



THE MOST IMPORTANT
INVASIVE PLANTS
IN HUNGARY

edited by

Zoltán Botta-Dukát and Lajos Balogh

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In honorem of Szaniszló Priszter

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ZOLTÁN BOTTA-DUKÁT AND LAJOS BALOGH

Institute of Ecology and Botany
Hungarian Academy of Sciences

Vácrátót, 2008

COVER PHOTO:
Helianthus tuberosus s.l. and *Solidago gigantea*
in the floodplain of Rába River
near the village Magyarlak, Őrség, Vas County, Hungary,
30 September 1997, photo: Lajos Balogh

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PREFACE

Biological – including plant – invasions belong to the major drivers of biodiversity decrease all over the world. In Hungary – according to the MÉTA-survey –, subspontaneous stands of perennial alien plants cover 5.5% of the country and it does not include the area covered by alien tree plantations and annual weed vegetation of disturbed areas and arable fields. It is only slightly lower than the half of total area of natural vegetation (BOTTA-DUKÁT 2008).

Hungarian Nature Conservation Agency recognized the importance of this problem, and started a project to collect the knowledge of the biology of invasive plant species. The results of this project have been published in Hungarian in two books (MIHÁLY & BOTTA-DUKÁT 2004, BOTTA-DUKÁT & MIHÁLY 2006). These books include 28 monographs of invasive plant species. These species are also invasive in other European countries and some of them outside of Europe too. Discussions with colleagues from other countries highlight that there is a demand on such monographs in English. Biological floras published in scientific journals include only some of the important invasive species, e.g. *Ailanthus altissima* (KOWARIK & SÄUMEL 2007), *Fallopia japonica* (BEERLING et al. 1994), *Solidago altissima* (WEBER 2000). Therefore, we decided to publish the monographs in English. We excluded some chapters because there was no enough information in literature for making a comprehensive description. We also exclude chapter on *Heracleum mantegazzianum*, since a book (PYŠEK et al. 2007) has been published recently on this species with new results of the Giant Alien project, and *Humulus japonicus*, since a monograph on this species has been published elsewhere (BALOGH & DANCZA 2008). We included a species non-invasive in natural habitats till now, *Phytolacca esculenta*. It is spreading in settlements and it may be invasive environmental weed in the future. Its congener *Ph. americana* is invasive in natural vegetation, and the two species are treated in the same chapter. Thus this book contains 21 chapters which deal with 31 species or species complexes. The order of chapters follows the order of families in the recent reconstructed phylogeny (HASTON et al. 2007, PODANI 2007).

Each chapter contains the following sections: Taxonomy, Morphology, Origin, distribution, Life cycle, Habitat preference (including autecological and phytosociological relations), Biotic interactions (allelopathy, competition, herbivores and pests), Economic importance (benefits and damages) and Nature conservation significance. Lengths of the sections and of the chapters vary considerably depending on the available information. Since the Hungarian version was a popular work made for students and nature conservationists, we departed from the scientific style, and used citations in the text only if it was unavoidable. It makes the text more easily readable. However, each chapter contains a bibliography which structure follows the order of sections. This property was remained in this volume.

This English edition is not a simple translation of the Hungarian one; the chapters were completed by the new results. The authors were asked to complete the bibliography with new publications, and to remove papers published in Hungarian except which contain information that inaccessible from other sources (e.g. distribution data). Section treating phytosociological relations were shortened, because this topic is more informative for Hungarian than foreign readers. Since more and more information available on the worldwide web, chapters finished a section of Web references that contains useful links.

We decided that the monographs would not contain information on the management of the invasive species, since the authors of the book are biologists, thus this section would be less comprehensive than the others. However, we hope that in spite of this fact this book will be useful for nature conservationists, and also biologists (researchers, teachers and students) who need basic information on these species or need bibliography on them.

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MÉŢA Survey homepage. <<http://www.novenyztiterkep.hu/en/>>

COAST SANDSPUR

(*Cenchrus incertus* M. A. CURTIS)

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TAXONOMY

At the present time the taxonomical and nomenclatural status of Hungarian coast sandspur populations is not clear yet. According to the present view, in Hungary *Cenchrus incertus* M. A. CURTIS species is present. In former Hungarian literature the same plant is mentioned as *Cenchrus pauciflorus* BENTH (nowadays this name is considered to be synonymous to *C. incertus*); while earlier it was identified falsely as *Cenchrus tribuloides* L. species. It was lately revealed that the Hungarian coast sandspur is identical indeed with *Cenchrus longispinus* (HACK.) FERN. species, furthermore the presence of the *Cenchrus echinatus* L. was mentioned too. Since the exact status of the species requires further researches, in present study we do not wish to take a stand on this. Hereafter, above all we are going to touch upon the knowledge regarding the two most probable (for that matter much similar in their biological properties) species (*C. incertus*; *C. longispinus*).

English appellation of the *Cenchrus* species is usually „sandbur”, but the „grassbur”, the „sand burr” and the „sandspur” names are often used too. *C. incertus* most often called „common sandbur”, „field sandbur”, „coast sandbur” and *C. longispinus* usually called „longspine sandbur”.

The latest monographic work distinguishes 20 species within the *Cenchrus* genus belonging to the Poaceae family, but because of the taxonomical uncertainty we may found significantly different number of species in other studies. Most of the species are of tropical-subtropical distribution, but some of them are typical in the temperate zone. Members of the genus occur either in the Old and New World too as native, and the secondary area of many species still under growth due to human impacts.

MORPHOLOGY

The coast sandspur is an annual plant with erect or recumbent stem, often rooting on nodes; hereby it is often an extended bunch forming grass. Its height can vary from 5 to 60 cm. The plant itself is hairless, only the margin of the leaf sheath is hairy, on the border of the leaves long hairs can be found sporadically, just as the spiny husk that surrounds the fruit has tiny hairs too. The ligula is replaced by a girdle consist of about 1 mm long hairs. The leaves are 2–7 mm broad, 2–18 cm long, they have definite, slightly bloated leaf sheath. The root consisting of numerous flimsy roots ranges into the soil relatively shallow (shallow rooted crop).

The most pronounced part of the plant is its floret, the so called ‘burs’. On the crooked arbor of the compound flower can the spikes be found intermittently, in smaller bunches or congested closed in a husk (henceforth fruit envelop) covered by extremely stinging spines. The fruit envelop is not analogous – contrary to some essays – with the chaff, but it is of shoot origin. The most important distinctiveness between *C. incertus* and *C. longispinus* is the fruit envelop. In case of *C. incertus* the number of spines is 8–40, while *C. longispinus* has 45–75. The longest spines in case of the aforementioned species are short-

er than 5 mm and in the latter one are longer than 5 mm. The different sized spines that are generally flattened and flared at the root are located diffusely on the fruit envelop, but characteristically the ones at the bottom of the husk are increasingly more dense and short. The fruit envelop and the roots of the spines are subtly hairy. There are 2–4 (commonly 3) stemless, bare spikelet closed into the fruit envelop. The spikelets are of two flowers: the upper one is fertile; the lower one is sterile, perhaps staminate. The grain crop is 5–6 mm long, ovoid.

The coast sandspur often shows purplish-red coloration, which can turn up on any part of the plant that is above the ground level (on the stem, on the leaf and on the fruit envelop) either just in spots, or on the whole plant. The coloration becomes more characteristic by the arrival of the colder weather.

ORIGIN, DISTRIBUTION

It is quite difficult to give the exact native range of the *Cenchrus* species as probably with the appearance of people their secondary spread started long ago. The original area of *C. incertus* contains the southern part of the United States and Central America, just as it is present in the subtropical and Mediterranean zones of South America. The distribution of *C. longispinus* runs along the southern part of the United States till the southeastern end of Canada, primarily it is typical in the central and eastern parts of the country, its occurrence in the western states, just as in Central and South America is secondary. Thus in their native range out of these two species *C. longispinus* rather typical on the temperate, while *C. incertus* on the subtropical and Mediterranean areas. Their altitudinal distribution is similar, both of the species is typical chiefly on the plains. Their highest occurrences: 900 m (*C. longispinus*), and 800 m (*C. incertus*); both of the data are from the Mojave Desert.

Several species of the *Cenchrus* genus are introduced to many part of the World, but unfortunately because of the taxonomical uncertainties it is hard to connect data to specific species. Thus either of *C. incertus* and *C. longispinus*, or both of them are present in South America, Australia, Oceania, South Africa and in the Mediterranean region. In addition it showed up as a casual species at many places in Europe; its steady-state occurrences expand from Hungary, through Romania and Moldova till Ukraine (here it is prevalent chiefly on the Northern coast of the Black Sea).

The first report on occurrence of the coast sandspur in Hungary is from 1922, its explosive propagation is considered to be follow-up the Second World War. In Hungary – just like in its native range – it primarily occurs on plains. The coast sandspur is a generally prevalent invasive weed of sandy regions of the Danube–Tisza Interfluve, its occurrence in other regions of Hungary is only casual. In a specific way it can be found on the ruderal soil along the railways with extreme habitat conditions at many different areas of Hungary (we have data from the railway stations of Pécs, Győr, Budapest, Nyíregyháza, Debrecen, Szeged).

LIFE CYCLE

The coast sandspur living in Hungary is an annual plant (it is a summer annual plant with C_4 assimilation type). According to literature *C. longispinus* is solely annual plant, while *C. incertus* can be short-lived perennial too.

The coast sandspur is a warm-demanding species; its germination starts up only in soil of about 20 °C of temperature. The species is able of self-pollination, its propagation formula is a fruit surrounded by spiny fruit envelops and containing 1–3 seeds. On a favorable habitat the plant can bring many crops: the literature reports about a maximum of 1000 concerning *C. incertus* and in case of *C. longispinus* they mention 3000 propagules. The yield of the individuals came up in spring is much higher than of the individuals came up under same conditions in summer. The propagules are spread by animals and people.

Of the two species the sprouting of *C. longispinus* was studied in detail. The plant's propagules contain two different kinds of seeds: usually the upper seeds germinate within a year, while the lower ones commonly remain dormant for a long while. The removal of the fruit envelop and the mechanical scari-

fication stimulate the germination, but under natural conditions probably it has only trivial role namely usually the germination starts up from the seeds closed into the fruit envelop. The viability and the germination capacity of the seeds fall back strongly after 3 years. The light and the long-lasting high temperature inhibit the sprouting; moreover it can induce a secondary dormant state of the seeds. Usually on the soil surface the plant germinates badly, the optimum depth is 1-3 cm, but in sandy soil even from the depth of 25 cm viable seedling can develop. Observing the Hungarian coast sandspur populations the crops deriving from 3 sequential years accordingly to their age they shown gradually descending germination rate under laboratory conditions (unfortunately it is not clear from the assay under what light conditions was the germination done) and those seeds that was wintering took place in laboratory and not outdoor, germinated with a higher rate. According to outdoor observations, in Hungary the beginning and the end of germination strongly vary, it can be from the second part of spring till the beginning of autumn. In case of *C. longispinus* the floescence follows the germination by 3-4 weeks. Counting from the shooting the crop maturation needs 7-13 weeks. Some of the seeds are capable of life already when the spiny fruit envelop appears. If the spring is extraordinarily hot we can find flowering specimens already at the end of April in Hungary.

HABITAT PREFERENCE

On its native range and in Hungary the most adequate habitat for the coast sandspur's demand is the warm, dry, flimsy and calciferous sandy soil, and even here primarily it is typical on the disturbed sites and open grasslands. Its biggest stands can be found on sandy arable fields, vineyards, new wastelands and forestations, around sand pits and on dirt roads. It can often be found around foxholes and rabbit-holes too. Of semi-natural habitats it can be found in abundance on strongly trodden, grazed sandy areas, in annual and perennial open sandy grasslands. (On the likewise disturbed areas of sand-drifts with deeper and more attached soil usually the coast sandspur is substituted by the carrot grass [*Tragus racemosus*]). It occurs on sandy loess and loess; however it is not recorded from the Hungarian acid sandy soils. It is light-demanding, this is probably connected with the fact that it does not live in elder, closed woods.

Characteristic habitat of the coast sandspur aside from all is the railway line's pitched „base soil” with extreme water and thermal management, as well as gritty-sandy building detritus. On these kinds of habitats it can be found all over Hungary, although it is not of frequent.

BIOTIC INTERACTIONS

We have no knowledge about allelopathic phenomena regarding the coast sandspur. Moreover we have no data neither about its competitive ability, although according to the descriptions under favorable conditions it can proliferate so much that in its dense stands it can supplant other weeds, the *Setaria* and the *Digitaria* too. Observations show that this species can get in this kind of competitive edge only on newly or regularly disturbed habitats; on not disturbed areas the coast sandspur stands can rarefy intensely in few years and the species can perfectly vanish too. Consequently we do not need to keep count of its stands forming effect in near natural substances.

We have not got any knowledge about the consumers and causative agents of the coast sandspur. Grazers consume it willingly till the appearance of the spiny flower.

On the roots of the coast sandspur there was no mycorrhizae detected under Hungarian conditions, we have no data from international literature. In the propagation of the crop and in the allocation of the seeds into the soil furry animals and people (directly and by means of vehicles) have an important role.

ECONOMIC IMPORTANCE

The coast sandspur has no factual utility for human. Its substances can be utilized as pasturage only for a short term (till the appearance of the spiny flower). We have no data about its traditional folk utilization.

The coast sandspur is a noxious weed of sandy fields and orchards. It can be a nuisance chiefly at the cultivation and harvest of crops that require manual labor. It can cause injuries to the livestock with its spikes and getting stuck into wool it can decrease strongly its availability of processing and value.

NATURE CONSERVATION SIGNIFICANCE

The nature conservation significance of the coast sandspur is symbolic. Because of its narrow habitat spectrum and pioneer nature it can cause problems only on the disturbed parts of sandy grasslands or on tender wastelands with similar habitat. Its presence renders more difficult the utilization of the landscape typical for sandy grasslands and the grazing animal husbandry. It can also cause problems that the coast sandspur can come to stay and often proliferate stoutly on dirt roads used by passengers, causing inconveniences to the tourists (by this the display function of the conservation areas mutilates).

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CDFA Encycloweedia. <<http://www.cdfa.ca.gov/phpps/ipc/weedinfo/cenchrus.htm>>

JAPANESE, GIANT AND BOHEMIAN KNOTWEED

(*Fallopia japonica* (HOULT.) RONSE DECR.,
F. sachalinensis (FRDR. SCHMIDT) RONSE DECR.
and *F. ×bohemica* (CHRTEK et CHRTEKOVÁ) J. P. BAILEY)

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TAXONOMY

A) Scientific name: ***Fallopia japonica*** (HOULTUYN) L.P. RONSE DECRAENE in RONSE DECRAENE & AKEROYD 1988; synonyms: *Reynoutria japonica* HOULTUYN 1777; *Polygonum cuspidatum* SIEBOLD et ZUCCARINI 1844; *P. sieboldii* DE VRIESE 1849, non MEISSN. in DC. 1856; *P. sieboldii* hort. ex MEISSNER (sensu CLEMENT & FOSTER 1994); *P. giganteum* hort.; *P. confertum* HOOKER fil.; *P. reynoutria* MAKINO 1901; *P. zuccarinii* SMALL 1895; *Pleuropterus zuccarinii* (SMALL) SMALL 1933; *Pl. cuspidatus* (SIEB. et ZUCC.) H. GROSS 1913; *Tiniaria japonica* (HOULT.) HEDBERG 1946; Common names: UK: Japanese knotweed, Sally rhubarb, donkey rhubarb, gypsy rhubarb, Hancock's curse, broad-leaved polygonum; USA: Mexican bamboo, Japanese bamboo, Japanese fleece-flower, wild rhubarb, crimson beauty, elephant-ear bamboo.

B) Scientific name: ***Fallopia sachalinensis*** (FRDR. SCHMIDT PETROP.) L.P. RONSE DECRAENE in RONSE DECRAENE & AKEROYD 1988; synonyms: *Reynoutria sachalinensis* (FRDR. SCHMIDT PETROP.) NAKAI in T. MORI 1922; *Polygonum sachalinense* FRDR. SCHMIDT PETROP. ex MAXIMOVICZ 1859; *Pleuropterus sachalinensis* (FRDR. SCHMIDT PETROP.) H. GROSS 1913; *Tiniaria sachalinensis* (FRDR. SCHMIDT PETROP.) JANCHEN 1950; *Reynoutria sachalinensis* var. *brachyphylla* HONDA; *R. brachyphylla* (HONDA) NAKAI 1938; *R. ×vivax* SCHMITZ & STRANK 1985 (sensu CLEMENT & FOSTER 1994, et KERGUÉLEN 1999); Common names: UK: giant knotweed; USA: Sakhalian knotweed, elephant-ear bamboo, Sacaline, Sakhaline.

C) Scientific name: ***Fallopia ×bohemica*** (CHRTEK & CHRTEKOVÁ) J.P. BAILEY 1989; synonyms: *Reynoutria ×bohemica* J. CHRTEK & A. CHRTEKOVÁ 1983; *R. ×vivax* J. SCHMITZ & K.J. STRANK 1985; *R. ×vivax* auct., non SCHMITZ & STRANK 1985 (sensu CLEMENT & FOSTER 1994); *Polygonum ×bohemicum* (J. CHRTEK & A. CHRTEKOVÁ) P.F. ZIKA & A.L. JACOBSON 2003; (= *F. japonica* × *F. sachalinensis*); Common names: Bohemian knotweed; hybrid knotweed.

The family of knotweeds (Polygonaceae) belonging to the order of Polygonales comprises about 40 genera. The taxonomy and nomenclature of species dealt with in the present study have changed many times. Taxa that were earlier classified into the genera *Reynoutria*, *Polygonum*, *Tiniaria*, *Pleuropterus* and partly also *Bilderdykia* – are recently specified, based on chromosome analyses, as belonging to the genus *Fallopia*

ADANS., divided into four sections². The section *Fallopia* contains annual plants with climbing stems, such as cove bindweed (*F. dumetorum* /L./ J. HOLUB) and black bindweed (*F. convolvulus* /L./ A. LÖVE). The section *Parogonum* K. HARALDSON includes perennial creeping plants, with no representative occurring in Hungary. Perennial or ligneous plants are categorized in the *Sarmentosae* (I. GRINTZ.) HOLUB. section, such as Russian vine (*F. baldschuanica* /REGEL/ J. HOLUB) and silver lace vine (*F. aubertii* /L. HENRY/ J. HOLUB).³ The *Reynoutria* (HOUTT.) L. P. RONSE DE CRAENE section contains Japanese knotweed (*F. japonica*), giant knotweed (*F. sachalinensis*), and their hybrid the Bohemian or hybrid knotweed (*F. ×bohemica*). Due to their synanthropic expansion, invasive and strong habitat-transforming nature, Japanese, giant and hybrid knotweeds have been in the focus of intensifying scientific and nature conservation scrutiny in the past 20-25 years. Because the three species are highly similar and because their distribution data are thus significantly overlapping and unclarified, it seems reasonable to deal with them together. The reason the authors introduce the three taxa sometimes at different depths is the limitations caused by different levels of international research into these taxa.

MORPHOLOGY

The three species discussed are robust, herbaceous perennial (geophyte) plants usually taller than a man. They have roots penetrating 1-2 m deep down from their base, and far-reaching, laterally spreading rhizomes, bearing buds on them. In the categorization system developed for clonal plants by KLIMEŠ *et al.* (1997), they belong to the “*Aegopodium podagraria*”-type. With their dense shoot system budding from the rhizome, they create connected offshoot colonies (polycormons) which are easily recognized even in the defoliated stage from the pectinated pattern of erect stems, coloured in dun when dried. Their stems are upright and thick, hollow at the lower section, and leafless at the bottom. Their leaves are large, broad or elongated ovate, more or less cuspidate at the apex, with entire margin. Leaf shape and size vary at different life stages and at different locations on the plant. The largest are the ones on the stem, their disposition being sparse. Ones located on the lateral ramifications are considerably smaller, placed oppositely. Their flowers are arranged in small glomerules, in multi-axial partial inflorescences with bracts, together making up axillary, short-axled complex panicles (pleiothyrus). In addition to the openly positioned main inflorescence atop the stem, there are also accessory inflorescences on the leafy paracladia. Functionally, these species are dioecious (sometimes polygamous, with mixed – unisexual and hermaphrodite – flowers), meaning that there is sexual dimorphism in flower composition and inflorescence structure. Staminate flowers are 9 mm long, whereas pistillate ones are only 5–6 mm, but the perianth can grow further on when the fruit is ripened. The five tepals are united at their base, forming a tubelet. The outer ones have three keels or are winged. The number of stamens is 8, and the stigmae on the 3 free-standing styles are fimbriated. On functionally male specimens the pistils are reduced, whereas on female plants stamens are vestigial. *F. ×bohemica* is an exception, because in this species hermaphrodite flowers (with fully developed stamens and pistils) can grow on male specimens. No fruit is produced, though, in this case. However, even fruit can be produced on the staminate (male) specimens of *F. sachalinensis*, because in this species pistils are only partially reduced. Apart from these exceptions, the enwrapped, three-edged or three-winged achenes are produced on female (pistil-bearing) flowers only, the fruits measuring about 10 mm. In case of *F. japonica*, the achene is 2–4 mm long, weighing 1.6 g per 1000 seeds. These species bear nectaria as well. Their floral nectaria are of the epithelium-type, whereas extrafloral nectaria located on the external surface of cicatrices belong to the trichoma and pit types. Further exomorphological features used for differentiation between the three species are listed in Table 1. From that it is apparent that the hybrid *F. ×bohemica* is located between the parent species (*F. japonica* and *F. sachalinensis*) not only

1 BAILEY *et al.* (1995) believe that the *Reynoutria* sectio of *Fallopia* genus includes *F. japonica* together with its varieties, *F. ×bohemica* and *F. sachalinensis*, but the category “Japanese knotweeds” describes only *F. japonica* var. *japonica* and *F. ×bohemica*. Later for convenience *F. japonica*, *F. sachalinensis*, *F. ×bohemica* and any backcrosses were referred to collectively as Japanese knotweed s.l. (cf. BAILEY & WISSKIRCHEN 2006).

2 This classification was not taken over by Flora Europaea and by the majority of Central-European literature. Instead, these knotweed species are still dealt with in the genus *Reynoutria*.

3 The taxonomy (and thus adventive distribution relations) of the two species are not viewed uniformly in international literature.

in respect of its chromosome number but also in certain morphological features. Phenotypic variability is mostly characteristic for the highly polymorphic *F. japonica*, especially in its native range where it remains shorter. However, it is typical of all three species and in all of their habitats that under arid circumstances the plants will have shorter stem and smaller leaves. *F. sachalinensis* is the most similar in size, and can be clearly confinable species both in its native and adventive range. For quite a long time, infraspecific taxa have not been described apart from *F. japonica*, and more recently in *F. sachalinensis*, from their native distribution area.⁴ Besides *F. japonica* var. *japonica* × *F. sachalinensis* = *F. ×bohemica* other hybrids are also known which are considered to be partly intrasectional (belonging to *Reynoutria* section)⁵ and partly intersectional taxa (belonging to *Reynoutria* and *Sarmentosae* sections)⁶. The basic chromosome number typical in species belonging to *Reynoutria* section is $n = 11$. The characteristic chromosome number ($2n$) of each species are shown on Table 1, but some literature records report different cytotypes (incl. aneuploids) too, e.g.: *F. japonica* var. *japonica* ($2n = 44, \sim 60^*, 66^*, 110^*$),⁷ *F. sachalinensis* ($2n = 66^{**}, 88^{**}, 102^*, 103^*, 132^*$), *F. ×bohemica* ($2n = 88^{**}$). The molecular genetic analyses performed in the United Kingdom and in the Czech Republic shows that the order of genotypic variability of these species is the following: *F. japonica* var. *japonica* < *F. j.* var. *compacta* < *F. sachalinensis* < *F. ×bohemica*, i.e. the hybrid is genetically the most diverse taxon in the study areas (HOLLINGSWORTH *et al.* 1998, MANDÁK *et al.* 2005). In attempts to genetically characterize knotweed species in Britain by molecular markers, including RAPDs and ISSRs, and to evaluate genotypic diversity in invasive *Fallopia* germplasm (HOLLINGSWORTH & BAILEY 2000), a single genotype of *F. japonica* was detected, suggesting all individuals were ramets of a single, but exceptionally widespread clone. The octoploid female (male-sterile) individuals of *F. japonica* var. *japonica* investigated by Czech authors proved to be genetically uniform and belongs to the same genotype that is present probably in the whole Europe (MANDÁK *et al.* 2005). On the other hand, the results of recent investigations carried out in the USA suggests the presence of intercrossing, segregating hybrids, and likely introgression between F1 hybrids and *F. japonica*. This study also shows the first evidence of bidirectional hybridization between parental taxa in the USA, emphasizing the complex structure of populations in that region (GAMMON *et al.* 2007). Hybridization and backcrossing within the species of

4 *Fallopia japonica* var. *compacta* (HOOK. f.) J. P. BAILEY 1989 (syn.: *Polygonum cuspidatum* var. *compactum* [J. D. HOOK./ L. H. BAILEY; *P. cuspidatum* var. *compactum* hort.; *Reynoutria japonica* var. *compacta* /HOOK. f./ MOLDENKE 1941, ead. comb. BUCHHEIM 1972; *Polygonum compactum* HOOKER fil.; *P. sieboldii* var. *nanum* hort.; *P. cuspidatum* 'Reynoutria' /sensu NAGY 1978/) is an alpine variety, being smaller and more compact than var. *japonica*; it is (30–) 50–60 (–100) cm tall, its stem being less upright; its lateral stems are dark red or reddish maroon; leaves are small (4–7cm), almost round (characteristically as long as broad), with thick and leathery blade, strongly truncated base, undulate margin, and abruptly cuspidate apex; the flowers in the compact (–6 cm), non-branching or slightly branching upright panicles are white, carmine or reddish. It is an alpine dwarf variant native to volcanic ash and scree habitats of Central and North-Japan. One of its forms – *f. colorans* – is a typical pioneer plant growing in cushions of several meters wide in the 300–500 m surroundings of active volcano craters. In its synanthropic range, it has been found growing wild very rarely, only in the British Isles and Czech Republic so far. It is usually grown in botanical gardens, and only rarely as an ornamental. $2n = 44$.

Fallopia japonica var. *uzenensis* (HONDA) K. YONEKURA & HIROYOSHI OHASHI 1997 (syn.: *Reynoutria japonica* var. *uzenensis* HONDA) is a variety with hairy leaf underside native to snowy areas of Japan, on the side of the Japanese Sea. It is also a rare garden plant in Japan and America. $2n = 88$.

Fallopia japonica var. *hachidoensis* (MAKINO) K. YONEKURA & HIROYOSHI OHASHI 1997 (syn.: *Polygonum hachidoense* MAKINO; *P. cuspidatum* var. *terminale* (HONDA) OHWI; *Reynoutria japonica* var. *terminalis* HONDA, *R. hachidoensis* var. *terminalis* HONDA) is an isolated endemism native to the Izu Isles located near Honshu, bearing larger leaves with waxy shine. It grows on windy, bare volcanic ashy terrain or lava fields in open tall herb communities. $2n = 44$.

Reynoutria japonica var. *spectabilis* MAKINO (syn.: *Polygonum cuspidatum* var. *spectabile* DE NOT.) grows somewhat smaller than var. *japonica* (–1 m). It is also more sensitive, bearing leaves with white variegation or ruddy, marbled shade. In Japan it is a rare garden plant too. (No synonymous combination shifted to *Fallopia* is known to exist.)

Reynoutria japonica var. *variegata* MAKINO is a rare garden plant in Japan; it has leaves with white and red striping. (No synonymous combination shifted to *Fallopia* is known to exist.)

Fallopia sachalinensis var. *intermedia* (TATEW.) K. YONEKURA & HIROYOSHI OHASHI 1997 (syn.: *Polygonum sachalinense* var. *intermedium* TATEW.).

5 E.g. *F. japonica* var. *japonica* × *F. j.* var. *compacta*, intraspecific hybrid, found in the UK and Germany, $2n = 66$; *F. japonica* × *F. ×bohemica* ($6\times$), backcross, found in Wales, $2n = 76-110$; *F. ×bohemica* ($8\times$) × *F. sachalinensis*, backcross, found in Wales, $2n = 66$ (cf. BAILEY 2003).

6 E.g. *Fallopia conollyana* J. P. BAILEY 2001 (*F. japonica* × *F. baldschuanica*) (cf. BAILEY & CONOLLY 1984, BAILEY 1992, 2001). $2n = 54$.

7 Numbers with a single asterisk refer only to the species' native distribution area; numbers with two asterisk refer only to the species' adventive distribution area.

Fallopia sectio *Reynoutria* in its adventive range, is clearly a significant and important phenomenon, offering as it does, the possibility of the production of individuals better suited to these non-native regions (BAILEY 2003). This case also render the suggestion by ELLSTRAND & SCHIERENBECK (2000), hybridization may act as a stimulus to invasiveness.

TABLE 1 Features of the three member of the species group

Feature	Japanese knotweed (<i>Fallopia japonica</i> var. <i>japonica</i>)	Bohemian or hybrid knotweed (<i>Fallopia ×bohemica</i>)	Sakhalian or giant knotweed (<i>Fallopia sachalinensis</i>)
Height	(1.0–) 1.5–2.0 (–3.0) m; in its native range around 1.5 m	(2.0–) 2.5–3.5 (–4.5) m	(2.0–) 2.5–3.5 (–4.5) m
Shape of leaves on middle of stem	broadly-ovate, triangular	broadly-ovate	elongated-ovate
Shape of leaf base	truncate or cuneate	upper leaves: mostly trun- cate or cuneate; lower leaves: slightly cordate	upper leaves slightly cordate, lower ones definitely cordate
Leaf tip	cuspidate, often curved	acuminate, often curved	acuminate or obtuse, not curved
Leaf size	length 5–15 (–18) cm width 4–10 (–13) cm	length 10–23 (–30) cm width 9–20 (–22) cm	length 15–35 (–43) cm width 10–20 (–27) cm
Leaf texture	leathery–stiff	intermediate	soft
Hairiness of leaf underside	underside appears glabrous, but with a hand lens, unicel- lular papillae are slightly vis- ible sitting on primary veins, on a swollen base; intervenal spaces are glabrous	if the underside is bent and held towards the light, a hand lens reveals 0.5 mm long, 1–4-cell stout hairs (trichomes) sitting on a swol- len base, mostly on veins; intervenal spaces are almost glabrous	the 1 mm long, 4–12-cell flex- uous hairs (trichomes) sitting on a non-swollen base, scat- tered mostly on the veins but also in intervenal spaces, are visible to even the naked eye
Position of pistillate inflorescences	the lateral axles of individual panicles lack further rami- fications, and are arranged loosely, sticking out straight in all directions	the lateral axles of individual panicles lack further rami- fications, and are arranged more densely, sticking out straight, slightly bent or sometimes arching downwards	the lateral axles of individual panicles lack further rami- fications, and are arranged more densely, uniformly pen- dulous
Position of staminate inflorescences	the lateral axles of individu- al panicles may have further ramifications, and are ar- ranged loosely and more or less pointing upwards	the lateral axles of individu- al panicles may have further ramifications, and are ar- ranged densely, forming an acute angle with the axis of the main inflorescence, and pointing up towards the light in bundles	the lateral axles of individu- al panicles may have further ramifications, and are ar- ranged densely and mostly upright
Flower biology, sexual expression	only pistillate (female) speci- mens are fertile (fruit may be produced); male specimens (bearing staminate flowers) are sterile (no fruit is pro- duced)	only pistillate (female) speci- mens are fertile (fruit may be produced); male specimens (bearing either staminate or hermaphrodite flowers) are sterile (no fruit is produced)	both pistillate (female) and staminate (male) specimens may be fertile (fruit may be produced in both cases)
Number of flowers in one cluster	2–4	3–5 (–6)	4–7
Position of anthers in male flowers	not exerted from the peri- anth	considerably exerted from the perianths	somewhat exerted from the perianths

Feature	Japanese knotweed (<i>Fallopia japonica</i> var. <i>japonica</i>)	Bohemian or hybrid knotweed (<i>Fallopia ×bohemica</i>)	Sakhalian or giant knotweed (<i>Fallopia sachalinensis</i>)
Flowering period	July – September	July – October	July – September
Shape of fruiting perianth (achene enclosed in the persistent perianth)	obcordate, broadly winged and abruptly narrowed into the pedicel	elongated-obcordate, broadly winged and first abruptly, then run almost parallel into the pedicel	elongated, narrowly winged and gradually narrowed into the pedicel
Width of fruit (including wings)	3–6 mm	2–4 mm	1.5–3.5 mm
Colour of achene	black, shiny	bronze, shiny	dark purple, shiny
Grown in Hungary	ornamental	ornamental	botanical garden plant
Degree of naturalisation in Hungary	naturalized, invasive	naturalized, invasive, transformer	casual
Most typical habitats in Hungary	survives firstly in areas it was formerly grown, mostly in ruderal synanthropic environments, or less frequently in degraded near-natural habitats	found firstly in degraded near-natural habitats (predominantly along rivers and streams, and in floodlands), and secondly in ruderal synanthropic environments	practically absent from areas outside the places it was grown
Distribution in Hungary	country-wide, but sporadic	found country-wide, being most common in hilly regions	practically in botanical gardens only
Typical chromosome number	2n = 88 (<i>F. j.</i> var. <i>japonica</i>) [2n = 44 (<i>F. j.</i> var. <i>compacta</i>)]	2n = 66 (<i>F. j.</i> var. <i>japonica</i> /2n = 88/ × <i>F. s.</i> /2n = 44/) 2n = 44 (<i>F. j.</i> var. <i>compacta</i> /2n = 44/ × <i>F. s.</i> /2n = 44/)	2n = 44

Identification key for species of the *Reynoutria* sectio of the genus *Fallopia*, growing in Hungary

1. a. Leaf blades are stiff leathery, only seldom longer than 15 cm (not longer than 18 cm and not broader than 13 cm), broadly-ovate, cuspidate at the apex, truncate or cuneate at the base, making leaf shape appear to be triangular, most strikingly on the lower and middle section of stem. Leaves are nearly glabrous, apart from unicellular papillae on primary veins of leaf underside, visible only with a hand lens. The number of flowers in one cluster is 2–4. Anthers do not exsert from the perianth. The plant seldom grows taller than 2 m. It is native to Japan, South Sakhalin, Korea, Central Eastern China and Taiwan; in Hungary it was originally planted as an ornamental and then naturalized. It occurs mostly in areas it was originally grown, primarily in synanthropic ruderal environments or degraded near-natural habitats, sporadically country-wide. (Data collected so far usually regards *F. ×bohemica*.) It is found in roadside weed communities and ruderal margin vegetation of shaded moist habitats. It is flowering from July to September.

***Fallopia japonica* (HOUTT.) RONSE DECR. Japanese knotweed**

b. Leaf blades are softer, their length often exceeding 15 cm (can be longer than 18 cm and broader than 13 cm); at least the ones on the lower and middle sections of the stem have cordate leaf base; they are more or less hairy on the underside. The anthers exsert from the perianth. 2–4.5 m tall, more robust plant

2. a. Leaf blades have soft texture, their length can be greater than 30 cm (–43 cm), width can exceed 22 cm (–27 cm); they are elongated-ovate, acuminate or obtuse, with cordate base. The underside is hairy – especially on the veins but also in interveinal sections –, well visible to even the naked eye. Trichomes are 4–12-cellular, approximately 1 mm long. The number of flowers in one cluster is 4–7.

Anthers slightly exsert from the perianth. It is native to South Sakhalin, North and Central Japan; in Hungary it is almost restricted to botanical gardens (e.g. Vácrátót). (Reports from its growing wild are mostly about *F. ×bohemica*.) It is flowering from July to September.

***Fallopia sachalinensis* (SCHM.) RONSE DECR. Giant or Sakhalian knotweed**

b. This plant is characterized with transitional features of the parent species. The leaves have intermediate texture, they are not longer than 30 cm and not broader than 22 cm, broadly-ovate, acuminate. The base of the upper ones is truncate or cuneate, and the lower ones – most strikingly on the lower and middle sections of the stem – are slightly cordate. Leaf underside appears to be glabrous to the naked eye, but, if examined with a hand lens, it has short, sparse hairs mostly on the veins, while the interveinal spaces are almost hairless. Trichomes are 1–4-cellular, approximately 0.5 mm long. The number of flowers in one cluster is 3–5(–6). Anthers exsert considerably from the perianth. This plant is a hybrid of *F. japonica* and *F. sachalinensis*, probably having been created in Europe. In Hungary, it might have been an ornamental some time ago which then escaped and naturalized. The majority of its populations in Hungary are male-fertile, do not produce seed and are reproducing vegetatively. It is found country-wide mostly in degraded near-natural areas or, more rarely, in synanthropic ruderal habitats, especially in hilly regions. It is a spreading, dangerously invasive species, which is apparently almost ineradicable. It is found in ruderal margin vegetation of shaded moist habitats and roadside weed communities. It is flowering from July to October.

***Fallopia ×bohemica* (CHRTEK & CHRTEKOVÁ) J. P. BAILEY Hybrid or Bohemian knotweed**

ORIGIN, DISTRIBUTION

A) The native range of *F. japonica* is in East-Asia, (from north to south) in Russia (South-Sakhalin, southern Kuril Isles), in Japan (Honshu, Shikoku and Kyushu; 0–2800m), Korea, Central-Eastern China (50–2500m) and Taiwan (2400–3800m).⁸ It is very common in Japan – the most precise data are from there –, occurring mostly in hilly and montane areas.

Its adventive range extends onto several continents. It was first introduced to Europe in 1823 to a Dutch botanical garden. Shortly afterwards, it was planted not only as an impressive ornamental, but in some places it was grown as a productive farmland green forage or in well-lit forests and forest edges it was grown as forage for game animals. It often escaped, and then naturalized in several places. By today it has spread into a significant proportion of Europe, including West,⁹ Central¹⁰ and partly in Southeast Europe. It is thought to have become naturalized in 99% of the British Isles, and 41% of European areas. It has insular occurrence in Scandinavia (up to 70° northern latitude), in the Baltic states, Ukraine and Russia¹¹. In South Europe it is practically absent from the Iberian, the Apennine and the Greek peninsulas.¹² Besides Europe, it has naturalized throughout North-America,¹³ from Alaska to Georgia, and it still continues to expand. There have been reports on its occurrence in Australia and New Zealand as well.¹⁴ As regards its altitude tolerance, in Europe it is considered to be a plant of colline or lower mountain regions not expanding to higher elevations: Scandinavian mountains (–480 m), South Wales (–320 m), Swiss Alps (–800 m, sometimes 1460–1650 m), Baden-Württemberg (90–1000 m), Erzgebirge (–900 m), Krkonose (Giant Mountains) (–750 m), Tatra (–860 m). North America: California (–1000 m), Utah (1220–1830 m). Only var. *japonica* has become naturalized. From Britain and the Czech Republic only a single female clone has been known. Currently, *F. japonica* is widespread in all countries of the Carpathian Basin, although no data are known from Serbia. The first information about its wild occurrence in the region (1923; cf. PRISZ-

8 Altitude limits of distribution are given in parentheses.

9 It was introduced into the United Kingdom in 1825, and it was first recorded as having escaped in 1886.

10 It was introduced into Germany in 1825, and it was first recorded as having escaped in 1884. It was brought into what is now the Czech Republic in 1892.

11 In Moscow's wider surroundings, in the Caucasus region, and in Vladivostok in the Far East.

12 But it occurs in the Mediterranean region of France.

13 USA and Canada; it first naturalized in the 1880s in the northeast states of the US.

14 First in 1935.

TER 1957) was reported in general by JÁVORKA (1924), and its subsynchronous occurrence was first recorded by KOVÁCS F. along Tisza river at Óbecse (Soó 1927). About a quarter of a century later, already 18 Hungarian settlements were listed (PRISZTER and Soó in Soó 1952). Its occurrence data have increased since then, especially in the most recent decade. According to UJVÁROSI (1973) – although it has sporadically established in the Great Hungarian Plain region –, it has become frequent in the middle-altitude mountain range and in Transdanubia, expanding most strongly in the latter regions (Soó 1980). PRISZTER (1985) considers it to have become completely naturalized, found almost everywhere throughout the country. However, the author of the current study believes, based on observations having been made for more than one and a half decade that this plant is much less frequent as reported in literature, because many of these reports probably relate to the hybrid species (BALOGH 1998).

B) The native range of *F. sachalinensis* is also East Asia: it is native to Russia (South Sakhalin, southern Kuril Islands), northern (Hokkaido) and central (northern sections and central part of the western side of Honshu; 0–1050 m) areas of Japan, being a relatively frequent plant there. (Occurrence and distribution data of infraspecific taxa of the above two species are listed in the section of morphology.)

Its adventive range is narrower than that of the congener species, but it also extends onto several of the continents. It was introduced into Europe in 1863: first into the Royal Botanical Garden in London, and into the Moscow Zoo. Like in the case of the former species, this one, too – although more rarely – was planted as an ornamental and as forage. It has naturalized in several parts of Europe, but has remained much more sporadic. The focus of its distribution is Northeast Europe¹⁵ and the northern part of Central Europe¹⁶. South of 45° northern latitude there are only Bulgarian occurrence data. It has other insular occurrence patches in the south of Scandinavia (up to 65° northern latitude), in the Baltic countries, in Ukraine and in Russia¹⁷. Shortly after its introduction to Europe it was imported to North America too, and from the middle of the 20th century it has had subsynchronous occurrence data (California, eastern-central parts of the USA). It was first reported from New Zealand in 1936, from Australia (Victoria) in 1954, from South Africa (Natal) in 1987 and from India in 2000. As regards its altitude preference, in Europe it is thought to be a species of colline and submontane regions: Scandinavian mountains (–250 m), Baden-Württemberg (90–710 m), Giant Mountains (Krkonoše) (–750 m, on Polica: –895 m); in North America: California (–500 m). From the Carpathian Basin there are only some sporadic occurrences in Austria, Slovakia and Romania. There are only few reports on its wild occurrence in Hungary (the first one: Vácrátót 1949 in PRISZTER 1957; PRISZTER 1985). It is probably that these data concern about hybrid species that were still not described at that time but were similar in many respects. Until today, its occurrence has been proved only as a planted, botanical garden plant (e.g. Vácrátót)¹⁸, and only in the most recent times was founded its small stand in the Gerecse hills (Vértetolna, BARINA 2006).

C) Surprisingly the hybrid between *F. japonica* and *F. sachalinensis* was not mentioned from Japan until 1997, when *Reynoutria ×mizushima* Yokouchi ex T. Shimizu was described. Its possible reason is that *F. japonica* and *F. sachalinensis* are either not sympatric or if and where they are, any hybrid progeny is poorly adapted. BAILEY (2003) found several examples of *F. ×bohemica* growing in ruderal habitats in NW Honshu in 1999 and 2000 (all were hexaploid, indicating a cross between octoploid *F. japonica* and tetraploid *F. sachalinensis*). Apparently these hybridizations were a result of the practice of planting *F. japonica* along new roadside embankments and cuttings for soil-stabilization purposes. In Europe *F. ×bohemica* was created probably spontaneously as a hybrid between the above two species. It was discovered in 1982 in Northern Bohemia and described in 1983 by CHRTEK and CHRTEKOVÁ. Its distribution was studied in only few of the countries. According to such research, it has naturalized in Belgium,

15 It was introduced into the United Kingdom in 1860, and it was first recorded as having escaped in 1896.

16 It was introduced into Germany in 1863 and into what is now the Czech Republic in 1869.

17 In Moscow's wider surroundings. First date of its introduction: 1864.

18 Botanical Garden of the Hungarian Academy of Sciences: Developmental History and Phytotaxonomy Garden, Polygonaceae plot. However, escaped populations along the stream Sződ-Rákos flowing in the Botanical Garden are not *F. sachalinensis*.

British Isles, Bulgaria, Czech Republic, Denmark, Finland, France,¹⁹ Germany, Hungary, Italy, Netherlands, Norway, Poland, Romania, Serbia,²⁰ Slovakia, Switzerland and Ukraine, but most likely in other countries as well.²¹ Available records range from 67° in the North to 43° (latitude) in the South and from 10° in the West to 25° in the East (longitude). Outside Europe it has been reported to occur in the USA, Australia and New Zealand also. It is probably cultivated and probably also escaped in China. As to the latitudes, European data are available from Norway only: Scandinavian mountains (–250 m). In Hungary it is mostly the functionally male specimens or populations of the hybrid knotweed, usually not producing fruit that are seen. In Hungary, where it is the most frequent among the three species it has continued to expand considerably in recent times too. To conclude, the synanthropic range of these three species, including their Hungarian distribution, is most probably expanding and becoming denser.

LIFE CYCLE

The life cycles and life histories of the three knotweed species – due to their high similarity – can be dealt with together, with the important differences being specified. They are probably the tallest polycarpic (flowering several times) perennial herbaceous plants of the Hungarian flora (apart from liana species). Being geophytes, it is their extensive, lignescent rhizomes that over-winter. In the native ranges of the parent species – especially as pioneer species of volcanic terrain – an effective generative way of reproduction has vital importance.²² However, this is not true in their synanthropic ranges and in the case of the hybrid species. As experience shows, the adventive “career” of these species is most likely to be relying primarily on their effective vegetative reproduction ability. The efficiency is so high that these plants were studied in the 1980s as the general empirical model of vegetative plant growth.²³ During the autumn and winter period, over-wintering buds are generated on the base of the stem and on the lignifying rhizome, to produce new shoots in spring, among which the strongest are the ones emerging on the crown of the stem base. Rapid shoot development starts at around late March – early April, depending on the weather. Young shoots might suffer damage from late spring frosts. According to French data, *F. sachalinensis* grows in the first three weeks at a rate of 3 cm/day; this rate increases to 5 cm/day by the third week of May. As the season proceeds, the densely positioned stems with lignified base, developing from the robust rhizomes, will become suberous on their lower sections. Later on, lateral ramifications will also develop, thus multiplying total leaf surface of the plant. By that time, however, leaves of the main stem become yellow, and then fall. Inflorescences start to develop as early as in June. The formation of functionally dioecious flowers is accompanied by the less intense development and retardation of the adequate parts of the hermaphrodite archaic flowers. Flowering normally starts in the second half of July, reaching its maximum in August when the plants are the tallest, and lasts until September–October, although plants that are injured can produce flowers and continue flowering until the first frosts. Flowers are predominantly insect-pollinated (entomogamous). The most frequent visitors of flowers, floral and extrafloral nectaria are dipterans (Diptera), especially syrphid flies (Syrphidae) and muscid flies (Muscidae). Also common are hymenopterans (Hymenoptera), beetles (Coleoptera), Rhynchota and moths and butterflies (Lepidoptera). If fruits are produced, they will ripen by around September–October, and are dropped in October–November. Earlier frosts can damage the abscission mechanism in the appropriate zone of the fruit pedicel, with the result that the fruits stay on the plant way into the winter season, until weather or the birds remove them. Their winged achene fruits are wind-dispersed (anemochorous).

19 In the Mediterranean region too.

20 Data from K. SZABADOS (pers. comm.)

21 Investigations to clarify actual occurrence data of the parent species and their hybrids in various areas are currently under way.

22 Germination happens above ground (epigeic), meaning that it is the stem section below the cotyledons (hypocotyl) that extends, rising up the cotyledons. When *F. japonica* seeds were investigated, dormancy was broken even at room temperature, but germination rate was then very low.

23 Recently published a correlated random model for the spatial spread of a rhizome network in *F. japonica*, which is able to the practical application in forecasting future disposal costs of existing stands (SMITH *et al.* 2008).

In Europe, however, instead of generative reproduction, they spread almost entirely vegetatively.²⁴ There are very few evidential data on generative reproduction (i.e. on plant specimens germinating and growing up under natural conditions). There are data of seedlings from Germany on the *F. ×bohemica* hybrid between *F. japonica* and *F. sachalinensis* (ALBERTERNST 1998), and from the British Isles on the *F. ×conollyana* hybrid between *F. japonica* and *F. baldschuanica*.²⁵ Studies in the USA were proved, while clonal growth is apparent, there is more evidence for sexual reproduction (FORMAN & KESSELI 2003, GRIMSBY *et al.* 2007). Germination experiments conducted in Belgium (TIÉBRÉ *et al.* 2007) were showed that *F. japonica* produced large quantities of seeds that had germination capacity, but in contrast to the American studies, they did not observed any seedlings in the field. The high occurrence of adult hybrids in the study area and the observation that there is high genotypic diversity in these hybrids (TIÉBRÉ *et al.* 2007), similar to that observed in Britain (HOLLINGSWORTH *et al.* 1998), indicated that seedling establishment does occur in the field, albeit probably at a low percentage in comparison to the total seed rain. Further experiments are needed to assess the best conditions for hybrid seedling establishment. The major dispersers of the reproductive parts (rhizome or sometimes stem sections) suitable for the development of a new individual are humans and water. These parts are usually transported away from their growing locations by human mediation (anthropochory), e.g. with garden waste, etc. If it getting to edaphically arid or ruderal habitats their populations usually become stable and gradually expand. From moist, waterside habitats, their – mostly vegetative – propagules are transported further by flowing waters (hydrochory). In addition to the fact that the size of the ligneous stem base (serving as a regenerative complex) grows with time, laterally expanding rhizomes with regenerative buds also develop even in the first year. These can cover a distance of as far as 15–20 m from the plant (of course, depending on soil compactness). The three knotweed species discussed are sensitive to prolonged dry spells during summer. Leaves fall from late October, or after the first frosts at latest (they are sensitive to frost early in the autumn), causing the stem to die off too. Regeneration ability is the most important characteristic for spreading in the species of *Fallopia* sectio *Reynoutria*. The regeneration rate and shoot mass were significantly affected by genotype in *F. ×bohemica* but not in *F. sachalinensis* (PYŠEK *et al.* 2003). Some phenotypes of *F. ×bohemica* exhibit high regeneration potential and the hybrid can be considered as the most successful representative of the genus *Fallopia* sectio *Reynoutria* in terms of regeneration and establishment of new shoots. *F. sachalinensis* shows the lowest regeneration ability. The regeneration from stems is less efficient than that from rhizomes except *F. sachalinensis*. It could be concluded that rhizomes are more crucial than stems for the spread of knotweeds through fragmentation and clonal growth, suggesting the importance of soil disturbance (BIMOVÁ *et al.* 2003). The examination for a variety of ecological and genetic parameters of some *F. ×bohemica* populations in north-eastern France (SCHNITZLER *et al.* 2008) indicates that some clones are more aggressive than others with a similar chromosome composition. Aggressiveness can be linked to the absence of seed production and possession of large leaves, which might allow higher storage of nutrients and greater volume of rhizome in the soil. It is illustrative to the differences in the viability of these species that during the last century in the Czech Republic *F. japonica* var. *japonica* has been spreading significantly faster than *F. sachalinensis* and the hybrid exhibits twice the rate of invasion of its parents (MANDÁK *et al.* 2004).

HABITAT PREFERENCE

Autecology

The distribution area of the parent species, including their Hungarian and synanthropic ranges, is limited to areas characterized with the following climatic features. Relatively wet summers, regular frost (*F. sachalinensis*: 120 days below 0 °C mean temperature; *F. japonica*: at least one shorter period below 0 °C mean temperature), long and mild vegetation period (about 210 days above 5 °C mean temperature), except for *F. japonica* occurrence in Northeast Utah (USA) where the summer is too dry. While the entire distribu-

²⁴ The role of *F. japonica* and *F. sachalinensis* fruits in the expansion of these species needs to be clarified in further studies.

²⁵ Cf. the footnote in the part of morphology referring the hybrids.

tion range of *F. sachalinensis* is limited to the temperate phytogeographic zone and sub-oceanic regions, that of *F. japonica* includes the sub-meridional–temperate zone and a wider area of oceanic regions: from oceanic to subcontinental. For this reason, no significant expansion of distributions is expected in their anthropogenic range – unless in the case of climate change –, although it is likely that occurrence frequencies will increase. It is remarkable the progressive spread of *F. ×bohemica* (and the absence of *F. japonica*) in the mesomediterranean zone of southern France. *F. ×bohemica* seems to exhibit an ecological ability that is – contrary to its morphology and physiology – not intermediate between its parents, but reveals new qualities of independent niche adaptation and range widening (BAILEY & WISSKIRCHEN 2006).

A) *F. japonica* has wide ecological amplitude. In its native range it is usually found in higher altitudes than its congener species. For example, its dwarf variety (*F. japonica* var. *compacta*) is one of the most typical plant species of open, sunny spots of new ash or lava surfaces in volcanic mountains (e.g. Fuji). This variety produce large amounts of seed, which regularly germinate, and the plants appear to grow as discrete circular stands with little evidence of lateral spread. The rhizomes grow straight down rather than laterally (BAILEY 2003). However the most typical habitat for the tall *F. japonica* var. *japonica* in Japan are edge of the forests or riversides in forests, on poor, fast-drying, gravely soils with bad water balance. Secondary it is frequent along roads, managed pastures too, especially where high nitrogen-level fertilizers are used. It often occurs not in compact stands, but as single well-separated stems, which had long rhizomes relatively close to the surface (BAILEY 2003). It can tolerate extraordinarily harsh environmental conditions (e.g. its rhizomes withstand months of frozen soil, and survives on extremely acid volcanic soils (< pH 4). With low absorption values, it also tolerates high sulphur-dioxide pollution present near active volcanic fumaroles. Its extensive rhizome system stabilizes moving stone debris. Being a plant that stores nitrogen and other important nutrients, it assists the development of soil, the establishment of other species, and increases the chances for the development of a more highly organized ecosystem.

In its adventive range, *F. japonica* occurs in various, relatively productive, usually man-made habitats with often disadvantageous features, which can be divided into three groups based on their edaphic characteristics. The first group contains more typically man-made, relatively dry areas or those with ill water-balance, which are partly pioneer habitats: railway embankments, waste heaps, empty yards, neglected or abandoned gardens, hedges, ruderal areas, roadsides, etc. The second group, on the contrary, comprises more near-natural, moister areas: areas along regulated (sometimes unregulated) streams and rivers, embankments and dykes, roadside ditches, forest edges, clear-cut sites, etc. The third main habitat type of its occurrence is sea coasts (e.g. Norway, Denmark) and salt marshes. All this indicates that indirect and direct disturbance can assist its expansion. The fact that its populations belonging to the first type group are concentrated in the close surroundings of human settlements is most probably related with its ornamental uses, with the effects of human soil disturbance, and with the rarer late autumn frosts and summer droughts. This species has wide pH-tolerance (3.0–8.5), but normally prefers limy soils. It is not choosy as regards soil type, and tolerates high levels of heavy metal and salt pollution. In North American investigations on *F. japonica* and *F. ×bohemica* were proved that plasticity in salt tolerance traits may allow these taxa to live in saline habitats without specific adaptation to tolerate salt (RICHARDS *et al.* 2008). Somewhat contradictorily with its Hungarian name (“floodplain Japanese knotweed”), this plant in Hungary is found primarily (as observed by the author) in places where it escaped from its former planting sites, mostly in settlements’ ruderal habitats, or sometimes in degraded near-natural habitat types. Thus, in Hungary it is rather urbanophilous species. According to GRIME *et al.* (1988) it has competitor strategy.

B) In its original distribution *F. sachalinensis* lives in forest edges, along forest trails, on scree habitats of montane areas, on seaside rocks, riversides, abandoned lands and along public roads. Generally, it prefers alluvial lowlands with higher temperature, lower elevation and constant water supply in the vegetative season. However, sometimes – similarly to the other species – it does occur as a pioneer colonizer of recently formed bare volcanic surfaces, or along alpine gullies and flowing waters.

In its adventive range *F. sachalinensis* is present in the first two major habitat groups mentioned above for the congener species. However, the occupancy rates of warmer and dryer ruderal habitats

in urban areas vs. wetter and colder habitats of mountainous areas vary highly and characteristically among areas within Europe. For example, in Poland it is known from forests mostly, whereas in France it is typically found on vast alluvial lowlands and islands of alpine rivers.

C) The habitats of *F. ×bohemica*, known so far from Europe, belong to three groups on the basis of edaphic features, similarly to the case of *F. japonica*.²⁶ The author has found it to be an urbano-neutral species in Hungary, although it is present primarily in degraded moist, near-natural areas (along rivers, streams of hills and mountains, floodplains, sometimes along intensively used forest trails, and only secondly in more strongly anthropogenic, ruderal habitats. It favors highly exposed situations with no coverage, but can appear in shaded forest areas too in which case its stands appear to be less dense.

Phytosociology

A) In its native range *F. japonica* is a pioneer species of riversides and shallows: the *Polygonum cuspidatum* association (*Penniseto-Artemision principis*, *Artemisietea principis*) is a 40-100 cm high, relatively species-poor one, characterized with the dominance of the name-giving species. It is found in other – mostly tall herb – associations too, where vegetation is somewhat higher (50–150 cm). It plays an important role in the succession of volcanic surfaces where it is a constituent of natural pioneer plant associations. During succession it is normally grass patches of *Miscanthus sinensis* that accompany this knotweed species, then, after about 50 years, this grass will become dominant with other grass species, to be followed by woody vegetation in the habitat.

In its adventive range, *F. japonica* (just like the two other species) has very low sociability. In the majority of cases it forms more or less continuous, homogeneous stands. For this reason, phytosociological literature treats these as associations signified by the name of the species only, or just as stands (*F. japonica* association, *F. japonica* stands). However, it can be additionally specified what types of associations these stands co-occur with. According to more recent Central-European literature (NEBEL *et al.* 1993, OBERDORFER & MÜLLER 1994) these are: willow and alder bushes, montane alder galleries along streams (*Stellario-Alnetum*, *S.-Petasitetum*), garlic mustard (*Alliarion*), burdock (*Arction lappae*) and sweet clover associations (*Dauco-Melilotion*). Applying the derived association concept which was first used about 25 years ago – and which focuses on the dominating species – Japanese knotweed tall herb associations are also differentiated (*Fallopia japonica-Senecion fluviatilis*) (MUCINA *et al.* 1993), comprising the *F. japonica* extreme facies of the *Impatiens-Solidaginetum* association and the *Polygonetum cuspidati* association. In the diagnostic species combination with dominant and constant accompanying species, the dominant species is *F. japonica*, whereas stinging nettle (*Urtica dioica*), bishop's goatweed (*Aegopodium podagraria*) and stickywilly (*Galium aparine*) are subdominant species. The latter are tolerant of shading; *Urtica* and *Aegopodium* are tough clonal plants. Coenosystematically, *F. japonica* has been classified in various association units, for example in Germany SUKOPP (1962): *Senecion fluviatilis*, OBERDORFER & MÜLLER (1983): *Galio-Urticenea*; in the Czech Republic HEJNÝ & SLAVÍK (1990): *Convolvuletalia sepium* and *Lamio albi-Chenopodietalia boni-henrici*. According to SOÓ (1970), Japanese knotweed in Hungary is typically found in gallery forests, oak woods (*Quercetum petraeae-cerris*), floodplain weed associations (*Cuscuta-Calystegietum*), forest edges and gardens; and is considered to be a *Calystegion sepium* species and a character species of alluvial weed associations (*Senecion fluviatilis*). BORHIDI (1995), too, classifies it as a *Calystegion sepium* species, but according to SIMON (2000) it is a *Calystegietalia*-type species, which is validly called today (BORHIDI & SÁNTHA 1999) *Convolvuletalia sepium* (moist, edge vegetation). The latter authors categorize all three species as new, floristically incomplete and unbalanced neophyte association elements of semi-arid and moist forest weed vegetation types. All these categorizations mentioned above provide a view of the phytosociological character of *F. japonica*.

B) In its original distribution, *F. sachalinensis* can be characterized with the following major vegetation-typical features. Firstly, it is a member of the so-called giant herb communities, that forms of

26 Cf. also with the establishment respecting the salt tolerance of *F. japonica*.

1.5-3 m height and nearly 100% coverage (*Angelico-Polygonetum sachalinensis*, *Cirsio kamtschatici-Polygonetum sachalinensis*) occurring in forest edges, mountain terrain covered with rocky debris, sea-side rocks and riversides. Secondly – similarly to the congener species –, it is one of the first colonizer species of newly formed volcanic terrain surfaces, establishing themselves in such areas within the initial couple of years.²⁷ Later on, trees that gradually settle in depending on knotweed density will shade out knotweed populations from such habitats within a few decades. Its almost homogeneous stands are found making up the pioneer vegetation of newly formed barren surfaces in human settlements.

In its adventive range the phytosociological characteristics of *F. sachalinensis* – just like its habitats – are similar to those of *F. japonica*, although exact phytosociological data are deficient. OBERDORFER & MÜLLER (1983) regard it as a *Galio-Urticenea* species, HEJNÝ & SLAVÍK (1990) as *Convolvuletalia sepium* and *Lamio albi-Chenopodietalia boni-henrici* species, whereas LOHMEYER & SUKOPP (1992) relate it with associations of moist forest weed associations along streams (*Aegopodion*), and, as an epiphyte, with associations of ruderal habitats. BORHIDI & SÁNTHA (1999) treat it together with the other two knotweed species, although valuable data are not available from Hungary.

C) The phytosociological relations of *F. ×bohemica* have been less studied in Europe. However, a considerable proportion of such data on *F. japonica* are probably about the hybrid species. Nevertheless, the occurrence preferences of the hybrid in Hungary (described earlier in the section on habitats) seem to be valid in this respect, too, and are thought by the author to be unlike those typical of *F. japonica*. Accordingly, it is most frequent in ruderal margin associations of rather near-natural, shaded and moist habitats (*Galio-Urticetea*), more specifically, in vegetation types characterized with alluvial weed associations (*Senecion fluviatilis*).²⁸ If all Hungarian populations are regarded, its proportions in highly anthropogenic roadside weed vegetation (*Artemisietea vulgaris*) have only secondary importance. It can be noted that already some populations growing in beech forests are known to exist. Communities dominated by *F. ×bohemica* recorded in the Mediterranean Sea (France) characterized by thermophilic species, which composition typical of the (meso-) Mediterranean region, especially at riparian sites (BAILEY & WISSKIRCHEN 2006).

BIOTIC INTERACTIONS

Allelopathy

Japanese knotweed species show a typical example of allelopathic mechanisms which are among the most effective means of competition between plants. Reynoutriin was separated from *F. japonica* leaves (Q-3-xyloside), whereas terpenoid: triterpene (sterol), phenoloid: tannin, flavonoid (quercetin glc), and anthraquinone (emodin) compounds were found in *F. sachalinensis*. The results of American experiments suggest that allelopathic interference or interaction with microbial soil organisms may contribute to the lack of native species in populations of *F. ×bohemica* (SIEMENS & BLOSSEY 2007).

Competition

Although in the adventive range, knotweeds have little in the way of competition from plants other than trees, in their native range (Japan) they must additionally cope with climbers, twiners and other members of the native giant herb communities. Even the commonly found grass, *Miscanthus sinensis* grows up to 2 m in height, parasitic *Cuscuta* taxa are strong enough to bring down the plants and *Pueraria lobata* with its vigorous smothering growth and *Wisteria* with its dense tangling growth provide worthy competition (BAILEY 2003). In the same time an interesting indicator of Japanese knotweed toughness and vitality is the fact that among species of species poor communities of areas depleted by the falling guano of cormorant (*Phalacrocorax carbo*) nesting colonies in Japan, the highest surviving coverage is made up by *F. japonica* (ISHIDA 1996).

²⁷ Owing to its strong ability to produce offshoots, it is capable of emerging from below 0.5-1.0 m thick volcanic sediment, rapidly creating dense stands, and regenerating older colonies buried under the sediment.

²⁸ Here it often co-occurs with other alien, invasive tall herbs or lianas, such as adventive *Aster* species, *Echinocystis lobata*, *Helianthus tuberosus* s.l., *Humulus japonicus*, *Impatiens glandulifera*, *Parthenocissus inserta*, *Rudbeckia laciniata* or *Solidago gigantea*.

In their adventive range, in addition to allelopathic effects, the success of these three knotweed species is ensured by other important features such as shading and subterranean nutrient depletion. With their early-starting and rapidly proceeding growth they occupy the air space before other species could develop, by shading them off gradually with their dense stems and foliage mass, eventually taking away almost all the available light. In addition, their rhizome system grows rampantly, and the plants intensively remove the nutrients from the soil, thus taking over the ground, too, from their competitors. All these together, result in an almost 100% inhibition of germination and growth in co-occurring species. There are only few exceptions from this, mostly plants growing and producing fruit in the early spring period (e.g. *Ficaria verna*, *Veronica hederifolia*). It is only a few liana species that sometimes are able to overcome its aggressive, monodominant stands, such as *Clematis vitalba*, *Humulus lupulus*, *Echinocystis lobata* or *Calystegia sepium*. Investigating the stands of the three *Fallopia* species along a north Bohemian river the authors concluded that the species richness of communities has no influence on the success of *Fallopia* invasion; the combination of environmental conditions and propagule spread is more important to the invasion success than the number of species in the host community. *Fallopia* invasion greatly reduces species diversity.²⁹ *F. japonica* invaded more habitat types than *F. sachalinensis* and *F. ×bohemica*. The hybrid *F. ×bohemica* out-competes the parental taxa at sites where both taxa occur (BIMOVÁ *et al.* 2004). American researchers used a factorial transplant experiment to assess whether light limitation, nutrient limitation, or allelopathic interference by *Fallopia ×bohemica* reduces growth or survival of two native species. The results in combination with the outcome of a cutting experiment suggest that *F. ×bohemica* achieves competitive superiority primarily by limiting access to light. Species-specific effects and significant interaction effects particularly of light and activated carbon suggest additional mechanisms (SIEMENS & BLOSSEY 2007).

Herbivores

A) The highest amount of data is available on *F. japonica*. In Japan its leaves were consumed by chrysomelid beetles which could reduce them to a delicate tracery of veins as well as various lepidopteran and sawfly larvae. Upper stems frequently bore the exit holes of stem boring larvae. Below ground, the large larvae of the Japanese swift moth (*Endoclita excrescens*) bored cylindrical holes through the thick rhizomes, and their damage and old exit holes were a common feature of knotweed rhizomes in Japan. Another herbivore the Asian longhorn beetle (*Anoplophora glabripennis*). Beyond these the aphid infestations and various rust infections decrease the leaf area (BAILEY 2003). Its herbivores known from Europe are the followings: mammals: in the British Isles, the epigeous shoots were grazed by sheep, cattle, goats, horses and donkeys. Rhizomes however are toxic to some farm animals. Grazing by sheep and cattle early in the summer had a significant negative effect on shoot density. Birds: house sparrows (*Passer domesticus*) were observed to feed on seeds. Acarids: *Tetranychus urticae* (Tetranychidae). Insects: only very few insect herbivores were identified on Japanese knotweeds; this may be one of the reasons for the success of knotweeds discussed; Butterflies and moths (Lepidoptera): *Spilarctia lutea*, *Spilosoma lubricipeda* (Arctiidae), *Apatele megacephala* (Caradrinidae), *Phlogophora meticulosa* (Noctuidae), *Taeniocampa gothica*, *Orthosia cellaris* (Orthosiidae), *Inachis io* (Nymphalidae), and other larvae belonging to the families Noctuidae and Geometridae, not having been identified so far; Beetles (Coleoptera): *Phyllobius pyri*, *Otiorhynchus sulcatus* (Curculionidae), *Gastroidea* (*Gastrophysa*) *viridula*, *Chrysolina fastuosa* (Chrysomelidae). Neither endoparasitic nor ectoparasitic nematodes have been found.

B) Data are deficient in the case of *F. sachalinensis*. One polyphagous moth (*Spilarctia lutea*, Arctiidae) and one aphid was found on this knotweed species in Europe (Germany). *Spilarctia lutea* was equally successful on this knotweed and on its original native host plant *Rumex obtusifolius*. It is an interesting aspect to this topic that this knotweed species (and maybe the other two as well) attract ants with their extrafloral nectaria, possibly increasing protection against insect herbivores.

29 Similar results have been found by Hungarian authors too (BALOGH & BOTTA-DUKÁT 2007).

C) Data on herbivores feeding on *F. ×bohemica* are available from Germany only. Moths (Lepidoptera): *Spilarctia lutea* (Arctiidae). Beetles (Coleoptera): *Gastroidea (Gastrophysa) viridula* (Chrysomelidae). Dipterans (Diptera): *Pegomya nigritarsis* (Anthomyiidae). Undetermined acarid species are also observed. *Gastroidea (Gastrophysa) viridula* had only 15% growth compared with its individuals feeding on their native host plant *Rumex obtusifolius*.

Pathogens

A) In case of *F. japonica*, no parasitic fungi have been found. Among pathogenic saprophytic fungi, the following have been identified. Ascomycotina: *Amphorula sachalinensis* (Great Britain), *Ceriospora polygonacearum* (Great Britain), *Chaetoconis polygonii* (Great Britain), *Cytospora polygoni-seiboldi* (Great Britain), *Glomerella cingulata* (Japan), *Myxosporium polygoni* (Great Britain), *Pezizella effugiens*. Basidiomycotina: *Puccinia phragmitis* (Japan), *Puccinia polygoni-amphibii* (Japan), *Puccinia polygoni-weyrichii* (Japan). Deuteromycotina: *Alternaria* sp. (Germany), *Cladosporium* sp. (Japan), *Colletotrichum gloeosporioides* (Great Britain), *Endophragmia cesatii* (Germany), *Epicoccum* sp. (Germany), *Fusarium* sp. (Japan), *Helminthosporium* sp. (Japan), *Phoma* spp. (Great Britain, Japan, Germany) incl. *Phoma anceps* var. *polygoni* and *Ph. polygonorum*, *Phomopsis polygonorum*. Further sixteen plurivorous microfungi have been reported from growing and dead stems.

B) In *F. sachalinensis* the following saprophytic fungi have been identified: Ascomycotina: *Ceriospora polygonacearum*, *Myxosporium polygoni*; Deuteromycotina: *Phomopsis polygonorum*, *Phoma polygonorum*.

C) No data are available for *F. ×bohemica*.

Symbiosis

No mycorrhiza was found when samples from *F. japonica* in the British Isles and *F. sachalinensis* in Poland were investigated.

ECONOMIC IMPORTANCE

Benefits

Due to their rapid growth resembling that of bamboo species, *F. japonica* and *F. sachalinensis* have been planted as ornamentals for quite long, especially in the lawn of gardens and parks, and on watersides. Because of the high protein content of their leaves, experiments were made for their cultivation as forage for domestic and game animals.

A) Several medicinal uses of *F. japonica* are known to exist.³⁰ In addition to that, there are also some ethnobotanical uses as well: for example World War II troops used its leaves as tobacco. Young shoots are said to have been used for salads, because their taste resembles that of almonds. If cooked, it is suitable for dishes prepared similarly to asparagus or as puree. It can also be used as a substitute for rhubarb, to be accompanied by a specially prepared sour sauce. Recently, its utilization for purifying soils contaminated by heavy metals was also suggested, because it can accumulate those metals in its leaves and stem.

B) *F. sachalinensis* used to be popular among German hunters because it was hypothesized that it is tastier for game animals than *F. japonica*, and it also seemed suitable for lurking during hunting. In Rus-

30 In traditional Japanese and Chinese medicine, its dried rhizomes are recommended for curing the following diseases: purulent dermatitis, gonorrhoea, favus, *Dermatophyton* mycosis and hyperlipemia. Some probable agents have been shown by KIMURA *et al.* (1983). One of the acting agents (resveratrol) is thought to have bactericidal and fungicidal impact, which had a reducing effect of cholesterol level in rats. The extracted drug called emodin had an inhibiting effect on the intestinal parasitic trematode *Schistosoma japonicum*. The active drug content of this species used in Chinese medicine also for healing burns was analyzed by MOLNÁR (1991) (partly supported by SZABÓ L. Gy.).

sia, it was used as silage too.³¹ In its native range, sometimes there are so many larvae living in the inter-nodal sections of the stem that they are often used by anglers as a source of bait. Its rhizome is thought to be suitable for curing a number of diseases; the active drugs are anthrachinone-derivatives. In some places of Japan its young and tender shoots are eaten. In Europe, recently it has been discovered that it is effective against fungal plant diseases. The extract made from its leaves proved to be suitable against mildew on apple, begonia, cucumber, wheat, and the botrytis of sweet pepper. In hot climates, its huge leaves are used for shading fruits in the market.

C) By taking advantage (not actively growing!) of the functionally male, non-fruiting *F. ×bohemica* stands, utilization ways similar to those of the parent species could be revealed: food, medicine, pesticides, purification of heavy metal contaminated soils, stabilization of waste heaps, etc.

Damages

F. sachalinensis was recommended in the USA for stabilizing embankments on riversides, but this later proved to be unwise, because wherever it was used for such purpose, its spreading went uncontrollable. It is also possible, although actually no such information have arisen yet, that *F. japonica* was also planted in Europe some time for the same purpose. These three knotweeds (incl. *F. ×bohemica*) are less recommended today for being used even as garden ornamental plants. High standard gardening books ornamental plant and botanical garden catalogues (index seminum) nowadays particularly call the attention to the difficulties and threat meant by the escaping and control of this (and similar invasive) species. Knotweed stands, spreading along flowing water bodies, cause problems in accessibility, flow rate, and increase the maintenance costs of regulated river sections, by damaging flood prevention engineering objects. In settlement environment they can damage traffic infrastructure: crack sidewalk surfaces, or can even penetrate through weaker paved roads. They can suppress plants and hedges planted in parks, along roads and watersides. Fortunately, they only very seldom appear as weeds in agricultural areas. In California, for example, both species are considered as harmful weeds, *F. sachalinensis* “forming densely infested areas” (HICKMAN 1993). However, it is not specified in the literature source mentioned whether these plants cause “only” nature conservation problems or they are also an agricultural weed.

NATURE CONSERVATION SIGNIFICANCE

Although such problems caused by these knotweed species are not new ones, the attention of nature conservation organizations has turned towards them only recently.³² With their expanding polycormons they form almost entirely homogeneous stands in which only few species appear occasionally, but even so the majority of these species are unable to reach generative stage. Through direct or indirect human mediation, they can establish well in natural or near-natural habitats as well or even spread there, depending on the vegetation type affected there. In the invaded areas they strongly inhibit natural succession and regeneration processes and spontaneous reforestation, but also drastically reduce the survival chances of herbaceous associations. By excluding members of the original flora and vegetation in the habitat, they reduce the biodiversity of plants, and through that, of animals too, and thus are detrimental to biodiversity in general. Their control is very difficult, and any intervention with chemicals brings about nature conservation concerns. For these reasons – although these knotweed species occur in a variety of habitats – the most problematic from the aspect of nature conservation is their expansion in near-natural, waterside habitats.

31 The first piece of such data is from 1864.

32 Occasionally, warnings have been released, for example the United States Department of Agriculture called the attention to the rampant, aggressive spreading ability of *F. sachalinensis* as early as in the late 19th century.

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Web reference

JKLIST: JAPANESE-KNOTWEED JISCMail list (The Japanese Knotweed Forum).
<<http://www.jiscmail.ac.uk>>

AMERICAN AND CHINESE POKEWEED

(*Phytolacca americana* L., *Ph. esculenta* VAN HOUTTE)

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TAXONOMY

A) Scientific name: ***Phytolacca americana*** L. 1753; synonyms: *Ph. decandra* L. 1763, *Ph. vulgaris* CRANTZ 1766; common names: American pokeweed, common pokeweed, pokeberry, poke, Virginian pokeweed, scoke, pocan, garget, pigeonberry, inkberry, American nightshade.

B) Scientific name: ***Phytolacca esculenta*** VAN HOUTTE 1848; synonyms: *Ph. acinosa* auct. europ. non ROXBURGH 1814, *Sarcoca esculenta* (VAN HOUTTE) SKALICKÝ 1985, *Ph. acinosa* ROXB. var. *kaempferi* (A. GRAY) MAKINO 1892, *Ph. acinosa* ROXB. var. *esculenta* MAXIMOWICZ 1869, *Ph. pekinensis* Hance 1869, *Ph. kaempferi* A. GRAY 1859, *Pircunia esculenta* (VAN HOUTTE) MOQUIN-TANDON 1854; common names: Indian pokeweed¹.

The Phytolaccaceae LINDL. family that belongs to the Caryophyllidae subclassis and holds ancient characteristics is classified to the Chenopodiales or Caryophyllales (Centrospermae) order. It is considered to be the evolutionary base group of the families belonging these orders. In between there is RODMAN et al. (1984)'s revision, who places the Chenopodiineae suborder into the Centrospermae order², whose Nyctagineae cohorts contains the Phytolaccaceae. 125 species of the family's 22 genus' are known. (TAKHTAJAN /1997/ classified them into more families, so in his terms the Phytolaccaceae contains only the 30 species of *Anisomeria*, *Ercilla*, *Phytolacca*, and *Nowickeia* genera.) They are herbs, shrubs, rarely trees or lianas. None of their species is native in Hungary. They are common in the tropical and subtropical parts of America, South-Africa and South-Asia, including the mediterranean parts too. Considering the number of species the hot spot of the family is America. In the Phytolaccaceae family the missing anthocyanins are replaced by betacyanins and betaxanthins or in summary by betalains. The species of the *Phytolacca* L. genus belonging to the Phytolaccoideae H. WALTER subfamily and to the Phytolacceae REICHB. tribe accumulate the purple (dark pink) dye in their vegetative and reproductive parts too, especially in their fruits. The chemical agent that is responsible for this is the phytolaccanin – it is a non-toxic chromoalkaloid – 95% of it is betanin, but it contains isobetanin, prebetanin and isoprebetanin too. The *Phytolacca*-species contains many toxic compounds – alkaloid (phytolaccin), resin (phytolaccatoxin), saponin (phytolaccagenin) and toxic protein (lectin) – which concentrate primarily in the roots, fruits and seeds. Beyond them they contain cinnamic acid- and flavonoid-derivates having physiological effects. The scientific name of the genus (*Phytolacca*) implies to the dye content of the fruits: phytón (Greek) = plant, lac (Latin) = varnish. Same meanings holds the English pokeweed or pokeberry (from the Algonquin Indian words 'pakon' or 'puccoon' = dye), the German Kermesbeere or Kermes (= crimson) and it's old Hungarian name too. Among the 35 *Phytolacca* species the followings

are better known in the European literature (brackets shows the places of their origin): *Ph. americana* L. (syn. *Ph. decandra* L., North America), *Ph. dioica* L. (South America; in the Mediterranean they are planted as an ornamental tree), *Ph. pruinosa* FENZL (Cyprus, Asia Minor).

The meaning of the *Ph. acinosa* agg. occurring in South East and East Asia is disputed for a long time. According to the most accepted view of nowadays the following – noticed even in the European literature – species belong to here: *Ph. acinosa* ROXBURGH s. str. (India), *Ph. esculenta* VAN HOUTTE (China), *Ph. japonica* MAKINO (Japan) and *Ph. latbenia* (BUCH.-HAM.) H. WALTER (India). Subspontaneous occurrence of the latter species and of *Ph. polyandra* BATALIN (syn. *Ph. clavigera* W. SMITH, China) only been mentioned from the British Islands. According to CLEMENT (1982) the species of *Ph. acinosa* agg. are well differentiated in their native range, while in British horticulture they constitute an almost continuous spectrum of variation. CLEMENT & FOSTER (1994) pose the existence of a complex of species that can cross and they talk about possible hybrids. It can be a special problem that *Ph. esculenta* is a problematic taxon according to the nomenclature too. Relative to the state of *Ph. esculenta* VAN HOUTTE and *Ph. acinosa* ROXB. belonging to the *Ph. acinosa* agg., in the literature there can be found different views, like 1: *esculenta* = *acinosa*, 2: *esculenta* = *acinosa* var. *esculenta*, 3: *esculenta* ≠ *acinosa*. Based on his studies SKALICKÝ (1972) consider them as well separable, substantive species. NOWICKE (1968) presumes that *Ph. americana* L. belongs to the *Phytolacca* NOWICKE section of *Phytolacca* NOWICKE subgenus, and *Ph. esculenta* VAN HOUTTE belongs to the *Pircunia* NOWICKE section of the *Pircunia* (MOQ.) H. WALTER subgenus. In Hungary the *Phytolacca* genus is only of adventive occurrence. Only those two species – *Ph. americana* and *Ph. esculenta* – in wild and naturalized occurs here those been discussed well in this chapter. Invasion of the previous species have been noticed for decades, whilst latter one become a typical invasive plant nowadays.

MORPHOLOGY

A) *Ph. americana* is a herbaceous perennial plant. Its root is thick, has several heads and strong taproot-system, its napiform root has been thickened like beet and its diameter at the ground level can reach the 12–15 cm. It is big-statured, 80–300(–350) cm high, glabrous, subdichotomously branched plant with upstanding stem. The stem is cylindric, fleshy, hollow inside, usually with purple patched or goes into red, it can be somewhat woody at the base. The leaves are darker green on the upperside and brighter green on the underside. They grow sparsely on the stem. They are petiolate, oblong- to ovate-lanceolate in shape, at the apex acute, 10–30 cm long, 5–15 cm broad, glabrous, entire and have striking winged nervation. The size of the leaves is decreasing towards the shoot's apex. Its inflorescences are 5–15 cm long loose racemous cincinnus, those can be erect or can lean over in ± bows, but by the time of ripening they are mostly hanging down. The flowers are small, 5–6 mm broad, hermaphroditous. The number of stamens is 10, the filaments are evenly fine. The 10 carpels are united at the base. Perianth-segments are white or greenish, on the fruit they turn into red; they are broadly-ovate in shape and about 2.5 mm broad. Its fruit is mildly articulated and green whilst unripe and it has smooth surface, first glossy dark purple and later black colour when it is ripe, it is 7–12 mm in diameter, depressed-globose, 10 seeded berry (bacca syncarpa). Its seed is reniform-orbicular, rather flat, shining, black, smooth, and 2.5–3.0 mm in diameter. Seed weight is 6.1–7.5 g/1000 seeds. Seedling: the stem underneath the seed-leaves is fleshly thickened, usually purple. The seed-leaves have oblong- ovate shape, tapering at the apex, big, 15–33 mm long, 6–11 mm broad, with cuneate base. The petioles of the seed-leaves are much shorter than the leaf blade is. The seed-leaves have reticulate nervation and the stem above is reddish. The first leaves are broader ovate in shape, tapering, alternate and they are bigger than the seed-leaves. It seems well that the leaf's nervation is loopy reticulate. The posterior leaves are bigger.

1 The English name used for the species *Ph. esculenta* and *Ph. acinosa* s. str. belonging to the *Ph. acinosa* agg. correctly behave only the *Ph. acinosa* s. str.; we never met the English name of the *Ph. esculenta* in this sense.

2 The recent cladistic analyses based on both morphology and molecular data support this way of classification (e.g. APG II 2003).

3 In the case of var. *rigida* (SMALL) CAULKINS & R. E. WYATT 1990 (syn.: *Ph. rigida* SMALL) that is known from the atlantic coastal areas of the USA, the infructescence remains ± erect.

TABLE 1 Comparasion of four Phytolacca-species
(by WALTER 1909, SKALICKÝ 1972, OHWI 1965 és LU & LARSEN 2003, completed)

<i>Phytolacca</i> (pokeweed)	<i>acinosa</i> agg. (Asian ~ species group)			
	<i>americana</i> L. (American ~)	<i>esculenta</i> VAN HOOTTE (Chinese ~)	<i>acinosa</i> ROXBURGH s. str. (Indian ~)	<i>japonica</i> MAKINO (Japanese ~)
Height	– 3 m	– 2,5 m	– 1,5 m	– 1 m
Shape of leaves	ovate-lanceolate	broadly ovate	oblongly ovate	oblongly ovate
Leaf base	narrow	broad		cuneate
Leaf apex	acute	obtuse or abruptly acuminate	acuminate	acuminate or acute
Surface of flower and inflorescence	glabrous	glabrous	coarse (bright ochre coloured, with fairly short hairs)	distinctly scurfy
Situation of the infructescence in ripening	nodding ¹	erect	erect	erect
Length of peduncles	± 7 mm	± 7 mm	± 5 mm	
Colour of perianth- segments	greenish-white, or white with a rosy tinge	white	moderately green, with white margins	pale rose or reddish
Apex of perianth- segments	slightly acute or rounded	rounded	acute	
Length of perianth- segments	± 2,5 mm	± 3 mm	± 3,5 mm	
Broad of perianth- segments	± 2 mm	± 2,3 mm	± 1,8 mm	
Number of stamens	10	8 (7–9)	8 (7–9)	10
Shape of stamens	cylindric-subulate	subulate, well de- pressed	linear	
Colour of stamens		white	white	
Colour of anthers		pink	white	
Number of carpels	10	8 (7–9)	8	6–10
Position of carpels	united at the base	free	free	united at the base
Styles	recurved on top	recurved	nearly erect	
Length of styles	± 0,8 mm	± 0,7 mm	± 1,2 mm	
Structure of fruits	united	articulate	articulate	united
Origin	North America	China	India	Japan
State in Hungary	previously naturalised	recently naturalised	absent (?)	absent

Intraspecific variation: both the broad lanceolate leaved var. *americana* and var. *lancifolia* H. WALTER 1909, which leaves are narrow lanceolate occurs in Hungary. The f. *leuocarpa* SCHUR 1866 recorded from Transylvania has white flower and berry. In North America the var. *mexicana* L. 1753 is known, together with the var. *rigida* (SMALL) CAULKINS & R. E. WYATT 1990 (syn.: *Ph. rigida* SMALL) which infructescence is ± erect at ripening, latter known from the Atlantic coastal areas of the USA. It has variegated-leaved (cv. *albo-variegata*), just as pale yellow striped and spotty (cv. *luteola*) ornamental varieties. Its chromosome number: $2n = 36$. It is often mistaken with *Ph. esculenta*, although aside from their morphology, their habitat and phenology are different too.

B) *Ph. esculenta* is similar to the preceding species, but usually it is lower, its stature is more squab, 1–2(–2,5) m high. The stem is more stout and less or not reddish at all. Leaves are broadly ovate, apex obtuse or abruptly acuminate, 10–30 cm long and 5–15 cm broad. The racemes are more compact, 5–20 cm long and they erect even at the time of ripening too. Flowers have 8 (7–9) stamens, the filaments widened at the bases. The gynaecium is of 8 (7–9) separate carpels. The berries, those develop from the apocarpic gynaecium, remain together even after ripening. The apocarpium (coccarpium) is of 10–15 mm in diameter and it is similar to *Ph. americana*'s in colour and it contains intense dyestuff too. Seed weight is 7 g/1000 seeds. Chromosome number: $2n = 36$. (Table 1)

ORIGIN, DISTRIBUTION

A) *Ph. americana* is native to the eastern part of North America (from Maine to Florida, in the west to the line of Minnesota, Kansas, Oklahoma and Texas), just as in Mexico (var. *lancifolia*). Nowadays its distribution is much bigger, so it occurs in the north up to Canada and in the west they can be found even in the states of Arizona and California. In the North Californian gardens it became a hardly controlled weed. It was introduced to South America (for example to Argentina). The plant got into Europe in the 17th century. Its cultivation begun areas around the Mediterranean sea (South Europe and North Africa), where it has been planted as a dye-plant since 1650. From 1770 it started to spread out from Bordeaux (France). At the beginning it occurred in the Mediterranean vineyards and later it started to spread to the northern and eastern parts too. It dispersed in the Mediterranean countries and in Macaronesia; and in the north in France, the Benelux states, Germany, Switzerland, Austria (in the latter two countries they occurs especially on the southern slopes and in the valleys of the Alps), Slovakia, Hungary, Croatia, Serbia-Montenegro, Romania, Bulgaria, Ukraine and southern part of Russia. In the Czech Republic it is a casual neophyte. It is not known yet from North Europe. It is common in Asia from Turkey to Iran, and present in India, China, Taiwan, Japan, and Indonesia (on Sumatra it was found on 1500 m a.s.l.), furthermore it occurs in Australia and New-Zeland too. Generally it can be said that this plant is naturalized in the wine-grower areas worldwide. The consequence of the confusion of *Phytolacca*-species is, that some of the floristic data of *Ph. americana* in Europe probably concern *Ph. esculenta*. On the other hand, the data about the occurrence of *Ph. acinosa* in Europe probably concern *Ph. esculenta*. *Ph. americana* is well know in Hungary for a long while as a useful and ornamental plant got into here in the 16-17th century. It is included even in the botanical garden-index of WINTERL (1788), a botanist from Budapest. KITAIBEL found this plant even in the wild on his Slavonian trip in 1808. It was cultivated in vineries and in castle gardens; we have data about its escape and naturalization. BORBÁS mentioned in 1879 that it started to escape around gardens and hedges in Budapest. DOMOKOS (1937) writes about it as a frequent plant in the Mecsek-alja and along the Lower Danube already in the first half of the 20th century. Recent distribution in Hungary is South Transdanubia (mostly Belső-Somogy, West-Baranya), Duna-Tisza Interfluve (Budapest–Csévharaszt, to the south from Kecskemét) and Hajdúság (Téglás–Hajdúhadház). Recently its presence has been noticed in South-Mezőföld too, but its smaller or bigger stands can be found in many other areas (for example eastern Vas County, Bakonyalja, Balaton-uplands, Gerecse, Külső-Somogy, Zselic).

B) The native range of *Ph. esculenta* is China, where it has been grown for a long while. According to some authors it is native in Japan too, but some consider it to be an other species, *Ph. japonica*. Anyhow in Korea it is considered as alien plant. In China it occurs in valleys, undergrowth of woods, fringes of the forests, by the roadsides, but it is grown in gardens and can occur as a weed too. It grows mostly on damp, fertile habitats. Its altitudinal range reaches 500–3400 m a.s.l. In the last decades its spontaneous occurrence as a casual species has been reported from many parts of Europe, and at some places it became naturalized (e.g. Romania, Germany, British Isles, the Netherlands, Czech Republic, Switzerland, Austria and Denmark). Probably a bit later than the American pokeweed, but definitely for the same reason of utilization, *Ph. esculenta* was brought in Hungary. It so far occurred only in botanical gardens, and rarely as an escaped plant in cities, as a casual species. PRISZTER'S (1997) literary

mention from 1920 probably covers data from Kolozsvár of Soó (1927) that, however does not regard to the recent area of Hungary. The herbarium data are scarce and the oldest collected specimen is from 1945 (KÁROLYI, Bázakerettye, Zala County). By now it became naturalized in many townships of Hungary – mostly in cities, but in villages too. As we studied it mainly in the West Transdanubia, most of the data we have are from there, but it occurs in Budapest, by the lake Velence, in Dombóvár, Miskolc and Nyíregyháza too.

LIFE CYCLE

Seeds of *Phytolacca*-species occurring in Hungary germinate in April–May. In the first year the plants develop a few cm thick primary root and lateral roots. The napiform root develops from the root, the epikotyl and other basal internodiums of the primary axis. The elder plants sprout from several buds of the napiform root in spring. Every mature individual can bring in up to 6–10 strong stems. The young sprouts can be damaged by late frosts. Generally in favourable habitats the plants reach their maximum size by the middle of summer. Their water regime is a bit unstable; in the case of permanent drought or on sunny summer days the leaves of the plants – and sometimes their shoots too – get a drooping habit, but they tolerate quite well the drought. Flowering starts in May, it peaks in July–August, but it can blossom in September–October too. The colour of the fruits is green at the beginning and during the ripening it gradually becomes dark purple (almost black), which is often followed by red coloration of their fleshy stems. Every individual can ripen up to few hundred seeds. According to the American publications, the seeds of *Ph. americana* remain capable of germination up to decades in the soil. In its native range one individual can reach even the age of 30–40 years. It is interesting to notice, in an earlier Hungarian reference book (Soó 1970) *Ph. esculenta* show up to be an annual plant, but nowadays it is definitely considered to be a perennial. It blossoms few weeks earlier than the *Ph. americana*, presumably because of the milder microclimate of the townships. Both of the species are frost sensitive. Following the first frosts the whole plant whitens and frozes down till the ground's level. Initially their upstanding and then their decumbent white remains can be seen from autumn till spring. Birds participate mightily in the propagation of the *Phytolacca*-species. Their infructescences with blackish-purple berries can be seen from afar, that attract the birds and which eat the fruits and defecate the seeds in far places (endozoochoria). *Ph. americana*'s (pigeonberry) name refer to it. According to North American and Hungarian observations, the seeds of *Ph. americana* is propagated well by water (hydrochoria) too.

HABITAT PREFERENCE

Like most of the pioneers, these species germinates mostly in disturbed soils too. They develop well on sunny and on shady sites alike. Although they can be found mostly under branches of trees or shrubs, nearby fences, according to that these are the landing places of the birds defecating their seeds.

A) In its native range *Ph. americana* primarily grows as a pioneer plant of disturbed and open surfaces of damp soiled forests (for example around badger's burrows), on the fringe of forests and on riverbanks. Of the antropogeneous habitats it can be found on cuttings, waysides, fields and fallows. They prefer the eutrophic, flimsy, damp soils. It occurs rarely on sites where the temperature goes under –15 °C permanently in the winter, propagation is favourable if the average temperature is around 20 °C in July. In its native range it occurs at 1400 m of elevation. Typical examples for its European occurrence are clear-fellings in Austria (Lajta hills), hedges and dumps in Switzerland. In Italy it was found on field sides, along canals, on seashores, and in black locust plantations. In Hungary it primarily shows up en masse in forestry plantations (black locust, black pine and Scotch pine) and on disturbed woodlands or shrubberies. It can be abundant in disturbed sandy grasslands and in alder swamp forests that has no surface water. It prefers the more humid habitats, and the half-shade; on sunny sites it grows usually under shrubs or trees. It favours loose soils that developed on acidic or neutral, sandy or pebble bedrock.

It can be found in uncultivated vineyards, orchards, and lately it has been noticed on arable fields and row crop cultures (paprika, tomato, sunflower) too. It likes the ruderal habitats too, it occurs in the cities (for example Kecskemét, Szeged).

B) In its native range *Ph. esculenta* occurs in forests, on cultivated fields, sunny borders and half-shade sites. We only have scarce data about its habitat preference so far. This species is considered to be a specifically township- (urbanofil, cf. WITTIG *et al.* 1985) and warm-prefering weed that chiefly colonize on open surfaces of half-shade habitats on loose, eutrophic, neutral or slightly calcareous soils. In Hungary so far this species has only been found in townships! Its occurrence in the more near-natural vegetation in the future can be expected on the border-associations of the (half-)shady habitats (*Alliarion*).

BIOTIC INTERACTIONS

Although we have not found yet any notice in the literature regarding to this behaviour, however it is quite possible that *Phytolacca*-species have allelopathic effect; where they grow it can be seen well that other plants get distinct.

The seeds of *Ph. americana* is eaten – at least the ones we have data about – among others by the following birds (by RIDLEY /1930/ and DEBUSSCHE & ISENMANN /1990/): in North America: American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), white-eyed vireo (*Vireo griseus*), red-eyed vireo (*Vireosylva olivacea*), Philadelphia vireo (*Vireo philadelphica*), yellow-throated vireo (*Vireo flavifrons*), American robin (*Turdus migratorius*), eastern bluebird (*Sialia sialis*), northern mockingbird (*Mimus polyglottus*), eastern kingbird (*Tyrannus tyrannus*), great crested flycatcher (*Myiarchus crinitus*), eastern hairy woodpecker (*Dryobates villosus*), yellow-bellied sapsucker (*Sphyrapicus varius*); in Italy: blackcap (*Sylvia atricapilla*), whitethroat (*Sylvia communis*), song thrush (*Turdus philomelos*), blackbird (*Turdus merula*), blue rock thrush (*Monticola solitarius*), robin (*Erithacus rubecula*); in South France: robin and blackcap; in New-Zeland: the pheasant (*Phasianus colchicus*). The publications imply that the birds occasionally regurgitate the toxic seeds. The surrounding of a lake in the state of South Carolina, in North America was polluted by radioactive substrates and it was perceived that specimens of *Ph. americana* significantly accumulate the radioactive cesium which accumulates in the muscle of the mourning dove (*Zenaida macroura*) too, the bird's main nutriment is the fruits of this plant. It means that the consumption of these pigeon's meat can be dangerous too. According to an observation in the Canadian forests devastated by the Asian gypsy moths, the American black bear's (*Ursus americanus*) main nutrition was *Ph. americana*. Ad hoc observations prove that the young shoots of *Ph. americana* is eaten by big games (red deer, fallow deer) living in the Hungarian forests. The sheep and the goat kept on sandy pasture-land consume this plant too. According to observations on the British Islands rabbits cause no damage to *Phytolacca* species. One of the densest substances of *Ph. esculenta* of Szombathely is under the plane-trees in a park of the city, on which rook's (*Corvus frugilegus*) nestles. However the urbanophilous character of this plant and our own observations suggests that the most common consumers of their crops can be the blackbird (*Turdus merula*) and the song thrush (*Turdus philomelos*), that became more and more common in the townships in the last decades.

Ph. americana is a natural perennial host plant of different plant viruses, for example the cucumber mosaic virus (CMV). Specimens that shows the symptoms of the mosaic- and annular patchiness was observed in Keszthely in 1989, later in Szentes in 1994. In both cases mechanically transmissible, but so far not yet identified viruses was separated from the diseased plants. Next to Berkesz (Szabolcs-Szatmár-Bereg County) – in substances living in the woods of Scotch pine and black locust – chlorotic and necrotic oak leaf-markings were found which suggests virosis. HOLLÓS described the imperfect fungus *Coniothyrium phytolaccae*, from *Phytolacca*. *Phoma sorghina* (Deuteromycotina) that causes phomal disease was lately observed on the *Ph. americana*. From the Japanese publications *Ramularia harai* and *Septoria phlyctaenoides* (Fungi imperfecti), just like the powdery mildew producer *Sphaerotheca fuliginea* and *Sphaerotheca macularis* truffles (Ascomycotina) are well known as agents of the *Ph. esculenta*'s leaf patchiness.

ECONOMIC IMPORTANCE

Benefits

A) The young shoots of *Ph. americana* are eaten cooked as a substitute for asparagus in springs, and its tender leaves were eaten as a substitute for spinach even by the North American (Delaware and Virginian) Indians. We can find this kind of utilization nowadays too: at markets in the southern states of the USA it is sold as „sprouts” even these days, and they sell its young, tender leaves tinned (Poke Salet Greens). At some places it is still cultivated, though only in small-scale. The tender, bright inner part of the stem is crumbed in cornstarch and fried. They use the young plants before crimson coloration, but the cooking water needs to be discarded. Its ripe berries are added to cake pastries. The roots and the leafy stems are traditionally used for purple-brown dyeing. This colour is not much permanent, after body painting it can be removed easily. The root contains much saponin so it can be used for making soaps. The leaf's powder or the leaves were used for external treatment of cancerous wounds. After it got into Europe it was not only planted as an ornamental plant, but its dark purple dye was used for food coloration. The liquor of the berries were pressed, fermented and cleaned up by straining and afterwards it was evaporated down to about honey density in China. The product was used at one for the coloration of foods, preserved fruits, sweets, liqueurs and wines; and for example as *Succus Phytolaccae inspissatus* it was sold in German pharmacies. The berries were used to colour the wines of poorer quality with such a success that the plant was widely grown in Portugal, Spain, France and Italy. An ethnobotanical fact about the plant in the Carpathian Basin is that the Transylvanian (Kalotaszeg, Kiskapus) people put the fruit in the barrel cabbage to give it a red colour. Thanks to its betacyanin content it can be used as an industrial dye, but its colour is not as persistent as the colour of the scarlet oak (*Quercus coccifera*) is. Rarely it was used for wool and silk coloration too. The crimson coloured sap of the berries was used as ink (for example by the soldiers in the World War), that is where English name, inkberry derives from. A limner from Missouri, BINGHAM used it as paint. Its therapeutic utilization has traditions too. The Delaware Indians considered it to which has cardiac restorative effect, and the Virginian tribes used it for its strong psychotic effect. They presumed it is useful against rheumatism, tumours and in smaller doses against syphilis too. Its therapeutic utilization is comprehensive. Earlier the European therapeutics used it too as an emetic: *Radix, Herba et Baccae Phytolaccae*. Its root, leaves and fruits are used in the homeopathy too. The plant is a pharmaceutical base material even nowadays. Its drug is used as an antirheumaticum, purgaticum and emeticum (alias “poke root” or „Phytolacca”) in the USA, besides the lush root may be used against breast cancer, too. The berries are utilized there for food coloration too, and with its leaves they adulterate, or rather substitute the „*Folia Belladonnae*”. The modern medicine started to show interest in it, thanks to the antiviral protein (pokeweed antiviral protein, PAP) that blocks the infection and reproduction of the HIV virus. The external use of PAP has an inhibitory effect on the plant RNA viruses too. The transgenic plants that contain the gene of this protein became resistant to a wide range of viruses. They impute that the root of the *Ph. americana* has blood cleanser, anti-inflammatory, expectorant, sedative, stupefying and purgative effects too. There are experiments for its utilization to cure the autoimmune diseases, especially the rheumatic arthritis. The plant contains toxic compounds against micro-fungi and molluscs too. The lectins extracted from it have toxic effect on the juvenile larvae of the southern corn rootworm (*Diabrotica undecimpunctata howardi*).

B) The species that belongs to *Ph. acinosa* aggregation are cultivated plants for a long time: *Ph. acinosa* s. str. in India, *Ph. esculenta* in China, while *Ph. japonica* in Japan. As the toxic compounds mentioned earlier are absent from or present only in a small amount in the juvenile plants (especially in *Ph. esculenta*), its fresh shoots are eaten as a substitute for asparagus, and its cooked young leaves are eaten as a substitute for spinach. The effect and the acidity of the slightly toxic (emetic and purgative) compounds tone down a bit by cooking. (According to data from 1852, *Ph. acinosa* was grown in Germany as „spinach”, and it was propagandized as a vegetable in France too, with little success.) The traditional East Asian medicine uses *Ph. esculenta* because of its several curative powers, for example in Korea as an antirheumaticum, in China as a strong purge and in Japan (the roots) as a diuretic. In addition its antiasthmatic, antibacterial, antifungal, anti-inflammatory, cough-relieving, expectorant effects are well

known too. The sap pressed from the leaves contains antiviral glycoproteins. Thanks to its edible leaves and berries *Ph. esculenta* is called „crimson spinach” too. Red dye can be extracted from the fruits of this species too. The saponins of *Phytolacca* species have repellent effect too. After all *Phytolacca* species – like other plants – synthesize many in itself useful and harmful compounds. The quantity can be dependent on the genotype of the individual, but – part-way – on the ecological factors too.

Damages

A) Beside the modes of utilization of *Ph. americana* mentioned above, it is important to emphasize that the toxicology keeps count of it as a *toxic plant*, it causes puke and diarrhoea while raw. Its use as a food dyeing is prohibited for a long while. The use for therapeutical purposes needs due foresight, medical supervision, not suggested to do it at home. The most toxic part of the plant is the root, which contains saponins, among them phytolaccatoxin that is toxic to vertebrates. In respects of human health the most dangerous is the lectin content. In the new roots of *Ph. americana* hemagglutinin compound was detected – which is similar to the ones in the seeds of castor bean and Calabar bean – that contains much cysteine (a sulphur-laden amino-acid) and has mitogenic effect. It can stimulate the abnormal cell division of the poise B- and T- lymphocytes, and it can damage the chromosomes too. From agricultural point of view *Ph. americana* is considered to be a weed its native range, for example in maize-, soybean- and other crops with no tillage. It is registered as a weed in Europe, Australia, New Zealand, Japan and China too. It occurs on the plow-lands in Hungary too, but it does not endanger the agricultural crops that gets regular and deep cultivation. The big bushes of the plant are remarkably maleficent, it extinguishes almost all the other plants around them. Recently the species weeds in even the horticultural areas. It weeds in the sparse and abandoned vineyards, and nowadays on arable fields and in the row crops cultures (paprika, tomato, sunflower) too. *Ph. americana* is worth considering as a lately spreading weed, and as a host of different plant viruses. As a sylvicultural weed it appeared chiefly not in the forests, but in the wood plantations, for example in the woods of black locust, black pine and Scotch pine. As a weed it occurs mostly on loose soils, sandy areas, on these sites multiple hectare of practically enclosed stands were observed. Its further spread on the cultivated areas is expected primarily on the plantations with less disturbed soils.

B) *Ph. esculenta* – as we mentioned earlier – so far appeared chiefly in townships. In private gardens and public premises, like parks, stream’s embankments, along fences and hedges they have started to spread nowadays. It is slightly perceptible that this plant is a weed, as with its imposing soliter or grouped habit, it appears to be an ornamental plant that has no need of gardener at blooming and even at cropping times. However its further spreading can make the work of park maintainer more difficult, and may the reaping of the embankments of the watercourses too. Primarily its further spreading is expected to be in townships and in their surroundings, and secondarily in sylvicultural plantations.

NATURE CONSERVATION SIGNIFICANCE

Ph. americana can propagate itself in large numbers on a slightly disturbed natural habitats. As a consequence of the different land use activities, there are some kind of disturbance everywhere so probably this species will be more common in the future. On sand grasslands it over-compete the native species by its shade and in the different forest communities its presence reduce the conservation value. Dispersion of *Ph. americana* in the protected area of Barcsi Borókás (originally with dominance of *Juniperus communis*) causes big problems, where along with an invasive tree, black cherry (*Prunus serotina*) it occurs en mass in open perennial grasslands (*Festuco-Corynephorum*), Molinia-Turkey oak forests (*Molinio litoralis-Quercetum*) and alder swamp forests (*Carici elongatae-Alnetum*) too. In West Hungary it also endangers the oak-hornbeam forests. While *Ph. americana* occurs mostly on semi-natural habitats, *Ph. esculenta* is spread on ruderal ones. Although, latter it appeared on semi-natural habitats too, like in alluvial forests (Ikervár, Vas County). According to the observations of population dynamics in townships, it is quite probable that in the future this species will appear more often in semi-natural habitats.

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ADVENTIVE GRAPEVINE SPECIES

(*Vitis*-hybrids)

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TAXONOMY

The grapevine family (Vitaceae) consists of some 12 genera and 700 species. According to recent studies the family is classified to a separate order, Vitales, which is placed among Core Eudicots. Formerly the family belonged to order Rhamnales, subclass Rosidae, class Magnoliopsida or Dicotyledonopsida, and phylum Magnoliophyta or Angiospermatophyta.

Genus *Vitis* comprises more than 60 species which are distributed on the northern hemisphere. Three centers of genetic diversity are separated: North American consisting of the most species, East Asian, and Mediterranean, the latter with few species. All species are lianas climbing with tendrils.

Genus *Vitis* is divided into two subgenera: inflorescences of *Muscadinia* consisting of only 3 to 30 flowers, while that of *Euvitis* has large, multi-flowered inflorescences. Berries of the former ripen not simultaneously and drop easily. There are conspicuously projecting lenticels. Pith within their wood is thin, and there is no diaphragm at the nodes. Their cortex is corky, but not peeling. Tendrils are not branching. There are two species here both native to North America of which *V. rotundifolia* MICHX (native to Texas, Florida and Virginia) is cultivated as table grapes.

Berries of subgenus *Euvitis* ripen simultaneously and do not drop. Pith of their shoots is wide and soft, there is a diaphragm in their nodes. Their bark peels in longitudinal stripes, tendrils are branched, and lenticels develop only on fruit pedicels, close to the berries.

After phylloxera plague grapevine (*Vitis vinifera* L.) could be grown safely on heavy soils only grafted on American grapevine species resistant to phylloxera. For this purpose as rootstock and primarily as so called directly yielding cultivars selected in North America the following species have been introduced into Europe and Hungary:

- V. rupestris* SCHEELE
- V. aestivalis* MICHX.
- V. labrusca* L.
- V. vulpina* L. (syn. *V. riparia* MICHX.)

Following species have been planted only as rootstock and ornamental purposes:

- V. cordifolia* MICHX.
- V. cinerea* NORONHA (syn. *V. flexuosa* THUNB.)
- V. longii* W. R. et B. PRINCE

Some of East Asian grapevine species are cultivated as ornamentals. A winter hardy species, *Vitis amurensis* RUPR. native to Manchuria has been used successfully for improving cultivars in Hungary as a parent species. Spontaneous hybridization of species not native to Europe and directed cross breeding serves cultivation of grapevine extending to almost all continents until today.

MORPHOLOGY

Neither of alien grapevine species can be separated easily, because *V. vinifera* escapes, *V. sylvestris* is forced back and partly hybridized, and escaped American species however are present as a hybrid complex today, therefore we would search for clear species in identifying books in vain, characteristic features suitable for their separation could not be found.

The wild European grape (*V. sylvestris* C. C. GMEL.) differs from grapevine in having basically dioecious flowers, similarly to adventive grapevines. Leaves of staminate (male) individuals of wild European grape are deeper lobed than that of pistillate (female) ones, leaf base is open or U-shaped. Leaves of pistillate individuals are scarcely lobed. Mean fruit diameter is 6 mm, slightly egg shaped, bluish-black berry of sour taste. Usually three seeds develop in each berry. They are more or less round with short, truncated beak. Fall leaf color is light yellow or purple. Leaf blade is wider than its length in both sexes, in this character it resembles only *V. rupestris* SCHEELE among American grapevine species. Leaf margin is serrated; teeth are short (wider than their length). Common feature of grapevine and wild European grape is alternating tendril development: after two nodes having tendril (or inflorescence analogous to tendril) there is a simple node having neither tendril, nor inflorescence (or reduced inflorescence, transition between tendril and inflorescence).

Common feature of American grapevine species is long teeth of serrate leaf margin, and continuous tendril (and inflorescence) development. This latter however is not fully regular: in case of *V. labrusca* L. all nodes have a tendril or inflorescence, while in other species it may be absent on some nodes.

ORIGIN, DISTRIBUTION

Land use antecedents – past of cultivation

Genetic material of *Vitis vulpina* subsp. *riparia*, considered *V. riparia* by the authors (identified as escaped *V. riparia* by TERPÓ) deriving from antecedents of cultivation, contains the genetic material of hybrid rootstock cultivars (*V. solonis*, *V. berlandieri*, *V. rupestris*, *V. vinifera*, *V. labrusca*, etc.). As a reason of it beside introduction of hybrids raised in their American native land we can mention that accidental crossing, which has happened in France among rootstocks introduced already as clear species. This process has been carried on intentional crossing and selection of hybrids of species in the second generation of rootstocks. Furthermore *V. riparia* is one component of cultivated directly yielding species complex too.

Possible process and chronological order of getting in invasive grapevines

Until discovery of America the only known grapevine species was wine grapevine, which was later described as *Vitis vinifera* by LINNAEUS. In the beginning wild growing populations later described as *V. sylvestris* have not been distinguished, then it has been classified under wine grapevine [*Vitis vinifera* L. subsp. *sativa* HEGI és subsp. *sylvestris* (GMEL.) HEGI]. Later it was approached also as escaped cultivated grapevine, which has caused considerable inconveniences in taxonomic interpretation.

“Official” discovery of America (1495) gives possibility of knowing, utilization and European introduction of large number species native to mainly to the Atlantic coast (From the Gulf of Mexico to Newfoundland). Appearance of landscape description of Vinland (Vineland) from the North American continent, belonging to fantasies in the beginning but later mentioned in Icelandic Sagas, is an interesting interlude. Remains of Viking settlements have been turned up, but today *Vitis* taxa do not live on this latitude in North America, that time however climate was warmer than today which makes the occurrence of most winter hardy grapevine species more north possible.

First documented introduction of American grapevine species into Europe are given by lists of botanic gardens and grapevine collections. The turning-point of European description of American grapevine species is “Species Plantarum” of LINNAEUS (1753), where there are two American grapevine species: *V. labrusca* and *V. vulpina*, presumably LINNAEUS has seen these two relatively hardy grapevines in Europe.

Before the 1848 Hungarian War of Independence there is already one *V. labrusca* hybrid named “Ananastraube” or “Erdbeertraube” in Hungary, which are usually identified as ‘Isabella’ today.

Three calamities

First American disease, grapevine powdery mildew (*Uncinula necator*) has appeared first in a grapevine-forcing house in England in 1845, it was indicated from France in 1850, and its first Hungarian mention is from Pál Bugát in 1853. Twigs of mildew resistant species have been imported from America in great mass, presumably the most dangerous pest of grapevine of that time, phylloxera (*Daktulosphaira vitifoliae*, *Phylloxera vastatrix*, *Viteus vitifoliae* or *Viteus vitifolii*) has been brought in with it, which appeared along river Rhône in the early 1860's. It has been observed first in the historical Hungary in 1875 at Pancsova (now Pančevo, Serbia); from 1885 its destruction has become very serious. Third American disease of grapevine growing, grapevine downy mildew (*Plasmopara viticola*) appears in Hungary in 1880 in village Medgyes; its damage is significant since 1891. This two latter has destroyed 60% of vineyards and decreased yield with 75% in 1894 in comparison with the base of 1886. Meanwhile in the knowledge of protection methods elaborated in France first grapevine restoration has been started. In 1881 state import of *Vitis* species (*V. riparia*, *V. rupestris*, species-hybrid table grapes — the first generation of directly yielding ones, e.g. ‘Noah’, ‘Othello’, etc.) and rootstock twigs from France has been started. Since phylloxera is not viable in sandy soils, re-plantation has been made with normal twigs (rooted cultivars) between rivers Danube and Tisza, while on heavier soils with scions grafted on ‘Riparia Portalis’ rootstock, which latter has been separated by the primer selection of *Vitis riparia*. First grapevine restoration has started gradually. First law (Act I, II year 1880) has been concerned to immediate protection; the second was Act V. year 1896 of “grapevine restoration” linking to the name of Ingác Darányi, minister of agriculture. On course of this form-rich clones (micro-populations) consisting of heterogeneous types have been used and got to rootstock plantations. Heterogeneity reflects also in contradictory synonymy of cultivars. Act V year 1896 of grapevine restoration already excludes some historical *V. vinifera* cultivars of low quality and yield, and allows some rootstock cultivars namely, these are primary selections (not yet hybrids) of *Vitis* species: ‘Riparia Portalis’, ‘Rupestris du Lot’, ‘Rupestris Metallica’ and *Vitis solonis* hort. (which latter has been thought to be a natural triple species-hybrid, but according to a more recent interpretation it is an own species, *V. longii* PRINCE).

From contemporary articles of Wine-growing News (Borászati Lapok) we know about several hundred kilograms of arriving *Vitis* seeds, which have been recommended to users in the first years of grapevine disaster. This we should consider in case of dioecious grapevines, because before selection both staminate and pistillate individuals have given chance to flower and set fruit, therefore to escape too, though originally in case of use as rootstock only the vegetative body of grapevine plant was necessary.

Hungarian Ampelological Station (predecessor of today's Ampelological Research Institutes) has been established in 1898, which has organized and supported rootstock Hungarian breeding adequate for local ecological conditions. Selection breeding of domestic rootstock cultivars has been started that time. It is confirmed that primary selections of species are not successful enough on calcareous soils, and they are not fully compatible with certain cultivars. Most successful species-hybrid cultivar selection is linking to the breeding activity of two generations of Teleki family at their works in Pécs then in Villány. After have prohibited the import of grapevine twigs because of black rot, Zsigmond Teleki has decided to grow lime tolerant rootstock cultivars from seed. He was informed, that *V. berlandieri* is the most suitable for calcareous soils, therefore — according to the documents — he has been imported about 40 000 seeds of hybrid origin from France, the parents of which were *V. berlandieri*, *V. riparia*, *V. rupestris* and *V. vinifera*. Seeds have been sown in Pécs in 1896, from the germinated seedlings he has destroyed individuals of *V. vinifera* type (presumably because of their phylloxera susceptibility), and then those of wild character he has divided into 10 type groups: № 1–3 of *V. berlandieri* dominance, which has been also destroyed. Among those of *V. berlandieri* × *V. riparia* phenotype glabrous internode ones he judged *V. riparia* character and divided into three groups (№ 4–6), among which he has propagated 3 individuals of type № 5, which have been sold as officially acknowledged rootstock cultivars under the name *Berlandieri* × *Riparia* ‘T.5A’. He named hairy internode seedlings of *V. berlandieri*

character (№ 7–9) among which he has propagated 5 individuals of type № 8, this is the base of rootstock cultivar named *Berlandieri* × *Riparia* ‘T.8B’. Seedlings having *V. rupestris* × *V. berlandieri* character complex have got into group № 10, from which he has selected rootstock cultivar named *Rupestris* × *Berlandieri* ‘T.10A’.

As cultivar material of the second grapevine reconstruction (decree with legal force № 23 of year 1959 and its enacting clauses) selected cultivars of *V. berlandieri* × *V. riparia* hybrids have been served, which are practically in use for grafting even today. Teleki have distributed a mixture of three types under the name *Berlandieri* × *Riparia* ‘T.5A’ and of five types under the name *Berlandieri* × *Riparia* ‘T.8B’ among rootstock cultivars bred by them, instead of starting from only one individual. So they have given a mixture of the same phenotype (a population fragment according to our interpretation) cloned to cultivation. This fact has made it possible, to select the Teleki cultivars further in other European countries, e.g. today widely known and propagated ‘T.5C’ and ‘T.5BB’ cultivars have been selected from ‘T.5A’.

According to the authors’ opinion we get an explanation here, why do pistillate individuals appear from time to time in stands of rootstock cultivar plantations declared to be staminate. KOZMA however explains the appearance of pistillate flowers on staminate individuals as an effect of hard pruning applied in rootstock plantations. Expanding populations could be dispersed by birds from these pistillate individuals even from rootstock plantations, and from cultivation relics of abandoned grafting vineyards. Majority of early escapes are rather relic of cultivation from rootstocks declared to have low performance of regularly yielding pistillate individuals sprouting and climbing on fences drawn along land borders. Second grapevine reconstruction have been made by using rootstocks of hybrid origin, among which the following ones are pistillate: *Berlandieri* × *Riparia* ‘Sz.157’, ‘Chasselas’ × *Berlandieri* ‘M-de G.41B’, ‘Mourvèdre’ × *Rupestris* ‘C.1202’, *Solonis* × *Riparia* ‘C. 1616’, *Berlandieri* × *Riparia* ‘T–K.5BB’. From these abandoned cultivars – similarly to *V. vinifera* – numerous successors have been originated in the surroundings of abandoned vineyards.

When North American grapevine species in question got into Europe verified?

According to Hilliers’ Manual of Trees & Shrubs (4th edition 1974: 453–454) *Vitis labrusca* L. “Fox Grape” has got into western gardens in 1656 with the aim of cultivation, while *V. riparia* MICHX. (syn. *V. vulpina* hort.) “Riverbank Grape” has already been cultivated in 1656. Time of its getting in is unknown, but as a conclusion earlier.

It is an interesting statement that berries of some wild growing “*riparia*” populations are of “foxy” taste. This has been considered as a result of crossing with *V. labrusca*. This latter species has not been seen wild in Hungary, only its directly yielding cultivars as relics of cultivation, or seedlings of cultivars. According to the authors of present article one should consider the origin of the name *V. vulpina* given originally by LINNAEUS, because it refers to fox.

Why do V. riparia – V. vulpina appear in two names?

We think here a duality of nomenclature, priority and morphology appears. Originally LINNAEUS used the name *V. vulpina* in 1753. The original description of LINNAEUS has been reviewed by MICHX, and ANDRASOVSKY (1925) mentions in the identifying key of genus *Vitis* that cultivated forms of the species *V. vulpina* L. are summarized under the name *V. riparia* MICHX. Among viticulturists in the nomenclature of rootstocks (see cultivar names) the name *Riparia* appears everywhere. ANDRASOVSKY (1925) at the same time does not mention the escape of any alien grapevine species, only that of *V. sylvestris*, which he considers not a native species, only the escape of *V. vinifera*. KOZMA (1991) uses both names in Latin and in English parallel, though he refers to many ecotypes of this species of wide distribution. In his early *Vitis* works TERPÓ (1962) writes about the frequent escape of *Vitis riparia* and *V. rupestris*, though real data confirm the great mass mainly of *V. riparia*. He writes about populations of *V. riparia-vulpina* along river Tisza and Bodrog (between Tokaj and Bodrogkeresztúr). TERPÓ takes a stand first on his academic doctoral theses (1988) concerning the taxonomy of native populations of *Vitis vulpina-riparia*, knowing the type specimen of MICHX he treats it as a subspecies named *V. vulpina* L. subsp. *riparia* (MICHX) TERPÓ, beside which the occurrence of this typical *V. vulpina* he considers doubtful.

He admits “hairy *riparia*” under the name var. *praecox* ENGELM. from the side of river Danube and Tisza (see “hairy” and “glabrous leaved” cultivated riparias KOZMA 1991), but he describes new taxa too, such as var. *pannonica* TERPÓ with V-shaped leaf base and small teeth, this is the most common; within it he separates f. *danubialis* TERPÓ, which is characterized by a straight braces ({} -shaped leaf base. He does not mention anywhere species *V. rupestris* got into the literature by his earlier publications. The authors can identify the population formerly identified as *Vitis rupestris* really in this subtaxon.

In addition he has separated var. *andreanszkyana* within *V. vulpina* L. subsp. *riparia* TERPÓ, in contrast with the former ones with rougher, crenate–dome shaped leaf margin.

He has expressed the taxonomic diversity of *Vitis vulpina* in the Hungarian flora by describing hybrids made with native species too: *Vitis* × *rathayana* TERPÓ (*V. sylvestris* × *V. vulpina*), and *V. ×andra-sovszkyana* (*V. vinifera* × *V. vulpina* subsp. *riparia*). Berries if this latter two contain diglucoside, which proves its (partly) American origin, but we think not surely of *V. riparia*.

Where do escaped grapes originated from?

- a) Import of original seed amounts (of partly hybrid origin) from France in the last third of the 19th century;
- b) Rootstock of first grapevine reconstruction is unambiguously *Vitis riparia*. The grape introduced to France from America in 1873 and 1878 was ‘Riparia Sauvage’ (unselected “wild” *V. riparia*). ‘Riparia Portalis’ as a rootstock cultivar of grate hope is one of the most successful of the first selections. Act V of year 1896 about grapevine restoration permits the following rootstock cultivars: ‘Riparia × Portalis’, *Vitis solonis*, ‘Rupestris du Lot’ and ‘Rupestris Metallica’ It soon turns out however, that lime tolerance of *V. riparia* is low, therefore clearly as a rootstock it is suitable only in limited scale, e.g. in the Tokaj district. Vineyards of ‘Riparia Portalis’ rootstock has been planted until 1920, later because of unsuitability a change of rootstock cultivar happened in this respect too.
- c) Rootstocks of unsuitable grafting combinations in plantations and rootstock nurseries. Rootstocks of plantations cut out are very virulent, they put out shoots again; they act as weeds on plantations or in fences, borders. Genetic material can get out from these plantations only by birds carrying fruits of pistillate individuals, since the possibility of carrying twigs is fairly low.

When did Vitis riparia escape so, that first it became naturalized, then invasive?

As first possibility great amount of unselected *V. riparia* seed imported for rootstocks of the First Grapevine Reconstruction can be taken into consideration, of which germinated seedlings might have been pistillate in 50%. As a characteristic feature of insensibility to nature conservation of the contemporary press, news about such escapes have not been seen yet.

The second possible way is the scattering of genetic material of selected *V. riparia*, also from pistillate individuals, the proportion of which is substantially smaller (occasional), since cultivars were officially staminate, but certain notes reported about scattered pistillate ones in rootstock plantations too. Fission of *V. riparia* hybrids has not been studied as we know, but it is possible, that from pistillate individuals of *V. riparia* × *V. rupestris* a gene spread could be happened. This can be the explanation not only of way of dispersal of *V. riparia*, but it can be the source of individuals thought to be *V. rupestris* too. This population is completed by the spread of seed material of also pistillate rootstock cultivar ‘Solonis × Riparia C1616’, its occurrence as relic of cultivation is reported by KISS (1939) together with *V. riparia*.

Appearance of riverside invasive stands

Large number occurrence of *riparias* at the bank of river Tisza is known in the literature from the description of PŐSÓ (1954). In his article he mentions, that local residents know it about for 10 years, which makes the large scale appearance of the species in World War II. There is a remark, that rootstock growers of Göngyös district were used it in large number – as an unauthorized rootstock – for making graftings. It is known, that its roots are weak and the tolerance of the species is not enough on dry, calcareous soil. (References concerning this question can be found in the memorials of villages in Gyöngyös district engaged in grapevine rootstock growing.)

Verbal communication of TERPÓ gets into the volume “The grapevine (*Vitis vinifera* L.) IV/1.” of the serial Cultivated Flora of Hungary, in which riverside escape of *V. rupestris* is informed by HEGEDŰS *et al.* (1966). He notifies it in Hungary only along river Danube and Tisza, in a substantially narrower area than *Vitis riparia*, but he adds no photo evidence in any information. TERPÓ publishes the escape of *V. rupestris* in KÁRPÁTI'S (1968) widely used identifying key beside *V. riparia* in a similar extent. Its use as a rootstock in large number has happened rather in hilly districts everywhere, its diaspora is uncovered so far. Though it is a plant growing originally along riverbanks in North America, the habitat is suitable, herbarium evidence however is missing. Theoretically its escape as successor line of pistillate 'Mourvèdre × *Rupestris* C1202' is possible, or seed dispersal from alien pollination of pistillate individuals of 'Riparia × *Rupestris* 101–14 M. et G.'

LIFE CYCLE

Adventive grapevines are long lived lianas. They tolerate cut back and disturbance very well. Those of wild character are rather dioecious, among of *V. vinifera* and *V. labrusca* origin bisexual flowered ones are in the majority. Their seeds are dispersed by birds and martens; however it is distributed mainly by marc. Fallen seeds germinate next spring, (seedlings are noticed in warm late spring, early summer), mainly in such places (e.g. in rock fissures, stone borders, stone heaps, gaps of covers, beside walls), where moisture remains for a longer time even in dry periods. They have a considerable yearly growth. A rooted, potted individual having only 50 cm twig in spring grew more than 4 meters till late autumn. They climb high (>8 m) in overstorey. Decaying branches of supporting tree died because of shading and even healthy, living branches under the weight if climbing grape often break easily in storms. Grapevine branches and twigs got to the ground root easily; therefore one has to reckon with its asexual propagation too.

There are no exact data concerning the time of its first yield. Three year old stocks of *V. vinifera* grown from cuttings are yield readily, this time should not differ very much in case of the *V. riparia* complex in question too. Fruit of adventive grapevines ripen already in august in contrast with wild European grape, which ripens in late autumn, in October.

HABITAT PREFERENCE

Seedlings of *V. riparia* can be found often in disturbed habitats, on the Hungarian Great Plains often in shady, moist-mesic habitats, where soil water table is not too deep (near rivers). It can be found in certain water determined (edaphic) communities (e.g. willow-poplar forests) and in plantations (black locust) too. *V. berlandieri* is more common in former vineyards of loess regions, at the edge of deep roads, where natural vegetation starts to conquer back its habitat, at about the same place, where seedlings of *Parthenocissus tricuspidata* appear. *V. berlandieri* is in a cultivation relic state yet, i.e. its seed dispersal happens mainly from abandoned stocks, not from seedling successors. *V. solonis* once have been recommended and planted on saline, wet soils.

BIOTIC INTERACTIONS

Their allelopathic effect has not been investigated. American grapevines live together with the leaf inhabiting form of phylloxera. A large riverside stand may take an effect on the genetic material of a nearby breeding work (since they are also wind pollinated in part). Their poisonous or harmful character is unknown. It is resistant against the most important pests and diseases of European species (*V. vinifera*, *V. sylvestris*).

ECONOMIC IMPORTANCE

In Hungary today the use of adventive grapevine species (basic species directly) in commerce as rootstock is prohibited, selected hybrids however are indispensable in plantations of heavy soils. Escaped plants of hybrid origin are investigated experimentally because of their dye, and are used as breeding

basic material in experiments. As a decorative trellis plant able to overgrow large surfaces and resistant leaf these grapes are widely used in restaurant terraces. Their presence in natural or semi-natural communities is harmful, and since it is difficult to distinguish them from *V. sylvestris*, they are often destroyed together with it.

NATURE CONSERVATION SIGNIFICANCE

All form groups of *Vitis viparia* are environmental weed of invasive character, which in spite of TERPÓ's works not only hybridizes with *V. sylvestris*, but grows over it and pushes it out from its identical habitat. On the same habitat it may hybridize with wild European grape, overgrows i.e. physically pushes it out. BORBÁS (1897) writes in Flora of Budapest, that in beech forests of several cadastral acres lying between Pilisszentlászló and Visegrád once all trunks of beech trees have been climbed by "*V. vinifera*", – i.e. *V. sylvestris*, because that time wild European grape has been considered the escape of wine grapevine. This native species has been extinct from this area because of liana-phobia of foresters (similarly to recent stage if ivy), and phylloxera plague, and *V. riparia* has not appeared instead (yet!?). Though beside more favorable conditions near riverbanks *V. sylvestris* could remain, its spreading ability is less (among others due to its late ripening time), its growth succumbs that of *V. siparia*, with which it hybridizes in part, but for the most part this latter overgrows, shades, and pushes it out. In riverbanks *V. riparia* has quasi "sit in the place of *V. sylvestris*". In moist forests its presence cannot be experienced so far, but we think its appearance is only a question of time.

For nature conservation judgement of *V. rupestris* it should be remarked, that it cannot be said to an invasive plant at all, its presence can be valued only as relic of cultivation (ergasiolipophyte). Publications of András TERPÓ, a man well-informed on a matter, refer to this chronologically too: populations identified as *V. rupestris* in the beginning disappear from communications (unfortunately they have infiltrated into identifying books and common knowledge in lack of scientific correction), on the other hand in infraspecific taxon of *V. riparia* with open bayed leaf – i.e. *V. vulpina* subsp. *riparia* var. *pannonica* TERPÓ f. *danubialis* TERPÓ – appear.

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FALSE INDIGO

(*Amorpha fruticosa* L.)

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TAXONOMY

The invasive false indigo now present in Hungary is identified as *Amorpha fruticosa* L. Its commonest English name is “false indigo”, but it is also called “bastard indigo” or “indigobush” too (the latter can denote several other shrubby members of the genus).

The genus of *Amorpha* comprising deciduous shrubs and semi-shrubs belongs to the Psoraleae tribe of the Fabaceae (legume) family. About 15-20 (according to the most recent revision exactly 15) species are differentiated within the genus native to temperate and subtropical regions of North America. Species are identified mostly on the basis of fruit size and shape, the shape of individual calyx lobes, and the amount of hair. Among all the species of the genus, *Amorpha fruticosa* is the most widespread and most varied in its appearance, and the highest number of taxa (species, subspecies, form, variety) with uncertain status also belong to the *A. fruticosa* form group. There is such a great degree of uncertainty among these forms that the most recent taxonomic revision does not even deal with them. In its native range, *A. fruticosa* can sometimes hybridize with its congeners.

No study has been produced on the variability of this species in its European range, yet several varieties described in America are reported to occur in Europe too. Several members of the genus are found in European botanical gardens, but we do not have information about these species having naturalized or having been cultivated at larger scales. In Hungarian botanical gardens we have knowledge about the occurrence of the semi-shrub *A. canescens* PURSH, the dwarf shrub *A. nana* NUTT., and also *A. californica* NUTT. in TORR. & GRAY which resembles false indigo but it has hairy calyx and legume.

MORPHOLOGY

False indigo is a shrub growing to a maximum of 3-4 m (some sources report 6 m). Its branches originating from the base are initially straight and upright, but later they lean outwards. Old, solitary specimens form wide bushes with loose branch structure. Fruits resulting from the previous year are visible on the apical part of the stems throughout the year. When many bushes grow close together, their older branches gradually die off. Due to freezing or cutting back, the bush becomes densely structured. The number of stems can be 5-10(-16). The entire plant (except from the flowers) has bad terpene smell.

Its continuously growing shoots are striated, and are greenish-yellow or grayish-brown. When young, they have fine hair, and exude rusty sap when wounded. Older stems have smooth, grayish-brown bark, with emergent suberose lenticels. Its buds are small, brown, rounded and fit snugly against the stem. Often there are two buds above each other. Leaves are 7-20 cm long, alternate, odd pinnate compound, comprising 11-25 (-35) leaflets. The 15-40 mm long and 7-15 (-20) mm wide leaflets are elongated elliptic, have short stalks, usually with a short aristate tip, and with translucent spotting. The leaflets are dark green on the top and have grayish down on the underside, although looking quite worn. The stipules are needle-shaped, sticking away, and can either cling to the stalk or break away. The terminally positioned

8-15 (-20) cm long, tightly packed, upright flower spikes grow either solitarily on the apex of the stems, or open in racemes of 2-5 (with an average of 150 florets in each raceme). The bell-shaped calyx of the small, nicely scented florets is woolly or almost bald, its lobes being much shorter than its tubular part. The upper two are broad and blunt, the lower three are triangle-shaped and pointed. The single corolla (the banner part of the vestigial legume flower) is bluish-violet, embracing the long, protruding anthers. The fruit is a 6-9 mm long, crescent-shaped, non-opening legume, containing 1 seed or sometimes 2. When fresh, the legume is green, and it becomes yellowish or grayish brown when ripening. Its surface is bald, characteristically warty due to small resin-glands. The inner side of the fruit is glossy brown, whereas the egg-shaped seed is shiny yellowish-brown. Seed weight is 6-11 g per 1000 seeds.

Cotyledons of the seedlings are elongated oval, with barbed base, and have vivid green color. The first true foliage leaves have only one leaflet, the following ones already bear three; they are wide obovate or even somewhat obcordate.

The root system of the false indigo reaches deep down in the soil, and is quite extensive laterally too, made up by several meter long roots running close to the surface. Generally there are no suckers produced under normal conditions.

ORIGIN, DISTRIBUTION

The false indigo originates from the eastern part of North America. It is native to the south-eastern states of the USA (Florida, Louisiana, Alabama), and to Northeast-Mexico, but the limits of its original distribution are not known exactly. Today it has become widespread and frequent east of the Rocky Mountains and in the southern states, and it is present in Canada and Mexico as well. In Asia it has been recorded in Iraq, Pakistan, China, Korea (in the latter two countries false indigo is planted at a high rate) and Japan. It has naturalized in most of Europe (except for Ireland, Spain, Portugal, Germany, Poland, Scandinavia and the Baltic countries), and its most eastern occurrences in Europe are reported from Russia and the eastern coastal part of Turkey.

This species was first brought into England in 1724 as an ornamental plant, and was then transferred to continental Europe as well. Its first occurrence data dates back to 1907. Starting after World War I in the Danube and Tisza valleys, the rapid spreading of the false indigo was related with economically based forestation activities. As early as in the middle of the 20th century it was generally present in all of the most suitable habitats of Hungary. Its radical spreading is associated with the change of traditional floodplain farming. The most recent expansion has been brought about by the fact that floodplain fields were abandoned and the amount of grazing and foddered livestock dropped, all these caused by the political and agricultural transformation and resulting economic insufficiencies.

The false indigo is sporadically present in almost all parts of Hungary. It occurs in masses in the Great Plain, especially the valley of River Tisza, its tributaries and canals. It is generally rarer along the Danube, but in the region of the Mohács-island it already has huge populations. It is only sporadic in gallery forests along River Drava. In Transdanubia and in the mountain (hilly) regions, as well as in Hungarian lowland areas further away from the rivers, it is usually found in hedges, earlier forestations, and in secondary grasslands. In suitable areas its expansion is continuous even today.

LIFE CYCLE

It is a short-lived shrub, maturing very soon. In suitable habitats it can reach a height of 25-35 cm within the year of germination, and can grow to 60-120 cm in the second year. On alluvium its growth can follow a peculiar pattern: shoots from the first year often lie flat because of the flood, and develop 1-3 new, upright shoots from the nodes. In the second year the root system of these plants grow thicker, and 4-7 new shoots appear, reaching 70 cm. In the third year the number of shoots is 10-12, their height reaching 100-150cm. Flowers first appear usually in the fifth year, sometimes earlier.

Budding and the appearance of offshoots on cut-back plants start in May. Flowering time is June-July, which, in the case of plants that were cut down the previous year, it is delayed by about 1 month. Oc-

asionally, flowering can be observed in September as well. Fruits start to ripen in late August. Fruits are dropped continuously; some may remain on the stronger stems until well into the following summer. The leaves are lost by late October. The stems often freeze back during winter.

Flowers of the false indigo are insect-pollinated. According to HEGI, autogamy is possible, but in Hungarian studies when complete inflorescences were isolated, fertilization did not take place (this does not exclude the ability for self-pollination, but the presence of pollinating insects may be essential). In the congener *A. californica* fruit production is greater every second year. In Hungary, it was observed that a population did not produce any fruit in a particular year, contrary to the previous season. An average plant with about ten stems can yield more than 12000 fruits a year. The fruits can spread with flowing water: first they float for quite long time, then sink to the bottom. It is possible that animals, too, can act as vectors.

Upon ripening, seeds are ready to germinate immediately, but later when they dry out, the resistance of the seed coat causes a dormant period. At room temperature germination ability is maintained for 3-5 years, this period being longer at lower temperatures (no field data are available, though). Concluded from experimental studies, germination percentage is known to be increased considerably by treatment with hot water, mild acids or by mechanic scarification. For nursery propagation, 0,8 cm sowing depth and 30/20°C D/N daily temperature variation is recommended. The shallow sowing depth optimum well explains the observation that false indigo has bad renewal capacities in dry areas or on easily drying soil. It has bad germination results in darkness. In its own (moderately shaded) stands, false indigo starts germinating from the seed, but after developing a 2-3 cm long radicle, its development comes to a halt (this can be partially due to allelopathic reasons).

The plant has a strong tendency to develop suckers (offshoots) from its base. Under normal conditions it does not grow root offshoots, but it has been observed that after intensive earth works that include the chopping of underground parts of the plant can cause it to send root offshoots too. False indigo can be easily propagated from cuttings and by layering. Similar ways of vegetative propagation are important under natural conditions too, because false indigo can grow from stems lying flat in floodplain areas or even from stems under cut down branches.

HABITAT PREFERENCE

Its spontaneous appearance in masses is expected in areas which are not too shaded, have light soil and are flooded occasionally. Thus, it is very typical in willow-poplar gallery forests, (although less characteristic in the willow stands of lower terrain), in cultivated poplar stands, in hardwood gallery forests of the less open kind, and in the margins, clearings and cut down patches of all such habitats. It appears in masses in high-weed plant associations of floodplains, in abandoned agricultural fields, on the side of canals and ponds, in sides of unattended embankments, in floodplain hayfields, pastures, moist shrubberies, willow marshes. We have observed that its situation is contradictory in willow bushes and in the vegetation of silty locations: at some places it is completely absent from such zones, whereas in other places it has become homogeneously spread in willow bush habitats. It is quite likely that such a difference is caused by disparities in water regimes or soil characteristics. The false indigo spreads also in not too heavily saline meadows, dry grasslands and marshes, especially in the silt dredged from canals, typically following temporary watercourses and renewing soil surfaces.

It is less typical in areas with stagnant water, it enters bogs and alder stands only when they are in the process of drying out anyway. Its establishment in high-sedge associations and reed stands is also limited.

Among habitats not being associated with flowing water, false indigo has been found to expand in various types of forest-edge shrubbery stripes, inside well-lit forests (even in forest-steppe woody stands!), in bushy forests, dry pastures, rocky grasslands, and in huge masses in a variety of secondary or damaged areas.

It has been planted in many places in the form of hedges, in embankments and in alleys. When it originates from earlier forestation activities its great masses are usually found in habitats with some extreme conditions, such as on saline soil, on sand or karst, often planted under pine in the latter two cases.

In addition to the most optimal, open habitats characterized with good water and nutrient supply and light soil structure, the false indigo survives under extreme conditions as well, and produces an

abundance of fruit. Due to its extensive root system penetrating deeply into the soil, it can complete its full life cycle – although reaching lower heights – even on dry drift sand soils. However, it can hardly reproduce and renew its population on dry sand, most probably due to the bad germination conditions. Its growth is limited on rocky, humus less soil too, but under such conditions it has been reported to expand spontaneously. Primarily due to its good osmotic regulation system, it can stand dry weather quite well. According to studies performed in China, its drought tolerance is approximately equal with that of *Hippophaë rhamnoides*. It tolerates extended periods of flooding, but floods lasting for exceptionally long periods with the total submergence of the plants can exterminate entire well-developed populations. It has been reported from several locations that ice drift in floodplains made false indigo to disappear from larger areas. It has been recorded that this species does not tolerate strong fluctuations of water regime, and stagnant water is very unfavourable for it, too. It is a light-demanding plant, but its stands that have grown up in shade can survive even under the closed canopy of the forest. Such specimens remain small, their stems are narrow, and the plants are less vigorous in producing inflorescences. Nevertheless, they can still produce fruit. Its older, large specimens, however, will die in the shade if the canopy becomes closed above them. After fires, false indigo will develop shoots from its base.

BIOTIC INTERACTIONS

Allelopathy, competition and population dynamics

The false indigo contains allelopathic agents with terpenic, phenolic and alcaloidic character. Based on preliminary results (CSISZÁR unpublished data), the aquatic extract of its leaves had a strong inhibiting effect of about 50% on the germination rate of mustard seeds. Allelopathic phenomena are likely to have importance under natural conditions, too; most probably this is one factor contributing to the species-poorness of closed false indigo stands, and to the fact that in thinner stands the surroundings of the base of the plant is strikingly poor in plants.

Closed false indigo stands suppress shorter plants (herbaceous plants as well as the seedlings of shrubs and trees) with their intensive shading. They have strong root competition, too. False indigo seedlings are grown over by closed, intact, high grass. Fully grown specimens can be forced out by the closing canopy of higher trees (shading), and climbing plants growing up in masses (vines – *Vitis* sp., hop – *Humulus lupulus*, blackberry – *Rubus* sp., wild cucumber – *Echinocystis lobata*) can also decrease their vitality. A number of observations have reported that false indigo is either absent from the immediate surroundings of the box elder (*Acer negundo*), or it has much more retarded growth even in otherwise open locations.

The false indigo is characterized with a particular type of interspecific competition and related special population dynamics. In its mature stands the number of specimens gradually decreases with ageing, together with the discontinuation of germination. The lower branches of surviving specimens gradually die off, to be followed by the collapse of certain patches of the 25-30 year-old stand. In the place of dead specimens, the colonization of competing woody plants can start (this process is usually preceded – and possibly also speeded up – by the fact that such dying specimens are usually totally covered by the climbing wild cucumber *Echinocystis lobata*). With some time, the entire population collapses, and the habitat having been dominated for long by false indigo gradually changes into a gallery forest (a similar succession process was reported, although with the details of the process not specified, from the Po River Lowland, Italy).

Consumers and pathogens

All parts of the false indigo contain an agent with repelling and highly toxic effect on insects, its principal component being amorphigenin (8'-hidroxirotenon), a compound belonging to the rotenoid group. Consequently, the false indigo is consumed by only a few, more or less specialized insects. In America there are 10 moths (*Agonopterix dimorphella*, *A. argillacea*, *Automeris io liliith*, *Catocala amestris*, *C. consors*, *Dasylophia anguina*, *Epargyreus clarus*, *Achalarus lycidas*, *Zerene caesonia*, *Walshia amorphella* – some of them being gall-formers), and three weevils (*Acanthoscelides pallidipennis*, *A. submuticus*, *A. floridae*) known to feed on false indigo. Among these, only the beetle *Acanthos-*

celides pallidipennis has established in Europe and Hungary (its first occurrence data is from 1972), and there are also two scale insect species (*Eulecanium corni*, *Neopulvinaria imeretina*) that have been observed on false indigo.

The only consumer insect species recorded in Hungary is the weevil *Acanthoscelides pallidipennis* which is now present in the entire country, and can be observed in great amounts on false indigo populations. As a seed-predator, this beetle attacks the fruits both when still developing and when already dry and fallen. Its adult specimens feed on pollen. In its native land, it can cause quite high damage in fruit production (30-90%), but in Hungary this rate usually remains much lower, i.e. normally less than 40% (these rates do not include damage that is caused to seeds already fallen from the plants). This beetle does not seem to have a significant parasite in Hungary. Its effect in restricting the invasive process of the false indigo is not known, but is most likely to be insignificant.

For grazing livestock, however, the false indigo is not toxic. Its leaves and stems are readily eaten, and it can be grazed by cattle, sheep and goats. Some studies have reported that after initially accepting it as a feed, goats later tended to refuse it. Game animals prefer rather not to feed on it.

In Hungary, patchy leaf necrosis caused by fungal pathogens is observed on false indigo, whereas in America mildew and rust are mentioned, without any specific pathogen being specified. Viral or mycoplasmal diseases may also occur such as wood cancer or blastomania.

Mutualism, symbiosis

In Hungary false indigo is pollinated mainly by bees (*Apis mellifera*), and also by its seed predator *Acanthoscelides pallidipennis*. Like most legume plants, false indigo, too, lives in symbiosis with nitrogen-fixing bacteria: *Mesorhizobium amorphae* WANG et al. was described from its root nodules in China. We have found no data on mycorrhizal associations.

ECONOMIC IMPORTANCE

Benefits

Because of its strong root system, false indigo is used effectively for bounding sand, against erosion, and for stabilizing steep embankments. Partly due to its high oil content, it provides good burning wood, therefore it is planted in places with limited natural wood resources as energy forests (e.g. in some parts of China at present time, and earlier in Hungary as well). It is also used in the recultivation of abandoned open-cast mines. By means of its nitrogen-fixing capacity, it somewhat improves the quality of very bad soils. It is planted as a windbreak, too, but due to its loose branch system, it is less suitable for such purpose. It can be used for bedding, as green manure or in compost. Its nutritive value is good, caused by its outstandingly high protein content. Experiments have been performed in the dry upland parts of Greece, for its summer utilization as a feed for livestock, and the results were promising. Along the Körös Rivers and along the Upper-Tisza in Hungary, its stems serve as raw material for hurdle-weaving and wreath-making. In Italy, it was used for wickerwork and producing wine-baskets. For barbecuing bacon, its stems can be used as grill sticks. Its smashed seeds can serve as a spice, and in China the oil pressed from them are utilised for glycerol production. In small amounts, the plant contains indigo pigment, therefore it was used for producing blue stain, but this turned out to be uneconomic. Several of its compounds are being tested in experiments, for possible utilization in medicine. It is also planted as an ornament. In Hungary, it is popular because of its good mellific characteristics, but the price of pure false indigo honey remains below that of locust-tree honey.

For its insecticide characteristics, false indigo is used in China for biological control against the agricultural and silvicultural pest beetle *Trematodes grandis*: if planted around nurseries and tree plantations, false indigo attracts the larvae of this beetle which are then killed by its toxic agents.

Damages

False indigo can seriously inhibit the process of forest renewal activities. Where it is present in masses, it overgrows young trees by its fast initial growth, and can be controlled only with high-cost solutions. It

causes serious problems in the renewal of floodplain forests, too. In forestry, today false indigo is almost clearly perceived as a weed species. Its rampant stands establishing on flood-protection dyke systems weaken the consistence of embankments, and the access routes along the rivers are also made impassable for machines. It accelerates the process of blocking canals and channels.

Judging its attributes altogether, there are no such characteristics that could economically justify its presence in Hungary. In practically all of the fields of its utilization, it can be replaced by native or harmless non-native species.

NATURE CONSERVATION SIGNIFICANCE

The most significant transforming effect of the expansion of false indigo is on natural treeless or shrubby vegetation in floodplains. By means of its fruits spread by the water during floods, it invades such habitats. If left growing up on hayfields and pastures, it can become monodominant unless treated, especially if the resistance capacity of these grasslands has been previously weakened by the lack of management (most typically), by mismanagement (e.g. overgrazing), or by prolonged floods. Under the dense, impenetrable thicket formed by false indigo growing to several meters high, the species of grassland associations are either incapable of surviving, or only very few of them survive. The habitat becomes unsuitable for the original nesting bird species (e.g. corncrake) as well as for birds of prey hunting in such open areas. The fauna of homogenous false indigo stands is very poor, anyway. Such a thicket is almost impassable for larger mammals (roe deer and red deer). These closed, monodominant false indigo stands in floodplains represent a succession "sink", a certain type of "green desert".

The fast-growing false indigo slowly replaces natural species in moist shrubby associations along grasslands, streams, canals, marshes, forests, and in marsh-type willow bushes too.

In floodplain forests, especially in the higher, poplar zone of softwood gallery forests, it expands to the detriment of natural shrub layer and renewing forest, although here its shading and other negative effects on natural vegetation are weaker than that of box elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*). It forms lower coverage in hardwood galleries and in the lower, willow zone of softwood gallery forests. It causes the greatest problems after large expanses of such forests are clear-cut: if no provisions are made, it will spread very rapidly, and monodominant stands will be established. The renewal of forests in such stands becomes impossible for extended periods of time.

If managed improperly, other natural habitats outside floodplains, including not too extreme open or just partially closed habitats, are also expected to be slowly invaded by false indigo, to the cost of natural species. It generally impedes natural recovery processes in all secondary or damaged habitats.

In near-natural habitats it damages the landscape aesthetically too, thus visitor zones can lose their functions. Study trails in open areas are often grown over by false indigo, making them impassable for visitors.

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BLACK LOCUST

(*Robinia pseudoacacia* L.)

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TAXONOMY

The currently accepted scientific name of the black locust is *Robinia pseudoacacia* L. Synonymous names are not used, deformed and invalid name is the *Robinia pseudacacia* L. Additional common names: Locust, False acacia.

The *Robinia* genus belonging to the Fabaceae family includes about 20 deciduous species which live in warm and periodically dry areas of North America and Mexico. Beside *Robinia pseudoacacia*, only the *R. luxurians* (DIECK) SCHNEID. and the *R. viscosa* VENT. are tree-sized but these not grow higher than 12 meters. The other *Robinia* species are shrubs with height from 20 centimeters to 4 meters. Only the *R. pseudoacacia* has white flowers and bare legumes all the other *Robinia* species has pink or purplish-red flowers, and the surface of the fruit is hairy, glandulous hairy or setaceous hairy.

The clammy locust (*Robinia viscosa* VENT.) has glandulous hairs, sticky shoots and fruits, pink flowers, thick and out sticking inflorescence is frequently planted in Hungary. The shrub sized bristly locust (*Robinia hispida* L.) with setaceous hairs and fruits, dark pink or purplish-red flowers is more rarely cultivated. The pink flowered locust (*Robinia ×ambigua* POIR.) which is bred as hybrid of the *R. pseudoacacia* and *R. viscosa* also has sticky shoots, light pink flowers with obvious yellow spot on the banner. The Hungarian nurseries sell the 'Decaisneana' breed which is abounding in flowers and has great nectar production.

The black locust has large area with diverse climatic conditions and its natural variation is less known. In its dispersion area three growth types are distinguishable: 1. Pinnata-type – with lengthy stem which can be seen in the foliage; 2. Palmata-type – the stem hardly recognizable in the foliage; 3. Spreading-type – almost not develop stem and low growth. From the viewpoint of forestry the most considerable is the “shipmast locust” (*R. p.* cv. *Rectissima*, syn.: *R. p.* var. *rectissima*) which belongs to the first type and has obviously straight stem that seems through the foliage, the branches are slender and standing in acute angle, rarely develop seeds therefore propagated with root cuttings. In Hungary 9 selected silvicultural breed are sold.

The majority of the horticultural varieties (breeds) were produced in Europe, mostly in France in the first part of the 20th century. The following are the most frequent:

cv. *Inermis* – the shoots are thornless

cv. *Microphylla* – small and narrow leaves

cv. *Pyramidalis* (pyramid locust) – the shoots are almost thornless, the shoots short and erecting, the crown is columnar

cv. *Semperflorens* – strong growth, two flowering periods in an each vegetation period

cv. *Tortuosa* (contored locust) – the branches are multiple curved, the shoots are spirated and the leaves are mostly hanging

- cv. *Umbraculifera* (globe locust) – slow growing, spherical crown, thornless shoots and smaller leaves than the base species and the plant is grafted onto a tree with higher stem
- cv. *Unifolia* – the shoots are thornless, the leaves are formed by only one, maybe 15 cm long leaflet and below that some small deformed leaflets can be seen.

MORPHOLOGY

In forest stands at good spots it can grow up to 30-35 m high. If standing free, the stem is dusky and in older age generally ribbed, strong branches start in low level, the canopy has irregular or domed shape. If standing closed, the stem is lengthy and columnar, only in the upper part splits into branches, clears up well, the shape of the crown is reversed cone. The stem is usually arched or tortuous, prone to furcate. In juvenility the bark is smooth with obvious suberous lenticels, and early forms netted crackling cortical bark. The older trees have very thick, grey-brown bark which is yellowish-brown in the cracks. The surface bark of the roots fibrillarly parted. The rootage is deep penetrating, later forms richly branching side roots. On loose soils the side roots run below the surface and are rope-like. On dry soils the lateral side roots outrange well the projection of the crown but on well watered soils the majority of the strong side roots usually do not outreach this. The rootage of the black locust can not penetrate the layers of compact soils and in cases like that the roots continue to grow horizontally and the root system will be layered.

The furcation system is sympodial, the shoots are pre- and neoformed. The twigs are reddish-brown, growing zigzaggy, at the apex corrugated with numerous suberous lenticels and beside the cicatrice on both side is a flattened, prickly stipular thorn. On the older individuals the stipular thorns are smaller or can be missing. The 3-4 standing buds are small, rusty hairy and protected by the light colored, suberous triangular cicatrice with a little knob at the centre. The true terminal bud is missing. The shoots at the end are more or less striated, zigzaggy, light green when young, bare or finely hairy. The leaves are odd-pinnate, 10-35 cm long and constituted by 9-19 opposite standing leaflets. The leaflets are elliptic, 2,5-4,5 cm long and 1-2,5 cm wide, at the base rounded or wide cuneate, the margin entire, the tip is rounded or slightly retused with a small arista. The leaf blade is thin, on the upper side light green or grey-green, on the under side bluish-green, the petiole is short, a bit swelling, the fibrous stipulae fall early. The midvein is striated and at the base abruptly widening, at the beginning finely hairy and covers the developing buds. The canopy of the black locust is loose; the leaflets can change their position on the petiole depending on the light circumstances. When the radiation is strong the leaflets stand more or less upright, when average horizontally and when the radiation is low the leaflets hang. This turgor movement shows decreasing tendency with the aging of the tree.

The perfect, proterandric, papilionaceous flowers have fine scent, opens in leaf axillary raceme, which are 10-20 cm long with 10-25 flowers. The inflorescences standing upright at the beginning, later hang and meanwhile the peduncle of the flower turn by 180 degrees and therefore the position of the flowers does not change. The peduncle is 8-10 mm long, the sepals are bell-shaped, reddish, with five teeth among them the two central almost coalescing. The petals are white, the banner is rounded, at the point retused, the margin often turn back, the throat is citrine, the wings have the same length as the banner and the keel is blunt. The stamens are diadelphian, 9 stamens are coalescing a tube and one is standing alone. The elongated, superior ovary has incurved and densely hairy style, the stigma is rounded, with rough surface, next below the stigma is a rim of hairs which deters the autogamy. The legumes hang in racemes, are dehiscent, straight, flat, at the abdominal joint a bit acuminate, 6-11 cm long and 1-2 cm wide, pergameneous and hold 4-8 seeds. The seeds are 3-5 mm long, kidney-shaped, appressed from the sides, blackish-brown colored, often variegated with very hard episperm, smooth and shiny surfaced.

The seedling has two comparatively large, fleshy, 2-2.5 cm long, reversed egg-shaped, at the base asymmetric, short petiolated cotyledons which central vein ending much before the point and the other veins are not visible. The first foliage leaf is not compound, rounded with long petiole. The following temporary leaf is trifoliate and the terminal leaflet is rounded and much larger than the two side-leaflets. The further leaves are typical locust leaves.

ORIGIN, DISTRIBUTION

The black locust is native in the inner part of Eastern North America. The area is crumbled into more patches. The largest is the central area in the Appalachian Mountains where the species finds its optimum between 150 and 1500 meters above sea level and common in the species rich forests. It is absent in the typical chestnut forests at the Southern end of the Appalachian Mountains. The Eastern part of the area extends from Central Pennsylvania and South Ohio to North-East Alabama and North Georgia. To West and South from here it can be found at smaller and isolated spots. The Western part of the distribution area lies between the Northern 32-37 degrees of latitude and the Western 90-95 degrees of longitude. Its centre is in South Missouri, the Ozark Upland, North-West Arkansas and East Oklahoma. Smaller distribution areas are in South Indiana, Illinois, Kentucky and Alabama.

In the present days the black locust is the second most frequently cultivated broad leaved tree species. Jean Robin, the royal gardener of Louis XIII brought it in 1601 from Virginia to France where it is attracted great attention for a long time. As ornamental and vista tree it became successful and around 1700 it was common in Germany. Nowadays the overall estimated area of the black locust plantations is 3.25 million hectares. The black locust is planted to avoid erosion in the steep slopes and chasmy hillsides in South-East Europe and Asia at many locations. The naturalization was unsuccessful on New Zealand. In Australia it was inhibited to plant because of poisonous effect for humans and cattles.

It was imported to Hungary between 1710 and 1720 and planted in the beginning as ornamental tree in parks and vista tree along roads. For afforestation it was used firstly in 1750 close to Komárom around the Fortification of Komárom-Herkály on 290 hectares. Because it proved successful the interest increased and it was started to plant on the most different soils like alkali soils, blowing sand. The first shelter tree belt was planted near to Pusztavacs in 56 km length. Between 1830 and 1848 on the treasury lands of Mezőhegyes black locust was planted on 750 hectares. In 1863 for binding blowing sand and afforestation in the countryside of Ásotthalom additional 2520 ha locust stand were planted. The time of bulk plantations in Hungary happened between 1865 and 1895. The afforestation law for the plains in 1923 proposed 110 000 hectares of forest plantation in the next 15 years on areas unsuitable for agriculture. Actually the plantations were realized on 52 000 hectares and 37 900 of this was black locust plantation. In the national afforesting programme started after the 2nd World War the black locus became one of the leading species.

Nowadays the black locust is planted about on the third of overall area of forests and forestry plantations. In 2003 the 22.1% of the all forested areas was black locust forests.

LIFE CYCLE

The black locust is a long living tree species, some representatives can live 200-250 years¹, and the stem diameter of the old plants can be 1 meter. The germination optimum under natural circumstances concluded from the optimal sowing time, i.e. the end of April. The synchronism of sowing and gemmation obviously not accidental and it is in conjunction with the soil temperature, but the scarified seed with the 7-10 days long germination can avoid the frosts in May belike.

Despite of that fact the collected seeds directly from the tree or the soil after scarification have germination potential above 90% under natural conditions only small fraction the fallen seeds germinate annually because of the hard episperm what is characteristic among the Fabaceae species. The hard episperm and the long period before the germination obviously is part of the survival strategy of the species but the hardness of the episperm is largely affected by the conditions. Under drier conditions it will be harder; if the habitat is moister the episperm is softer. The cold and the high level of humidity

¹ The tree known as the oldest individual in Europe lives in Paris and its the 350th birthday was celebrated at the beginning of the 1980's. The tree allegedly was transplanted by Vespasien, son of the royal gardener Jean Robin after the father's death from his garden into the Royal Medicinal Plant Garden (Jardin Royal des Plantes Medicinales) in 1635. The tree was over 100 when Linnae have seen the beautiful specimen of the species named after Robin when he visited the de Jussieu brothers in 1738. The existence of the tree not but the age and the legend dramatized by the French with the name of Linnae can be query on the base of some contemporary literary source and logical reasoning.

together can shorten the dormancy of the seeds what is acknowledged with freezing experiments in relation to the black locust. The natural germination is possibly helped by the low temperature and snow cover for example. The thinning, cracking or damage of the perisperm can be affected by many other abiotic or biotic factors for example the acidic or alkaline medium, the thermal fluctuation, treading, etc. The natural germination in black locust stands is noted by the silvicultural literature many times but also noted the seedlings die in a year generally. The death of the seedlings originate is possibly due to root concurrence and lack of the light, although the 1-2 year-old locust seedling has lower demand for light than generally thought. In the breeding of younglings the species is prone to the weed concurrence what is very important information from the viewpoint of natural renewal too. Naturally the behavior in stands does not preclude that the seedling can grow up at opened habitats.

The seedlings can hit 1 meter in height in the first year. The growth in height culminates in 2 meters per year in the 2nd-5th years and growth in thickness culminates in 7-10 mm per year in the 8th-10th years. The height growth is very dynamic until the 20th year, between the 20th-30th years it definitely decreases and above 35 year it is not considerable. The growth in thickness is most intensive in the first ten years, after that gradually decrease, the width of the age-rings fall to 1-1.5 mm but it can thicken even at 50 year-old age. The growth characteristics of the offsets do not differ considerably from the seedlings. The full-grown trees can be 13-35 meters high with 30-100 cm stem diameter. The growth of course depends largely on genetic potential and the environmental conditions. The young black locust tree often brings flowers in the fifth year and from the sixth year open lot of flowers. In forest stands the seed production begins between 10-15 year-old age. Under disadvantageous conditions – as it is usual among plants – the seed production begins earlier and more seeds are produced.

The earliest notes about the phenology of the black locust originates from the middle of the 19th century and a 81 years long data series are available from between 1850 and 1930 from the overall area of the Carpathian Basin. These data were completed by the observations carried out by the Silvicultural Research Institute between 1937-43 and 1955-61 which covered more phenophases than earlier observations and concern to the all area of Hungary.² Both of the data show that the opening of the buds happen between end of March and middle of May, the mean is 22nd of April. For the development of the foliage 1-1.5 month needed which take until the beginning of May and beginning of June, meanly 23rd of May, when the flowering starts. The average duration of the flowering is 18 days.³ The black locust is an entomogamous species. Superb melliferous plant, therefore beside the natural represents of the Hungarian insect fauna, the activity of the beekeepers ensure large numbers of bees and this obviously increase the possibility of the fertilization and amount of seeds. In Hungary the flower racemes firstly open at the Southern part of the land than the flowering goes in North-Westward and elevating with the level above the sea and in 10-30 days all of the Hungarian black locust forests shoot flowers except of the highest mountainous areas. Albeit the seed-crop is determined mainly by the first flowering, it worth mention the locust often has second flowering in September and some trees flowers in other periods of the vegetation period. The coloring of the foliage begins at 24th of September as mean, the yellowing of the leaves in summer connected to the droughty weather and the lack of water. The defoliation begins in October on the mountainous areas and ends at the beginning of November but often happens that because of the early frosts the natural physiological processes stick, therefore the leaves freeze and stay on the tree. The mean time of the ripening of the seed and fruit is at 17th of October; the seeds collected at this time show hard endosperm in 93.5%. In the matter of falling of fruits and seeds the publications show some differences. In the different notes it begins at the end of November and hold through the winter until February and March or from the next spring to the next autumn, by other authors the fruits stay on the trees in the winter and the legumes open up in the spring (it is approved by other authors too) and the falling of the seeds continues through the summer. The differences between the observations can be referable partly to genetic differences and mostly to the

2 The end-values of the phenophasal times generally noted at the South End and Hungarian Great Plain or at the Uplands respectively in the mountainous areas.

3 It is contradicted in a measure the flowering time endure 8-15 days that is published in some literature. The difference originates probably it is not consider the opening of the flowers but the beginning of nectar production as the beginning of flowering. The fact is that the bees also start to visit the flowers in the second week of the flowering because of this.

different environmental conditions, in many cases especially to the very characteristic aberrations of the different years. The authors observations show that it is not rare phenomenon at the time of the fruit ripening most of the fruits from the previous year are still on the tree. From the viewpoint of the spreading, it is important that the opening of the legumes only in an insignificant part mean the outfall of the seeds, the legumes fall from the tree together with the seeds, but there are contradictory observations also which show that half of the seeds fall freely and only the rest together with the legumes.

As the summing of the three most important phenophases we can say that the opening of the buds happens in the second half of April, the flowering between middle of May and middle of June (second flowering in September) and the defoliation happens in October.

From the viewpoint of phenological knowledge beyond the written above very advantageous the work of some researchers determined thermal values for the phenophases and examined the amount of days which befit some thermal criterions. Because of the more simple use in this work only the latter is discussed in details. By this the opening of the buds come after 20-25 days with daily average temperature higher than 3 °C and the highest temperature at least 10 °C. Until the beginning of the flowering, 28-33 days with higher minimum temperature than 4 °C degrees are needed. The calculated data show that from the bud-opening to the defoliation the black locust need 177 days which means the vegetation period is 5,5-6,5 months long what is accordant to the 180 days experienced at its native distribution.

The fruits and seeds of the black locust spread with anemo- and endozoochory. The spreading with the winds naturally does not exceed few hundred meters. Along the ways (highways and railways), where the black locust is common, the wind caused by high-speed vehicles possibly increase the efficiency of spreading.

The seed production was examined with collecting from fallen trees and by the examination of top soils in locust forests. The data earned about the soil seed bank can give important information about the survival strategy of the plant what is especially important from the viewpoint of invasiveness. The black locust yields in average 0.28 kg seed/year/individual in closed stand. According to the average 18.5 g weight of thousand seeds it means 15 000 pieces of seeds every year! (Counted with eight seeds in every legumes on a tree can hang about two thousand fruits.) Data concerning this fact were not published, but on the base of the behavior in forestry it is likely the examined trees were not older than 40 years. This all mean that the trees of margins, smaller groups or free standing and older trees can produce much more seeds! Some examinations show that – in a good year – after the clear cutting⁴ of one hectare locust forest averagely 200 kg seeds can be collected but the experimental data say only 125 kg/ha in average. On the base of the calculation above, it means about 7 million seeds/ha per year. According to some investigations, close relation of the seed-crop with the seed or offspring origin of the black locust stands not provable.

The useable seed crop collected from the topsoil in a 25-30 year-old black locust stand is about 770 kg/ha, in a 30 year-old stand 35 seeds can be found averagely on 10 by 10 cm. The seed-crop grows exponentially with the age of the stand (!) and the seed stock of the soil in a 50 year-old black locust stand can be 2200 kg which means 1 billion (!) seed/ha. Because under conditions of the widely used technology the collected seed have 92-96% germination ratio and the correlation of the seed-crop with the age of the stand was established on the base of samples of seed stock of the soil, it can be considered as proved the seed of the black locust keep its vitality in the soil for decades. The investigation of a 50 year-old stand showed that the increasing of the viable seeds is unbroken, so with the deduction of the time of the first yield it is sure the duration of the life of soil seed bank is longer than 44 years.

The result derived from indirect proof is strengthened by the abundant germination of black locust in a Scotch pine forest planted after the clear-felling of black locust when it was burned in its 17 year old. On other site after the felling of the 30 year-old pine plantation at the spots where the twigs were burnt many black locust seedlings grew. Beyond the ascertainments above it is likely in the soil of the offspring originated stands the seeds of the earlier stands also presenting because in some 20 year-old stands can count seed amount of 50 year-old forests. From the viewpoint of nature conservation the mast-like black locust forests have much less seed.

4 It happens at 25-35 – on better habitats at 40 – year-old age.

The seed production increase from the margins toward the centre of the stands, the border effect is perceivable to 8-10 meters from the outline of the stand. The vistas and smaller groups of trees show phenomenon like it is seen at the margins of stands. Maybe the plants living here flowers and fruits more abundantly but the seed mass is smaller which can have more reasons. It is sure the wind has considerable role as it blows the falling legumes away, but the much stronger activity of the animals compared to the inner parts of larger stands (birds, rodents, etc.) also can have effects on the seed stock with deporting, destructing and because of the damaging of the epispERM in germinating, additionally at the margins the danger of frost is also increased.⁵

About the drift and layering of the seeds in the soil it is ascertainable the seeds are in the largest number in the soil layer between 1.5-3 cm which is the decomposing humus themselves, the frequency here is about 30%, but almost the third of the all seed bank can be found below 4-5 cm depth. By other sectioning the half of the seeds are in the upper 3 cm deep layer of litter and humus, between 3 and 6 cm 35-36% and between 6 and 12 cm additional 13-14%. The vertical drift of the seeds can show differences between habitats but it is not depending on the soil structure as expectable (the differences among sand, loam and clay soils is in 5%) but on the temperature and humidity of the habitats. The primary reason of this is the composition of the soil-microfauna for what the more moist soil is more favorable and from this viewpoint the earthworms have very significant role. The more worm-hole and the more intense mixing of the soil increase the drift of the seeds and at the habitats of this type the seeds get deeper layers easier. Naturally the biotic effects on the seed drifting are completed with abiotic ones like the cracks of the soil, rain-wash, etc. These circumstances together can not change that fact in the upper 20 cm of the soil the seed-amount can treat as a constant value (deeper than this the seeds of the black locust can get exceptionally, for example through deeper cracks) and differences can only detect in this layers. At dry habitats in the up most 6 centimeters of soil, that is the humic layer can be found the 90% of the seeds but at humid habitats only the 60% accumulate here.

The hard epispERM helps the accumulation of the seeds as well as its small size, rounded kidney-shape and smooth surface what makes the slipping in the holes of the soil easier. By some opinions into this depth only along more years can descend the seeds. Storage the soil ensure more balanced humidity conditions that is inhibit the drying out and decrease the fluctuations of the temperature. Beside these the amount of oxygen is low, the CO₂ is high, the light lacks and possible bactericide and fungicide effects work. The sum of these effects is very advantageous for the surviving of the seeds. The 22 g/1000 seeds weight of seeds originating from the soil is higher by 3-4 grams than the seeds collected from trees and this denotes the larger seeds live longer. According to the classification of seed bank type systems the black locust has long-term persistent seed bank type. The classification is accordant with the establishment which says about the initiative species of the succession are members of the seeds bank for long times and it supports also the pioneer behavior of the black locust what is characteristic in the original distributional area too.

The black locust brings offshoot well from stem and root too. In its native range at high altitudes above sea level the primer propagation form is the bringing root suckers. The damage of the above-ground part or expanded damage of the roots generate bringing numerous root suckers which grow from the sleeping buds of the horizontal, rope-like roots near to the soil surface or the additional buds starting from thin and young roots. The rope-like roots can expand over 20 meters. The root suckers grow more intense than the stump sprouts. The stump sprouts and the root suckers of the thick roots grow very fast in the first years because they use widespread root system. The root suckers starting from thin roots only in the first one year can grow really fast then the growth decrease for a period until the development of the own root system. The plant regenerate well at individual level by its root suckers and stump sprouts and on the base of number of root suckers and its distances from the parent tree can say propagate well in vegetative way. The inclination to form polycormon strengthens the role in the early stadium of the succession. About the growth and development of root suckers and stump sprouts we have information from the 50's of the 20th century from offshoot renewal experiments. The experiments

⁵ The richer herb layer also play a role because the sampling is more difficult and therefore the efficiency of the discovery is worse and the possibility of the fault is larger.

covering the Transdanubia and the Hungarian Great Plain investigated the renewal of the black locust what was ensured with offshooting the thick and thin roots with root suckers, stump sprouts and completing the offshooting with youngling plantations. The size and number of the occurring offshoots was associated with the quality of the habitat. At the good black locust habitats generally the root suckers of the thin than the thick roots developed most intensely, it was followed by the planted youngling and after that the stump sprouts. In the third year of the experiment by the viewpoint of flowering intensity the stump sprouts were followed by the root suckers and the less flowering were the planted younglings. At the experimental plot near Balástya the offshoot numbers which exceed the 1.3 m was between 14150 and 19450 per hectare. The most outstanding offshoot was 4.4 m high at the end of the first year and 1.8 centimeter thick and at the place of some felled trees raised as many as 70 offshoots. The above shown data illustrate well the dynamism of spreading with offshoots of the black locust.

HABITAT PREFERENCE

As it is shown by the growth of the black locust in the native distribution area and the European, Asian and East Asian synanthrop areas the species is not adherent to narrow, strongly limited climatic conditions. Compared to Hungary the natural distribution area of the black locust lies more to the south with 5-10 degrees of latitude where the species adapted to a relatively moist climate with hot summer and mild winter. The early and late frosts partly limit the distribution on the south. Where at the end of April and beginning of May the frost may occur the black locust is presenting but where the frosts in mid-May a common phenomenon the plant is lacking. The early frosts have not so big consequences the black locust endure the frosts in the end of September and beginning of October but the earlier not. In Hungary the precipitation is less, the mean annual temperature is similar to the American chiefly at the Great Plain. In the original distribution range the temperature is about the same as at the northernmost areas of the black locust in its native range. In Hungary the northern limit of the species coincide with the zone of freezing days continuing to 25-30th of April because the later frosts induce the death of the leaves.

The black locust is very demanding to the air of the soil and can not bear the too high soil moisture. At areas flooded or with ground-water near the surface can not live. Above the up most level of the optimal ground-water needed 100-120 cm soil. If the soil is compacted and the water not drained therefore the water can accumulating on the surface the conditions not favorable and if the water is stagnating the black locust can not survive. The moving water on the surface and chiefly the well oxygenated trickling water of slopes do not create airless conditions and this is good for the black locust. The stagnating water of pseudogley soils also unfavorable for the species. With annual 600-700 mm precipitation the soil hold enough moisture for the black locust, at drier habitats the species absorbs the needed water partly by her roots from the ground-water.

The intake of nutrients compared to the beech, pedunculate oak, sessile oak, red oak and Turkey oak is the lowest. The black locust need for nutrients is low and it has the largest demands at the beginning of the vegetation period. The black locust gives relatively small amounts of organic matters to the soil and therefore not serve good base to the forming of humus. The annually falling foliage and other organic matters are not decomposed in one year. An experiment of the leaf-litter near Gödöllő showed that in a black locust forest presents 8 tons per hectare of air-dry organic matter at the time of defoliation in the autumn. Only a part of this is leaf-litter the most of the mass is built up by fallen wigs, petioles and died herbs. Compared to other species the only one leaf-litter with higher nitrogen content is that of the alder and the black locust shows more than two times higher value than the oaks. The phosphorus content is low, generally half of the other broad-leaved species and sometimes only fifth of that can be found in the litter of black locust.

The black locust demands much of light but at the first 6-8 years can bear some shade. In strong radiation of the sun it close together the leaflets and with the loose canopy can let many light go through. It does not bear the shade and the shaded trees die relatively fast.

In the case of the black locust the limiting factor are the water supply and the soil airiness meanwhile the soil nutrient content plays secondary role.

BIOTIC INTERACTIONS

The nitrification effect of the black locust causes serious problems. Nitrification is owing to the activity of nitrogen fixating bacteria like the *Rhizobium leguminosarum*, *R. tropici*, *R. meliloti*, *R. trifolii*, *R. japonicum*, *Mesorhizobium amorphae*, *M. loti*, *M. huakuii*. The bacteria „infect” the black locust already in the seedling stadium and encourage forming root nodules in which the fixating of the nitrogen happens. The root nodules grows to 1 mm in two month and the diameter of the older, partly over-wintering root nodules may be more than 10 mm. The nitrogen fixation is generally the most intense in the upper 15 cm of the soil and the number of root nodules decrease continuously with depth. The beneficiating of the nitrogen below 3-4 year-old black locust stands can achieve 100-300 kg/hectare but by other authors only 30 kg. The soil enrichment leads to the establishment of characteristic nitrofreqvent vegetation.

The forest stands of the black locust are mostly unmixed, from the tree and shrub species the common hackberry (*Celtis occidentalis*), black cherry (*Padus serotina*), common hoptree (*Ptelea trifoliata*) and the native common elder (*Sambucus nigra*) is capable to live in these forests. Into the plantations made on very dry habitats the common xerofrequent shrubs also can penetrate like the common juniper (*Juniperus communis*), hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), and dog rose (*Rosa canina*). In the semi-moist, repeatedly renewed from offshoot stands in the shrub layer the common elder (*Sambucus nigra*) can propagate well. The herb layer is poor in species and very characteristic. Because of the nitrogen fixating bacteria living on the roots, the loose canopy and the easily decomposing leaf litter the nitrogen level of the soil is considerable what is clearly indicated by the large proportion of nitrofreqvent plants.

The species growing in large abundance in the early spring aspect are the greater celandine (*Chelidonium majus*), common chickweed (*Stellaria media*), red dead nettle (*Lamium purpureum*), Robert geranium (*Geranium robertianum*), stickywilly (*Galium aparine*), chervil (*Anthriscus cerefolium ssp. trichosperma*), ivy leaf speedwell (*Veronica hederifolia*). In this aspect – also thanks to the high nitrogen content of the soil – some bulbous species also occurring like the lesser celandine (*Ficaria verna*), sand leek (*Allium scorodoprasum*), meadow gagea (*Gagea pratensis*), tassel grape hyacinth (*Muscari comosum*), green Star of Bethlehem (*Ornithogalum boucheanum*). At the drier habitats the grass species are dominant with representatives like the poverty brome (*Bromus sterilis*), chee reedgrass (*Calamagrostis epigeios*), and narrow-leaf meadow grass (*Poa angustifolia*). At moist and semi-moist plots in the spring and summer aspect thanks to the good nutrient and water supply the tall herb species propagate well and some liana also occur. The first group is represented by the giant goldenrod (*Solidago gigantea*), annual fleabane (*Stenactis annua*), stinging nettle (*Urtica dioica*), common motherwort (*Leonurus cardiaca*), common milkweed (*Asclepias syriaca*), hemp (*Cannabis sativa*), black horehound (*Ballota nigra*), garlic mustard (*Alliaria petiolata*), hempnettles (*Galeopsis* spp.), and the latter by the hop (*Humulus lupulus*) and the black bindweed (*Fallopia convolvulus*). The stands planted on very dry habitats miss the above listed, mostly nitrophilous and disturbance tolerant species but the plants of the dry grasslands propagate well.

With the comparison of the herb layers in Hungarian and Italian black locust forests it seems on the base of the analysis of the binary data the stands form groups of different locations. The analysis of the cover data show the high degree of similarity between the stand at the Small Plain and the Nyírség in Hungary but the stands of the Danube-Tisza Interfluve have high variability, and in contrast to the expectations the Italian data was not differentiated sharply from the Hungarian ones.

Black locust has known allelopathic effect; the metabolites of the plant (fenoloids and derivatives of amino-acids) inhibit the growth and development of other plants. The birch trees living in black locust stands bring smaller leaves, the shoot-ends start to dry then the trees die. Similar but less obvious phenomenon is observed on beech trees also. In Russia is observed the black locust delay the growth of the elm species and the agents washing out from the roots of the black locust decrease the photosynthesis of the pedunculate oak.

Hungarian researchers demonstrated the inhibitory effect of the black locust root extract in the germination of the leek (*Allium porrum*), the capsicum (*Capsicum annuum*) and the papaver (*Papaver somniferum*). The water extract of the living black locust roots inhibit the mycelium growth of the annosum root disease (*Heterobasidion annosum*).

For long time after the naturalization of the black locust in Europe it had no significant consumers or pathogens and the presenting food source was firstly discovered by the polyphagous arthropods.

As seedling the black locust occasionally dies because of infection of fungi (*Phytophthora* spp.) but the occurrence of this type of infection is dispersed. The chafer-grubs, mostly of the common and forest cockchafer (*Melolontha vulgaris* and *M. hippocastani*) and at sandy habitats the grub of the June beetle (*Polyphylla fullo*) impair the roots of the younglings and young trees. After the chewing the roots regenerate well but the younger trees react more sensitively to the lost of roots and therefore the grubs can result great damages. Less frequently than the chafer-bugs, the grubs of the click beetles (Elateridae), and sometimes the snout beetle (*Otiorynchus ligustici*) harm the roots. Among the putrefactive polypori of the stem and root of the black locust most frequents are the ash tinder (*Perenniporia cytisina*), the robustus conk (*Phellinus robustus*) and the chicken of the woods (*Laetiporus sulphureus*). The ash tinder occurs primarily in offshoot originated, old or overgrown black locust stand and the sporophore can be found often below the leaf-litter at the base of the stem or at the head of the rootage. It infects usually at the hurts of the roots and the white putrefaction can go up to 2-2.5 meters in the stem. The robustus conk also bring white putrefaction of the roots, usually penetrate at the knags and in forest stands occur dispersedly but in vistas of streets it can be much more frequent. The polyphagous chicken of the woods penetrate through the hurts of the root-head and the stem and bring the red putrefaction of the stem – this impairment is occasional. Over the above mentioned species on the older black locust trees the wound parasitic artist' conk (*Ganoderma applanatum*), and sometimes the big smoky bracket (*Gloeoporus adustus*) and the tufted bracket (*Phellinus torulosus*) can occur. Some insects harm the stem of young trees like the red-backed ground beetle (*Dolichus halensis*) which chew the stem and causing yellowing, drying and falling of the younglings or the hempseed beetle (*Peritelus familiaris*) which eat the buds, young leaves and shoots therefore delay the frondescence or because of the drying of the leading shoot the younglings retrograde. On the trunk of the older trees rarely impair insects but these are mostly polyphagous species like the walnut longhorn beetle (*Aegosoma scabricorne*), the ash bark beetle (*Leperisinus fraxini*) or the goat moth (*Cossus cossus*). The mammals – primarily on the long and cold winters– harm the buds of the black locust and chew the bark. Among the mice and voles (Muridae) principally the Orkney vole (*Microtus arvalis*), bank vole (*Evotomys glareolus*), wood mouse and striped field mouse (*Apodemus sylvaticus*, *A. agrarius*) and the water vole (*Arvicola terrestris*) can cause hurt. The hare (*Lepus europeus*) and the European rabbit (*Oryctolagus cuniculus*) chew and clear the bark mostly in the young stands. In the next stage of the stand the large deer stocks can make heavy harms with the bark clearing. On the branches and on the bark the primitive fungi can settle and infect. The *Diaporthe oncostoma* causes the death of the bark and cancerous phenomenon, the pycnidiums can occur especially on the younger shoots with smooth bark and the perythecic stroms show up on the thicker branches. The *Pseudovalsa profusa* ascomycota is common saprobiotic on the lower, drying branches of the black locust but in case of draught or frosts can occur as weakening parasite and can speed up the dying of the branches. *Camarosporium robiniae* is also saprobiotic; it lives on dying branches and only rarely causing bark-death as pathogen. Beyond the above mentioned species on the branches of the black locust the presence of the *Cucurbitaria elongata*, the *Nectria cinnabarina*, and the *Tubercularia vulgaris* already were observed too.

Principally the branches of the dispersedly standing trees can be covered by the mistletoe (*Viscum album*). Its spreading in large numbers can cause the death of the trees step by step, but if the mistletoe presents in lower density only the branch above the semiparasite die back because the lack of water.

The characteristic tessellated pattern on leaves, decrease in their size and deformation of the leaflets can be caused by the locust mosaic virus. Because of the effect of the virus the internodal length decreases, the axillar buds opens up and the tree crown shape will have deformity. Also a virus can cause the so called witch-broom in which case many small-leaved, broom-like shoot grow and the leaflets color into yellowish or orange except of the veins. The symptoms sometimes become localized only for few branches but the hardly infected trees stay behind in growth, partly dry out and finally die. Characteristic leaf deformations can occur on the black locust due to virus infection: the leaflets will be contorted and chlorotically light along the midvein and in the autumn this leaves fall earlier than the healthy.

Among the fungi the leaf blotting *Phloespora robiniae* and the powdery mildew forming *Trichocladia robiniae* have to be mentioned. The harm of the former can cause significant defoliation in the beginning of the summer, while the latter can be detected only rarely, mostly on the leaves of the offshoots.

The European fruit lecanium (*Parthenolecanium corni*) introduced to Hungary in the 1880's and proliferated very heavily. In that time, some theories presumed the possible extinction of the black locust from Hungary. Indeed, only the plantations at unfavorable habitats were damaged strongly where in the weak stands it could cause significant decrease of the growth and maybe death of the trees. The harm of the European fruit lecanium at the end of the 1800's participated in the calamity of black locust but in the last decades its consequence decreased. Imagoes suck the thinner shoots and larvae on the leaves. The extraction of the honey-dew helps the settling of the smoke mould (*Apiosporium salicinum*) and because of this the photosynthesis intensity and the shoot growth decrease. The black bean aphid (*Aphis laburni*) sucking on the shoots, leaves and fruits is less important despite of that it can cause the atrophy of the leaves, drying of the shoots and decreasing in the fruit yield. The black locust mite (*Vasates* sp.) cause symptoms similar to the powdery mildew: the leaves and the shoots have glaucous cover, the leaflets roll up and fall at a touch, the end of the shoot thickening and become fragile.

Among the leaf miners two introduced North American species harm the leaves of the black locust in Hungary. The caterpillars of the locust digitate leaf miner (*Parectopa robiniella*) chew palmately branching shafts along the midvein and also palmately branching shafts chew below the epiderm without defecation. The pupa overwinters in white cocoon on the margin of the fallen leaflets. The species is everywhere presenting in Hungary and in warmer years the infection can be 100%. The caterpillar of the leaf blotch miner (*Phyllonorycter robiniella*) lies at the margin of the leaflet and the patch shafts containing defecation usually did on the underside, the pupa overwinters in the cocoon inside the leaf. Beyond the three chafer the common and the forest cockchafer and the June beetle also can chew the leaves. The weevils (*Sitonia* spp.) leave meeting hemicyclic bites at the leaf margin; the damage usually not considerable but the bean weevil (*Sitonia lineatus*) can cause the death of the seedlings by the chew of the cotyledons.

The caterpillars of moths can harm the black locust by chewing leaves, shoots and roots. The most frequent pests are the owlet moths [garden dart moth (*Euxoa nigricans*), archer's dart (*Agrotis vestigialis*), turnip moth (*Agrotis segetum*), broom moth (*Mamestra pisi*)] the moths [common spring moth (*Biston hirtarius*), spotted birch moth (*Amphidasis betularia*), brown-tail moth (*Euproctis chrysorrhoea*), Asian gypsy moth (*Lymantria dispar*)].

The seeds and fruits have only few known pests. The second generation of the limabean pod borer (*Etiella zinckenella*) oviposits on the legumes of the black locust; the caterpillars intrude to the fruit and feed on the developing seeds which can cause considerable loss of fruit yield in some years. The larvae of the broom weevil (*Bruchidius cisti*) develop in the seed and the imago set itself free by the biting through the legumes which also can impair the seed-yield.

Pathogens of the felled and processed wood can be the hard white rot (*Phellinus contiguus*), the chicken of the woods (*Laetiporus sulphureus*), a Turkey tail (*Trametes versicolor*), and the hairy parchment (*Stereum hirsutum*). The core of the black locust is resistant to the dry-rot fungus (*Merulius lacrymans*) but prone to the infection of the cellar fungus (*Coniophora cerebella*). In the freshly felled wood sometimes the *Xyloterus domesticus* wood-beetle species and in stored wood the European lyctus beetle (*Lyctus linearis*) occurs.

Literary data about the use of locust seeds as food by animals is not known. The consumption is unlikely because it contains heavily poisonous proteins robin and phasin, which harm the haemocytes and the vascular walls.

ECONOMIC IMPORTANCE

The black locust is used for forest plantations from the last decades of the 17th century. The volunteers returning from the American civil war emphasized the advantageous characteristics of the species. The time of the radical spread stretched from 1865 to 1895 when it became the most important species in the forestation of the Great Plain. The growth of the area got strong drive with the national forestation program started in 1949 and nowadays it is the most voluminous species in Hungary. (Table 1.)

TABLE 1. *The area of black locust plantations in Hungary*

Year	Area (thousand ha)	Proportion in the total area of the forests and plantations (%)
1885	24,2	2,1
1923	110,6	10,1
1953	191,1	15,3
1993	291,7	18,8
2003	380,6	22,1

Black locust is a typical plantation species because easy to plant and can nurse without difficulties. These are owing to the following characteristics: 1. grows very fast (the cutting age is 30-35 years) 2. the wood is heavy, hard and enduring (exceptional firewood, column or post for fruit trees, vineyards, good for parquet floor, cartwright work and currently favorite in making supporters, ceiling parts, and in the pulpwood industry), 3. it lives on soils poor in nutrients and water, 4. it has good vegetative renewal potential (from root suckers and stump sprouts it renew inexhaustibly), 5. by its expansive rootage it binds loose soils and substrates.

Beyond the listed advantageous characteristics the black locust gives the base of the Hungarian honey production, about half of the merchandised honey is coming from this species. According to some guess-work the bees collect the fifth of the overall accessible nectar production.

Previously the black locust was used in plantings outside forests and it became main species in vistas, shelter-belts, tree groups and in farms but its decorative value is much lower than the native and some exotic species. Currently because of its pioneer character and nitrogen fixative ability it is used in recultivation of bare soils, burrows and piles.

The products made from black locust can have importance in therapy too; the essences of the flowers and fresh bark are used in the medication of gastrorrhagia, gastritis and headache.

The folk medicine recommends the black locust flower as antispasmodic, cough sedative and for therapy of gout.

NATURE CONSERVATION SIGNIFICANCE

Where the black locust settles practically not possible to eliminate. Its ability to form offshoots, the colony forming vegetative propagation and the accumulating, minimum for a half century vital seeds assure not only the regeneration but exceptional conservation and gain on area of the species.

On the base of national forest stand data we can say the black locust presents (and spread) on the all areas of Hungary where the environmental conditions make it possible.

From the viewpoint of the scale of this problem it is important to make estimation about the national seed bank of the black locust as one of the determinants of the survivorship and invasion. The database of the State Forest Service showed about on 364 thousand hectares black locust stand in 2001. If we count with the 770 kg/ha seed stock value for the mid-aged stands and the concerning 22 g/1000 seeds weight the total amount will be 280280 tons and 12739 billion seeds in Hungary. This estimation is apparently rough but the true situation is possible worse than better this because the calculation above include only the registered forest stands.

The frost sensitivity and the demand for airiness of the soil are the only limiting abiotic factors for the colonization of the black locust. The species can not find the necessary conditions on the sub-mountainous areas, at frost recesses and where the ground water is too high, the floods are frequent or the soils too compacted. There is room for uneasiness at the spread of the species at higher and higher elevations in the mountains. We have only untested hypotheses about the reason of this

phenomenon. It can be generated by climatic change or gradual adaptation, but it must not forget in its native range the black locust presents above 1000 meters, on latitudes 5-10 degrees more south compare to Hungary.

For black locust cultivation more than hundred habitat type is capable in the hornbeam-oak, turkey oak-sessile-oak and forest steppe zones. On the one hand, it confirms the wide ecological tolerance of the black locust, and on the other hand shows what a large range of the Hungarian habitats are endangered by the species. As illustration worthy of examination the (potential) vegetation map of Hungary and summarizing the area of the above listed habitat types. The result is more than third of all Hungary.

The black locust converts its habitat considerably. To the very intense evaporation the expanded rootage ensure the water and by this way decrease the possibilities of the neighboring plants for water intake. The mass of the leaves is small and decompose fast, it gives nitrogen and calcium abundantly but phosphorus and potassium in very small quantities to the soil. Partly due to the high nitrogen content of the falling litter, around the black locust individuals the nitrogen content of the topsoil is high. At the most habitat types the repeated cultivation of the black locust results considerable fallback in growth what can be caused by the soil exploitation of the species or by the unfavorable microbiologic processes. Either of them is acting, the basic element of the process is the black locust. Beyond its effective water intake, the conversion of the soil nutrients and the allelopathic effects can explain the low species richness of the herb layer dominated by nitrophilous plants or plants with wide ecological tolerance range for which the loose structure of the canopy also favorable.

The stands on unsuitable habitats or repeatedly grown stands show weaker or stronger impairment, on the worst habitats typical is the formation of the so called locust cemeteries. Beyond the mentioned decreasing of the diversity the characteristic changes of the habitat serve for some fungus species, like the sand truffle (*Terfezia terfezioides*), which has queried *mycorrhizic* partnership with the black locust and the black locust armillaria (*Armillaria rickenii*) described from the Hungarian black locust stands.

The low species richness of the vegetation foretells the small number of the animal species the number of consumer-impairing insects is limited, most of them are polyphagous. It is interesting the fast decomposing leaf litter of the black locust create really favorable conditions for the soil fauna and inside this especially for the earthworms.

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BLACK CHERRY

(*Prunus serotina* EHRH.)

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TAXONOMY

Scientific name of the black cherry: *Prunus serotina* EHRH. Synonyms: *Padus serotina* (EHRH.) BORKH. and *Cerasus serotina* LOIS.

The black cherry belongs to the Rosaceae family and inside this into the Prunoideae subfamily and genera *Prunus*. The Prunoideae subfamily is a taxon of woody plants with simple leaves and stone fruits. The endocarp of the fruit is almost always hard and woody, the mesocarp is fleshy and juicy, and the exocarp is very thin and leather-like. The species, more than 200 of the genus *Prunus* are distributed all over the Northern hemisphere (with great number of species in Asia Minor) but represents of the genus can be found in the tropic America too. By the characteristics of their fruits the species are known as plums, cherries, sour cherries, apricots, peaches, almond etc. The black cherry is classified inside the genus *Prunus* into the subgenus of *Padus*. The species can be detached from the other members of the subgenus by the sepals staying on the fruit and the dentation of the leaf-margins.

In its native land the black cherry is divided into the following five subspecies:

subsp. *serotina*, distributed at the Eastern part of North America;

subsp. *hirsuta*, at the states Georgia and Alabama;

subsp. *eximia*, at the middle part of Texas;

subsp. *virens*, from the mountains of Western part of Texas through Arisona to North Mexico;

subsp. *capuli*, distributed at Middle America.

The variability of the species is not researched in detail in the European distribution area.

MORPHOLOGY

The tree has average growth, in Hungary the detected highest specimens are 25-45 meters but normally lower and frequently shrub sized. Prone to strong branching, the canopy is wide and the stem frequently crooked. The bark is smooth with linear cracks and vertically elongating lighter colored lenticels. The bark of the older trees dark grey with linear cracks and the tiles with cocked margins are characteristics. The young shoots are green, on the base finely hairy, later reddish-brown with many ascendant lenticels. The two year-old shoots are covered with grey periderm. The buds are projecting, depressed conical, bare, reddish-brown with green-yellow spots. The leading bud is larger than axillary buds.

Their leaves are alternate standing, simple, the shape is egg-form or elliptic, 5-12 cm long and 2,5-5 cm wide with rounded or cuneal shoulder and acuminate. The edge of the leaf is finely toothed, the teeth are archwise forward standing, slender and at the apex with gland. The leaf-blade is thick and gloss, leather like, dark green with fine veins, smooth. The underside of the leaf is goose-green with rusty hairs along the middle vein. The leaf-stalk is 1-2 cm long and has irregularly placed glandular lenticels. In autumn the leaf color changes into bright yellow or red. The flowers open at the apex of the leafed side branches in the beginning as erected but later floppy, 8-14 cm long, cylindrical clusters. The

cluster is reminiscent of the hackberries one – which is native in Europe – but narrower, more loose and smaller than that. The petals are cream-colored, with long oval form. The pinnas of the calyx are wide-triangular, long staying and red. The flowering begins after the total developing of the foliage at the end of May. Diameter of the globose fruits is 8-10 mm. Their color is red before ripening later dark bluish-lilac and black shiny when ripe. Their taste is austere. The five-toothed calyx stays on the fruit. The nutlet is egg-shaped, smooth and inside the lonely seed is black. The fruit ripens in September. The whole plant (leaves, branches, shoots, bark and seeds) include cyan-glycoside.

The black cherry in general effect is very reminiscent of the native European hackberry (*Prunus padus*). The later species lives dispersedly in alluvial and mesophilous broad-leaved forests all over Hungary, it is common in the Western and South-Western part of the country and rare on the Great Plain (Alföld). It is also planted as ornamental tree. The leaf-blades of this species are thin, the surface of the leaf is beamless, little plicated, fresh green. The veins of the leaves are marked, upside recessed and reticulately running, at the margins anastomosing. The underside of the leaves is bluish-green without rusty hairs along the middle vein. The flower cluster is more dense and larger than the black cherry's is. The fruit is glossy black, sweet but with disgusting taste. The calyx is caducous. The bark has aromatic smell.

The also North American choke cherry (*Prunus virginiana*) is sometimes planted in Central-Europe and this species can naturalize too. Its fruits are dark red and the calyx is caducous. It is smaller; its height can be maximum 5 meters. Its bark is not aromatic. Its leaves are considerably pointed with only 8-11 side veins (on the leaves of the black cherry are at least 15 side veins).

ORIGIN, DISTRIBUTION

The native area of the black cherry is the Eastern side of North America; the distribution area extends on the South onto the mountains of Central America (from Mexico to Guatemala). The climate is optimal for the species in areas south from the Great Lakes. The five subspecies described in the native area have partly overlapping distribution areas. *Prunus serotina* was among the first species of trees were brought from North America to Europe. First time it was planted in 1623 near Paris. In the following decades it was diffused in numerous European countries. In Germany it was mentioned at first time in 1685. In the following two centuries it was planted as ornamental tree in gardens, parks because of its beautiful flowers and lively autumn colors. Its use in the forestry began only at the end of the 19th century. After the first forestry experiments in Germany it was considered as advisable timber producing species which grows faster on poor soils than native species. Contrary to the expectations it did not produce marketable timber but formed dense level of shrub in short period, at first in mixed oak-pine forests, and later it was penetrating other forest types. It was especially well spreading on poor soils. Today in most of the European countries it propagates spontaneously. It is known as an inconvenient and troublesome species everywhere, because it impedes the natural renewing of the forests and decreases the species diversity of the undergrowth. It gives many problems from the viewpoint of intensive forestry too. Nevertheless it was planted some places till the last decades because of its believed advances. Its leaf-litter is decomposed fast therefore in Germany it was hoped the species will increase the humus content of soils in pine plantations. Between 1920 and 1950 in Netherlands it was planted everywhere for amelioration as well as protection against fire and storms. It is frequently hard or even impossible to discover the history and key points of the spreading of black cherry in Europe. Many authors are in doubt that this fast dispersion is exclusively the result of the aggressive invasion but think it is mostly connected to the planting practice.

Today *P. serotina* presents on most of the plains of the European continent and it is especially frequent in Germany (mostly in the Northern part of the country), in Netherlands, in North-East France, in Denmark, in Poland and in some parts of Austria. It is present in North Italy, in Hungary, in Romania, in Bohemia and in the Southern part of England. It seems that by this time not presenting in Russia and the ex-soviet states, in the Mediterranean area and in Scandinavia. The distribution maps made in some countries show that the distribution in general coincides with the presence of sand-soils.

The first data of presence in the Carpathian Basin originates from 1897 (lived in the garden of a holiday home at Pusztaszentlőrinc). Between 1934 and 1949 it was mentioned more times as species of the forestry experimental ground at Gödöllő. Later it was planted mostly on sandy soils (in the Nyírség, Belső-Somogy, Kiskunság), but at the other parts of the Alföld and at some places in the hill countries also occur as planted and escaped species. At the Southern part of the Belső-Somogy at the end of the 1950's and beginning of the 1960's it was planted in large quantities in scotch pine (*Pinus sylvestris*) plantations because it was hoped making better pine trunks without side branches and increasing the growth. At the beginning the game stocks a bit impeded the growth of the plants because the younger shoots are less poisonous and assumable the species was a kind of delicacy for the large herbivores. Later the under planting were going on spontaneously, with native species reforesting abandoned grazing areas with less closed canopy. The second generation of the black cherry occurred in the Belső-Somogy at the beginning of the 1970's and the explosion-like spread holds on till today. In the Nyírség nowadays the species is widely distributed and at some places in smaller numbers occur in the forests of the loess plateau of the Hajdúság. It is frequent in the forestry plantations (mostly black locust and Scotch pine) but spontaneously occurs in other forest types too. In the Kiskunság the species is less frequent, rare in planted pine forests but in some locations near Kunadacs and Kunbaracs it grows in great quantities. The spreading can be detected chiefly in disturbed forests (disturbed might be 50 years ago) and it is independent of the species composition of the affected forest.

LIFE CYCLE

The seeds of the black cherry germinate in the soil. The first foliage leaves are oval-lanceolate with aristate-dentate margin, the one year-old shoots are slender, bright lilac-brown, glossy, hairless with many lenticels. The branches are short and standing at right angles. The strong nature of growth in juvenescent is characteristic. As free standing specimen the tree develops numerous side branches, frequently became bushy but few years later the trunk will become strong. The generative phase of the life begins early, in its native area flowers and gives fruit as 5-6 year-old (in Hungary it begins at 8th year). After the 10th year the fruit giving is frequent and abundant. The seeds are carried for long distances by animals but most of the seeds stay near to the mother trees. The European researches show that 75 percents of the seeds can be found within 25 meters from the tree. Indirect evidence of the travel of the seeds is the distance of the dense seedling stock from the mother tree. With consideration of carrying by animals by these researches 1) the distance between the seed growing tree and the seedlings is maximum 600 meters 2) more than the half of the seedlings are closer than 200 meters 3) the distance between the tree and the seedling generally less than 400 meters. The black cherry renews well with offsets of the trunk, it has good regeneration ability and the cut out older trees offset also. The growth of the offsets is dynamic. It does not throw out suckers. The frondescence begins relatively early in April and at sandy habitats it is in advance of most native tree species. The flowering begins after the complete development of the foliage at the end of May. The fruits ripen late in September. The foliage autumn colors are flourish yellow and red. In Central Europe the species is not long-living, after 50 years its vitality decreases fast.

HABITAT PREFERENCE

In its native area the black cherry presents from the plains of the seaside to the 1800-2000 meters high mountains in different height levels. It grows among very different climatic conditions. The average annual precipitation is between 500 and 2000 millimeters. The average temperature in January changes from -15°C to +13°C, and the average temperature in June is between 17°C and 28°C. The water requirement of the plant is average, the rootage goes deep and therefore it tolerates well the short droughts. Soil needs is wide enough, it grows on the soils from the compact clays to the loose sands. The plant finds its optimum in the deep and humid alluvial soils. On dry and poor sand soils the tree will be dwarfish.

P. serotina is widely dispersed in many different forest types of the eastern side of North America. In the center of the native area it grows in deciduous forests, on North it extends into the transition zone to the boreal forests. Near to the Atlantic Ocean the tree grows in pine forests but on the West near to the border of the prairie in the savannah of oaks. In North America it is described in 24 forest associations as presenting species. It does not form forest type in its own but very frequent in beech (*Fagus*) and maple (*Acer*) dominated forests at the Northern part of the deciduous zone. In the foothills of the Appalachian Mountains it lives in the oak-hickory (*Quercus-Carya*) forests. At the Southern areas it is rarer and not presenting in the boreal forests. In these wide range of forest types the black cherry is not a frequent species of the canopy or it stays in the shrub level because does not grow to the canopy. In the centre of its native area (Pennsylvania, New York, West Virginia, Ohio) its frequency is small, but presents large specimens as hold-over trees in remnant forests that grew up after clear fellings two hundred years ago when in the early part of the natural renewing the black cherry had dominant role.

In Europe it was planted as ornamental tree on many types of soils but in forestry it is used mostly at sandy areas. In Hungary the black cherry was planted also on sand-soils, in plantations of black and Scotch pine, black locust, hybrid poplar stands and at some locations in spontaneously reforesting abandoned pastures. The species spread fast after start to bring fruits (8-10 years). It is written by numerous authors that the disturbing of the habitat is important and favorable for the black cherry either natural (like thunders) or anthropogenous disturbing.

At the Southern part of Belső-Somogy in sand soil habitats it can be mass producer in all of the plant associations from the alder swamp forests (*Carici elongatae-Alnetum*) to the dry sand grasslands (*Festuco dominii-Corynephorretum*). The best growth is discernible in the border zone of the moor lakes. It endures the periodic inundation but can not bear the abiding flood (2-3 month) in the vegetation period. It is dominant or common element of the shrub level in the Nyírség and it can form homogenous shrub level in degraded forests and plantations. It penetrates into the natural oak forests of sand soils, chiefly in the "semi-mesophilous" and mesic-steppic oak forests (*Festuco-Quercetum* and *Convallario-Quercetum*). It can appear in the markedly mesophilous forests, in alluvial and swamp forests but in these habitats is not characteristic its proliferation in the Nyírség. The observations in the Kiskunság show that the species spread chiefly in the disturbed parts of the forests independently of the original species composition of the forest stand. Somewhere it is mass producing and over-competes the natural renewing seedlings. In the older stands of pedunculate oak forests, birch forests and in the near natural forest-steppe habitats it can not or barely can be found (in these habitats the herbaceous level is strongly closed and/or the shrub level is also dense). The observations of these area show that it settles at the locations with close ground water at first and then from these places radiates to the drier habitats.

BIOTIC INTERACTIONS

In Europe dense population of the black cherry seedlings grows over the native plants fast (herbaceous plants, seedling of trees and shrubs) and repress them by its strong shading. Studying the occurrence conditions of the different sized seedlings in North America it was found that under the elder trees there are many small sized seedlings, but the larger seedlings appeared only on sites where the old trees were absent, so the tree-layer was open. This behavior is known for many tree species: having short-lived seed these trees do not form seed banks (or only for short term) like many other forest species do, but instead build up a layer of regeneration underneath the canopy that can be called "seedling bank". These seedlings can survive the repressed, less sunny conditions for long, without height growth. Their growth starts only after the light conditions change – for example after storm or wood-cuttings – and then develop the next generation of the canopy-layer. This behavior (after the character of G. Grass's novel, who stops growing at the age of three) is called "Oskar-syndrome". The advantage of such an "Oskar strategy" is that these tree species do not have to conquest the habitat that time when the conditions are favorable for the tree growth, but they fill the space in advance and therefore they can be more successful than their competitors. The light-demand of the black cherry's seedlings is high and it limits the success of the species in woods those are constituted by trees tolerating shade, like the Amer-

ican beech (*Fagus grandifolia*) or some maple (*Acer* spp.). Consequently in its native range *P. serotina* become dominant in the canopy only for a limited time during succession (pioneer species). The demographic analysis of the species in the woods around Berlin shows similar pattern to the ones observed in North America. It has the same typical “Oskar-behavior”, but the “Oskar seedlings” are larger in Germany what is ascribed to the light surplus, because the oak-pine mixed forest provides better growth conditions for the seedlings.

In its native range main consumers of its foliage are the eastern tent caterpillar (*Malacosoma americanum*) and the cherry scallop shell moth (*Hydria prunivoreta*), these species can cause complete devastation of the tree by the consumption of the leaves. The above-mentioned species are not present in Europe, but there are data about the relation of black cherry and some insect native in Europe too. The main proved consumer of its foliage in Europe so far is a leaf beetle (*Gonioctena quinquepunctata*), whose larvae and imago were found on the black cherry in Germany about 10 years ago. Occasionally significant leaf damage was observed, but it was not proved yet if it has any negative effect on the development of black cherry. Originally this leaf beetle occurs in woods of moist areas (its host plants are *Sorbus aucuparia*, *Sorbus aria*, *Prunus padus*, and *Corylus avellana*) and it was observed that by the consumption of the black cherry located to drier habitats the distribution of this bug increased. Other bugs observed on the black cherry: Elateridae: *Athous haemorrhoidalis*, *Athous subfuscus*, *Dalopius marginatus*; Curculionidae: *Otiorynchus raucus*, *Phyllobius calcaratus*, *Phyllobius pyri*, *Polydrusus cervinus*, *Furcicus rectirostris*. On the black cherry different species of spiders, flies, diggers, butterflies and even the *Meconema thalassinum* grasshopper species have been observed.

The fruits of *P. serotina* are consumed by many bird, some authors enumerated around 60 bird species of this kind in Europe. A variety of small mammals such as marten, weasel, badger and fox consume the fruit. In the propagation of the black cherry the badger is the most efficient of them, because it often buries the fruit and so the seeds get into a favorable position for sprouting. Other parts of the tree are not eaten by vertebrates, because those are toxic for them. The leaves, buds, seeds, the bark and the boughs contain hydrocyanic acid and cyanogenic-glycosids (amygdaline, prunasine). However the fresh leaves, the seedlings and the saplings contains far less toxins, so these parts can be eaten by games in small quantity without any harm.

ECONOMIC IMPORTANCE

The black cherry shoot up in Europe is not suitable for industrial purpose wood culture because the size of the tree and its unfavorable structure. The timber is quite hard, it cracks in slew while drying out and it is pinny. In the Hungarian forestry practice it was used mostly in case of alien plantations to under deploy the substances, constituting the lower canopy-layer, hereby to intensify the quality's accretion and to aid the protection of the soil. It was also used to fill in the deployment holes, because it subsists even on lean production sites and it is not often eaten by games. However the practice usually did not justify the prospects about its favorable effects, moreover its unexpected negative effects are higher than the possible utility of the species. The black cherry can be a nutriment and water competitor of the planted and natural tree species; hereby it reduces the yield of tree species of economical interest. By its fast juvenile growth the black cherry planted in the deployment holes often overgrow and shade the primal tree species. The native shrubs and herbaceous plants are pushed into the background fast and get extinct, hereby the amount of the natural game nutriment decrease significantly. The substances of the spontaneously propagating, fast growing, dense black cherry stall the forest's resurrection and the development of other planted tree species. The logs of the black cherry – those been cut during the cleaning process preceding the logging – block the movement of the machines and its hard wood can prick the tyres of vehicles. In the aspect of the forestry practice the black cherry is unambiguously a weed that makes the forestry difficult.

Beyond its planting for wood culture purpose, it was planted for aesthetic purpose too. Thanks to its autumnal foliage coloration, it was used to construct the fringe of the forests and to piping the roads. It was planted in keen game preserves too, because its dense shrubs can give shelter for games. Out of

the forests, it was planted for afforestation purpose, for parks, greenbelts and along the roads, occasionally it was used for plant in the refuse of mines. It can be said that the black cherry has no any special utilization field – that could justify its presence – that can not be replaced by other native or less maleficent alien species.

NATURE CONSERVATION SIGNIFICANCE

The black cherry in the European forests - thanks to its dense, close shrub-layer – stalls the renewal of the native tree species, reduces the biodiversity of the undergrowth and has negative effect on the forests dynamics. It has unfavorable effect mostly on the renewal of the more light-demanding tree species, like the oak and the birch. Monitoring related to the diminution of the undergrowth's biodiversity held in Germany have found explicit coherence between the presence of the black cherry and the biodiversity: whereabouts the black cherry is present in the upper layer of the vegetation, the biodiversity of the sward layer decreases with the increase of the black cherry's domination.

On the protected natural areas situated on sandy sites the penetration of the black cherry causes serious problems. About one third of the protected area of Barcsi Borókás (SW-Hungary) is strongly infected; it means that the black cherry changed the native shrub species on 400-500 hectares. It can be big concurrency to the tree species of the lower canopy-layer too; moreover here and there it over-competes the earlier dominant tree species. It is a strong competitor of the native pioneer shrubs and trees in grasslands and abandoned pastures. It only absent from sites covered by stable open water, if the water's overlay lasts at least 2-3 months. It propagates substantially in the Nyírség (NE-Hungary) too and probably it will cause more serious conservationist problems in the near future. It propagates in forest-steppes on sand too, supplanting the native shrubs, the common and rare native species of herb layer (for example, *Iris aphylla* subsp. *hungarica*), just as it stalls the natural renewal of oak.

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RUSSIAN OLIVE

(*Elaeagnus angustifolia* L.)

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TAXONOMY

Elaeagnaceae family consists of shrubs or trees, whose branch system is usually thorny, shoots are covered with stellar and scale hairs and the leaves have unscathed margin. Their flowers are commonly four-parted and the corolla is missing. Three genera (*Elaeagnus*, *Hippophaë*, *Shepherdia*) with 69 species belong to the family. While the species of the Eurasian *Hippophaë* and of the North American *Shepherdia* genus are dioecious, flowers of the species of *Elaeagnus* genus are monoecious or hermaphrodites. This genus has some 45 species among those there are evergreens too. It occurs in Asia and North America and the centre of its origin is in South East Asia.

Elaeagnus angustifolia has high morphological diversity. Commonly four varieties are distinguished among those however geographical or habitat differentiation can not be observed:

var. *angustifolia* (*E. inermis* MILL.). – leaves are lanceolate or linear, silvery on both sides but without stellate hair;

var. *spinosa* C. K. SCHN. – leaves are ovate or elliptic and the shoot system is usually thorny;

var. *songerica* FISCH – leaves are softly felt, usually with stellate hair;

var. *orientalis* DIPP. – shoots have no scale hairs, but they are softly fleecy or felt.

In Europe (just as in Hungary) two further *Elaeagnus* species are planted in parks and gardens. The American silverberry (*E. commutata* BERNH., syn.: *E. argentea* PURSH.) native on the eastern part of North America is a 2-4 m tall shrub with multiple strains which colonize with its tillers. Its shoot system has no thorns, leaves are ovate or elliptic (they are 2-3 times longer than their width, whilst at the *E. angustifolia* this relation is 4-6), they are permanent scale haired even on the upper side, silvery-grey, on the abaxial surface among the silvery-grey scales sporadically brown squamas can be found too. It easily escapes from cultivation and settles down durative. Usually people do not distinguish it from the Russian olive therefore we have deficient knowledge about its occurrence in Hungary. The cherry silverberry native in East Asia (*E. multiflora* THUNB., syn.: *E. edulis* CARR.) is also of shrub stature, shoots are thornless, leaves are elliptic and 2-3 times longer than width, they get bare early on their upper side, they are dark green, usually with undulate edge, on their abaxial surface the sparse brown scales also can be found. Contrary to the Russian olive and to the Silverberry it flourishes early (in the first-half of May), fruits have long pedicles, they are succulent and have sourish taste, when mature their color is red. It gets wild rarely.

MORPHOLOGY

It is a tree with diversified conformation that can grows up to 8-10 m high, but often remains shrub-statured only. Mostly the trunk is spatial-crooked, almost always of slant position, low branching, furcating into coarse side branches. The root system is statuesque, it develops deep penetrating taproot from the

beginning whose first rank side roots are horizontal and making their way far. On steppe areas its roots do not fathom deeper than 2 meter, but the upper 20-30 cm of soil is rootless even in this case. In autumn the growth of roots stops later, than the growth of the shoot system. The bark is reddish-brown, thin, covered by lustrous and suberous verrucae while young, and its dark brown or grayish brown, soft, stringy riving and comes off in elongate fibrous strips, when elder. Its treetop is built up by bigger frame-branches, the branch system is loosely splayed, when elder it spreads in bow, and because of its strong phototropic quality usually it shifts towards light. Its shoot system is sympodial, is of specific build-up. On its frame-branches vigorous long shoots are growing those are capable of subsidiary expansion, and on them thin, 10-20 cm long dwarf shoots which grow 1-2 mm of diameter in the next year. These dwarf shoots are fugitive and they bear a significant part of foliage. Some of the dwarf shoots are of intermediate type; they can become woody and form further dwarf shoots. On the middle and bottom nodes of the long shoots, 1-5 cm long, simple thorns can be found. The thorns of individuals grown on dry and nutrient poor production site are of particularly robust growth. The boughs are bald, sleek, greenish brown and later reddish brown, the stick is lustrous, silvery hairy. The buds developing on the long shoots are vigorous, of diffused standing, oval with rounded tops, 4-7 loosely standing, and it is covered with silver-grey bud scales. Beside the advanced developing main buds, sub-buds are often. The buds of the lateral shoots are tiny with scarce scales, unable to develop forward.

Leaves can hardly be distinguished from other *Elaeagnus* species. The 3-8 cm long and 0,5-2,5 cm broad leaves are lanceolate or stringy lanceolate, their broadest part is their lower tierce, leaf base is acute, margins entire and leaf tip obtuse. The leaf blade is covered by scale hairs, fully developed they are green, sleek, the abaxial surface is silvery white, their main vein swells robustly, but their lateral veins are not well-marked. The petiole is 3-8 mm long, silvery, also covered by flake hairs and have no stipule. The treetop is bushy while young, but at an elder age it gets scanty. Light-leaves are smaller, narrower and thinner than the shade-leaves, the latter ones are dark green above and the previous ones are silvery grayish green.

The flowers are axillary, one-three of them form a cluster. Their peduncles are 5-25 mm long. The flowers are four-parted, their petals are missing, sepals form tubular calyx, and the pinnae are triangular, spreading at blooming time. Polygamous, the calyx of the staminate flowers are tubular, at the hermaphrodites it is lanced above the torus, and then flares in bell shape. The perianth is silvery white on the outside and yellow, slightly golden colored on the inside. The number of stamen is four, the filaments are short, and the stamens are located in the throat of the tubular calyx. The ovary is inferior, the style is strand-like, slightly bended, the discus is strongly attached to its basis, and the stigma is small and rounded. Its flower has strong fragrant.

Its drupe is 10-16 mm long, ovoid or elliptic, silvery grey colored, densely covered by scale hairs. On the top of the fruit sepal remains can be found. Following the maturation the color is yellowish or reddish brown, it is balding, the fruit flesh is farinaceous and acerbic flavored. The pit is arbor shaped, 8-12 mm long, bright brown colored with 8 dark brown lengthwise stripes. The seed has no endosperm.

ORIGIN, DISTRIBUTION

The Russian olive is native on the warm continental areas of Asia; it has a typical Turanian type distribution. Its distribution area starts at the eastern basin of the Mediterranean sea, and across Little Asia it covers West and Central Asia whereabouts its area spreads till the Altai-mountains and the desert Gobi. In the biggest mass it can be found on the Caspian Lowland, on the areas of the Lake Aral and the Lake Balhas, where it is a typical plant of the vegetation following the watercourses of the sandy semi-deserts. European part of the Mediterranean sea, just as the most Southern areas of Central Europe is often included to its native range. However most probably it was only naturalized here, as it is grown in cultures in West Asia and in Europe for centuries, from where it often escaped into the wild. It is willingly used in many other countries too, like in Egypt, Algeria, China, Italy, Spain and it is gladly planted on the Southern part of France. Probably it got into Hungary in time of Turkish domination (16-17th century).

LIFE CYCLE

At the beginning it is fast growing, the length of the seedling's taproot is 20-40 cm, shoots are of 15-20 cm, by the end of the third year the height of individuals approximates 1 meter. The height growth last out till its 10-12 years of age, but from the third year it is of smaller scale, rather the formation of lateral shoots is more dynamic. The root's growth in thickness is perpetual; the diameter at breast height can top even the 60 cm in case of elder trees. In spring in line with the shoot formation, the root formation starts too, but the development of roots continues even after the formation of shoots is stopped. Main period of its blooming is in May and June, the ripening of the fruits lasts from August till October, and the fruits stay on the tree even in winter time. The production of fruits starts at 3-5 years of age. The seed weight of the species is 100 g/1000 seeds (SCHÜTT & LANG 1994), according to other authors it is 140-180 g/1000 seeds (MAGYAR 1960). The average weight of the air dry fruits is 0.1725 g. We have found different data regarding the germination ratio of seeds: 30-60%, 50-60%, or rather 70-100%. The dried fruits or the cleaned up putamens of 6-14% water content and on 1-10 °C, kept in closed pot can keep their germinating capacity even for 3 years. Because of the inhibitors in pericarpium and the undeveloped embryo dormancy develops in winter. The dormancy can be broken with 1-3 months long stratification (1-10 °C) or with 30-60 minutes long treatment of undiluted vitriol, a one hour long vitriolic treatment results 66-98% germination ratio. According to PÉCH's (1903) suggestion seeds need to be kept in sachet for 2-3 months, in between fertilizer previous to sowing, seed them at the beginning of April and the seedlings come up till the beginning of July. The vegetative expansion of the species is weak, it brings only root sprouts, in case the plant gets injured it regenerates from the offshoots flushing from the root collar and from the farther roots, it is covered over shoots take root. Its life expectancy is 65-85 years, but it can even reach 100 years of age.

Its propagation, besides sowing, can be made from woody cuttings too, but from green cuttings it does not take root or does it badly. The most favorable period for cuttings is February. It can be pruned nicely, it can be trained for hedgerow, and its availabilities of use are: in parks, on dry areas, sand, saline area, inner urban places and industrial locations. The micro-propagation of species can be worked out too by taking segment of node from the full-grown individuals, by induction of shoot formation from the adventitious bud. Individuals regenerated on substrate can successfully transplanted into soil after acclimatization.

In nature the scarification of seeds is made by animals by means of their digestive chemicals, just as by the alternation of humid and dry, and of warm and cold periods, furthermore by saprobionta organisms. The spreading of the seeds and fruits can happen in many different ways. By gravitation the seeds do not get too far. According to American observations 86% of the seeds were fallen in the zone of tree-top, and only 14% were fallen in the inter-foliage area. The fruits and the seeds can be dispersed by water, by floating on the water surface, and by being buried in the river drift. It is proved that smaller mammals, birds and fishes disperse the seeds too.

According to experimentations carried out by BROCK (2003) in Arizona, out of 100 seeds that seemed to be viable only 60 were proved to be viable. The germination ratio of samples deriving from different monitored areas was altered between 14-54%; the germination percentage was on the average 21%. The number of seeds per square meter and the viability of seeds were considerably different in the five monitored unit: the average number of seeds per square meter was 415. 63% of seeds turned out to be fresh and capable of living, the other 37% of seeds were elder ones or of zero percentage of germination. By the results of examinations we can presume that, if 415 seeds can be found on one square meter and 63% of them are potentially germinable (including the dormant ones too), it means 216 potentially germinating member of the seed bank. However out of the seeds seemed to be viable, only 60% were germinable, thus the number of viable seeds per square meter decreased to 156, and forasmuch the authors observed an average of 21% germination ratio in case of humid soils, therefore this means 33 seeds per square meter according to the example above. This is more than enough for the subsistence of a population, and it insures the propagation of seeds too, by what the species can colonize new areas.

HABITAT PREFERENCE

According to a literature deriving from the area of the Former Soviet Union, the Russian olive survives a frost of -30°C , but at -20°C the terminal shoots freeze down strongly. According to North American authors the species can tolerate frosts of -45°C and $+46^{\circ}\text{C}$ heats too. As it is drought tolerant, salt tolerant and tolerates the cold winters, it has an important role in the erosion protection of arid areas. This provides a possibility to spread in wide range and if it settles down once, it is hard to keep its propagation under control. Its big volume root compared to the shoot system, its strong osmotic suck and its leaves covered by scales show its xeromorphic structure. During a long lasting drought it can loose 70% of its foliage. It tolerates the inundation of watercourse for 40 days, in North America its healthy substances occur even in river basins where sometimes the water level exceeds 60 cm; but in oxygen-poor water of clayey soil it perishes fast. It is quite undemanding concerning the nutrient supply and structure of soil, it subsists on many different type of soil from sandy to clayey soil, but in consideration of its development the most favorable soils the species is the deep sandy or loamy soils with low salt content. Although the species subsists on soil with high salt content, generally on saline soils it remains shrub-statured, on the soils with lower or medial (100–3500 ppm) salt content its development is more intensive. Concerning the soil reaction the lowest bound of its toleration ranges till pH 6. MAGYAR (1960-61) mentions it as the most important tree species that indispensable in the afforestation of the saline areas. The author suggests that the species is not fastidious regarding the soil; it tolerates saline soil, the aridity and the clayey soil, but suffers for the inundation. The root system of the Russian olive enmeshes richly the saline soil. The seedling has typical taproot that can reach even the 105 cm depth. In saline soil the root of the two-year-old common oak can reach the 95 cm, the Turkey oak the 70 cm, the Common hackberry the 55 cm and of the three-year-old Russian olive the 302 cm depth. It is strongly light-demanding; its shade toleration is moderate. The morphological and anatomical diversity of the leaves provide such an adaptive advantage to the species that allows of the development and function of leaves even in habitats those strongly differs in respect of sunlight, air temperature and aridity. As the species tolerates well the air and soil contamination, it is often planted in cities and industrial locations. The species is slightly sensitive even of other emissions – like for example the sulphur-dioxide, ammonia compounds and the fluorhydrogen.

BIOTIC INTERACTIONS

The Russian olive lives in symbiosis with a nitrogen-fixing Actinomycetes species, the *Frankia elaeagni*. This species occurs in nodules found on the root of the Russian olive, and able to transform the atmospheric nitrogen – that is unavailable for plants – into nitrate – that is available for plants -, and by this it contributes significantly to the nitrogen content of the soil. Thanks to their symbiosis the Russian olive is able to subsist even on nitrogen-poor soil. The roundish nodules of an about 2 cm of maximal size can be found on the bushy, short, thick and branching side roots.

Diseases harm the Russian olive less often within its native area than they do outside of it. So kind of diseases are mostly known from North America those can principally be originated in pathogen fungi. One of the most notable diseases of the Russian olive is a fungus, *Phomopsis arnoldiae* (syn. *P. elaeagni*) that causes cancer and the necrosis of peripheral parts which is strongly pathogen and attacks even the vital individuals, although other authors consider them to harm only the elder specimens. The disease was introduced into America from Europe. Although the fungi rarely kills off the tree, but it looses its attractive appearance and becomes weak, hereby other causative agents can attack it more easily. In case of aridity or hailstorm the fungus-disease spread more rapidly too. Firstly the wilting of the leaves can be noticed and this is followed by the mortification of the bark and the cancer of the trunk. The leaves wither on the branches and on the rods, then the shoots die down. The cancer can attack any sized branches, the leaves shrivel on the affected branches, involute and discolor, but stay on the tree in the growing period. The size of the bark cancer is varying; it is of orange-brown – reddish brown color with a darker brown margin. For the time being there was no efficient fungicide found or used against the disease, usually the concision of the damaged parts, the removal of the strongly affected

specimens, or rather the planting of healthy seedlings is recommended. It is hard to save the badly infected trees, especially if there are other diseased trees about and the danger of re-contagion holds. The Russian olive damaging *Tubercularia ulmea* (Deuteromycotina), wrote down at the Siberian elm, is a bark parasite too, firstly it causes wilting, then the mortality of the branches and the trunk. It is a facultative parasite that usually attacks trees washed out by aridity, frost damage or root injury, but can cause serious problems. On the moist and badly drained areas of Eastern part of North America the devastation owing to the *Verticillium* wilt is common. The attacked branches start wilting, the leaves turning brown. The *Verticillium* wilt is usually fatal and it attacked many plantations in the American central west. The *Cercospora elaeagni* is less dangerous, but widespread and damages the leaves, causes 1-2 mm wide, bright patches. The *Lasiodiplodia theobromae* (conidial form of the *Botryosphaeria rhodena*) is a notable pathogen fungus of the Russian olive too, its damage affects equally the leaves, the branches and the trunk (bark necrosis). In America the weakening and the gum forming of the specimens of Russian olive became more and more common in the last years and mostly among the elder individuals. A yellow, gum-like material comes up on the branches that later becomes solid. The reason of weakening is primarily the environmental stress (too little or too much water, extreme temperature rates). Commonly beyond the gum forming branch devastation and leaf wilting show up, then the devastation of specimens eventuates usually 1-7 years later. The Russian olive forms gum if it is in stress. The reason of it can be a fungi infection (*Lasiodiplodia* (*Botryodiplodia*), *Nectria* (*Tubercularia*)), but it can mean the malfunction of the roots too that can be a result of disease or of unfavorable environmental factors. On the roots of the weakening specimens *Fusarium* and *Phytophthora* fungi were found, but it is not known yet whether or not these fungi are the chief reason of the depression.

The leaves and the shoots of the species contain much tannin; therefore it has quite a few harmful agents. Insects barely harm the Russian olive, but at blooming time an abundance of insect seek out the tree. Its foliage is consumed by leaf-beetles, weevils and sucked by plant-lice, field bugs. In North America a scale-insect species causes the biggest problems. The Russian olive is a host plant of the Asian *Anoplophora glabripennis* (Coleoptera: Cerambycidae) which beetle causes the devastation of hardwoods, but its many other host plant is known besides *Elaeagnus*. It causes enormous economical damages in North America, because of its injury thousands of urban trees was necessary to be removed from New York and Chicago and the amount of importable wood was strongly reduced too. The larvae beds itself deeply into the trunk or rather into the branches, therefore it is hard to defend against it. Other Asian *Aeolesthes sarta* (Coleoptera: Cerambycidae) beetle species that is absent in Europe, beside numerous other plant species damages the Russian olive. It causes wilting and leaf drying, it makes holes in the bigger branches and trunks. The larvae of the *Hyalophora gloveri* (Lepidoptera: Saturniidae) butterfly species feeds on the Russian olive too.

In Central Europe 16 bird species consume the crop of Russian olive that compared to the other not native tree and scrub species is a relatively high number. In Hungary the crop is consumed by birds (starling, pheasant, and carrion-crow) and by smaller rodents. The Fieldfare's (*Turdus pilaris*) winter nourishment is chiefly the crop of the Common hackberry, the Japanese pagoda tree, the Russian olive and the Rosehip. The species does not suffer game mastication.

ECONOMIC IMPORTANCE

The Russian olive is utilized widely and for a long while for the sake of its many advantageous features. As it blooms richly, it is a valuable bee meadow, but the sugar level of its nectar is relatively low. However its flowers blossoming following the black locust blooming elongates the getting in period, its spicy flavored honey beefs up the black locust honey. Some people can be allergic at its pollen. The fruit of the Russian olive having high vitamin C content (0.33 mg vitamin C / g fruit flesh). It is consumed in Turkey, Persia and Greece as fruit, and it is used for making alcoholic drinks. The taste of fruit is due to the main sugar components (fructose and glucose), just as to the phenolcarbon acids (4-Hydroxybenzoic acid, coffee acid, ferulic acid, benzoic acid, protocatechin acid, vanillin acid and the 4-Hydroxycinnamic acid). The species is widely grown thanks to its edible fruit. Its leaves and flowers are used in vernacu-

lar medicine because of its diuretical and antipyretic effects and its fruit is used as a whet, appetizer in winter. The infusion of the fruit of the Russian olive is proved to have gastric mucous membrane immunizing activity (antiulcerogenic effect) too.

According to observation carried out on mice, the flavonoid components of the Russian olive's seeds cause muscle relaxation, the infusion made from its fruit reducing inflammation in case of acute inflammation and the infusion of seeds is effective in case of chronic inflammation. The different infusions of the Russian olive have antinociceptive effect (work against the algogenic stimulus); they extend the pain limen depending on concentration.

The fruits contain brown paint material, as well as oil that is used as prandial oil (*Oleum sancteum*) on the East. Its wood is of poor quality, flimsy textured, at best used as firewood. Its other beneficial feature is that game do not damage it, its fruits are eaten by birds in autumn and winter time. Root is bushy and bulky, and specifically because of its drought tolerant feature it is used for binding flimsy soil of arid-semiarid areas, that is how it became the typical tree species of sand-afforestation. Because of its low nutrient requirement it was widely used even on lean sandy soils. In turn by right of its salt tolerance it was one of the most often used species in the afforestation of saline lands, in the still afforestable saline soils it was planted together with *Tamarix*-species. By virtue of its nitrogen fixing capability it is often applied on ruderal soil, in erosion control and in recultivational afforestations. Because of its short trunk and bushy branch system it is a beloved and common element of shelter belts, wayside windbreak tracts and lowland forest borders. Owing to its good capability of regeneration it can often be trimmed, so thus it has role in making hedgerows and forming median strips of motorways. It is one of our most city tolerating plant, that tolerates well the polluted air, salting of roads, the drier urban environment, but because of its architectural structure it can be used as a hedge tree, only as a soliter element of greater areas. Its strong pioneer feature (its light-demand, fugitive feature and its strong root concurrency) partly forestalls its usage in the earlier mentioned fields of application, in consequence of that it is not or only slightly able to live together with other woody plant species.

The applicability of the species as biomonitor was tested by the detection of lead, cadmium and zinc from the washed and from the unwashed leaves of the plant. The difference of samples deriving from the washed and unwashed leaves varied accordingly to the metal-contaminations. Significant correlation was found between the heavy metal concentration of the upper layer of the soil and the washed leaves. In virtue of these the Russian olive can be a suitable biomonitor of heavy metal contamination. Its use as a biomonitor is suggested by some authors because it is very tolerant (temperature ranges, type of soil), its leaves are able to accumulate a big quantity of contamination, the measure of the air and soil contamination can be easily separated (by determining the heavy metal content of the unwashed or rather the washed leaves), it is a widespread species or rather it can be identified easily.

NATURE CONSERVATION SIGNIFICANCE

The Russian olive is one of the primarily appearing plant species in the succession of disturbed floodplains and riverbanks in North America, after its sedentation it remains even in the subsequent stage of succession; it becomes dominant in the communities supplanting the native poplar species. According to observations the growth vigour of the Russian olive is more by about 3 times than of the native Green ash. It advanced the propagation of the species that comparing with the native poplar species; it is less damaged by beavers. Because of its adaptive features (drought tolerance, salt tolerance, fast germination, continuous germination in humid terms of vegetation period, symbiotic nitrogen fixation, fast growth and early fruiting) the species is considered to be a factor of the most negative effect that affects the riverside biomes on the south western part of the USA. In America the communities dominated by the Russian olive are generally more unfavourable for animals than how the natural vegetation is. Because of its spread, the willow-beds used as nesting place by endangered birds were retired.

Compared to native tree species, it consumes more water causing diminution of water level that reduces the habitat of rare fish species. Its widespread planting near by roads with heavy traffic can cause high mortality rate among the birds that eat its fruits.

The Russian olive spreads dynamically also in Ukraine, in the Northern region of Black sea. At the beginning the main sources of its running riot were the Russian olive hedges planted by roads, nowadays the Russian olive spreads spontaneously, and it occurs sporadically on the area in form of bigger or smaller substances. In an artificial environment only solitary specimens or smaller alignments can be found, but on near natural habitats it appears on grasslands, open sandy areas, sand-dunes, riverbanks, in pitched abysses, and it can penetrate into the swardy and bushy areas too. On the seaside dunes it can become the dominant species of associations, but in the riverside willow-poplar woods it spreads together with the *Catina rosie* and the Desert false indigo. On this area the Russian olive behaves similarly to weed species, it appears chiefly on the open soil surfaces of disturbed habitats, it can spread significantly on sandy steppes and on open sands, the space it occupies in the tree-layer is 10-50 (70)% and it can reach even 40-80% in the herb layer.

On the concerned areas the rate of sandy and steppe species can be reduced significantly, the proportion of mesophilous species can increase, that is why the Russian olive can be a possible competitive danger to the previous species.

In America (Idaho, Snake River) BROWN (1990) compared the natural alluvial willow forests along rivers with the Russian olive ones: smaller diversity of species, less possibility of nesting and feeding and the absent of insects typified the Russian olive ones. The comparison of fauna of the natural riverside vegetation and the Russian olive ones gave similar results: on the previous habitat 505 specimens, 56 species; on the latter one 458 specimens and 40 species were found; moreover the diversity of birds was far smaller. The beavers privileged the natural willow and poplar species in front of the Russian olive, subserving the persistent staying of the Russian olive woods on the area. In New Mexico some bird species (*Zenaidura macroura*, *Icteria virens*) privileged the Russian olive in front of natural species in the course of nesting.

In Hungary the Russian olive appears primarily on moist meadows, alongside rivers and channels, or rather on saline areas, especially where it has domiciled substances. At the deployment place the Russian olive abides permanently, and thanks to its good capability of regeneration, in case of lesion of top parts, it sprouts from the adventitious buds those regenerated on the roots. Because of its appearance on treeless habitats the light-demanding species takes a back-seat locally and thanks to its nitrogen-fixing bacteria it can subserve the sedentation of nitrofreqent weeds.

The environmental problems caused by the Russian olive can locally be pretty much different in Hungary, but at some places of the country it can be of outstanding importance. In the years of 1930' and 40's on the area of the Fertő-Hanság National Park the Russian olive was planted in shelter belts in between the plough-lands to prevent them from soil deflation and erosion. As the fruit of the Russian olive is consumed by many bird species, the species spread by leaps and bounds, and by the end of the 90's it generated woodlands all over the saline areas. Because of the sweeping changes of habitat caused by the spreading of Russian olive numerous rare and protected species is pushed into the background, for example following the cutting of Russian olive on the National Park's area the number of the *Ophris sphegodes*, that was known to be extinct long before, throve nicely, and the recovery of the habitat proved to be favorable for many orchid species (for example *Orchis morio*, *O. palustris*) too. The presence of Russian olive can cause serious problems in the Kiskunsági National Park too. There it spreads mostly on saline lands. Along saline lakes the presence of the Russian olive's shrubs can assist in the diminution of number of the waterfowls living in that area, namely the nest predator magpie willingly nestle in them, just like other raptorial bird species, which birds consume often the eggs and the nestlings of the waterfowls. On some areas of Hungary the Russian olive does not cause any remarkable environmental problem yet, however its suppression can be necessary even here just for guard.

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COMMON HACKBERRY

(*Celtis occidentalis* L.)

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TAXONOMY

Celtis genus belongs to Ulmaceae family, in which about 150-200 species of 15 genera are categorized. The present-day propagation centers of the family are the tropical and subtropical areas of the Northern hemisphere, particularly in Asia and America. All members of it are woody plants, some of those got to the Northern temperate zone too. The number of species of *Celtis* genus, categorized into Celtidoideae subfamily, is not known exactly, most of the dendrological studies mention 70-80 species, but lately ones presume that around 100 species belong to here. Among the hackberries there are evergreens too, these are all of tropical spread, others are deciduous. Some more curiosity of this genus is that among its species some shrub and liana can be found too, and the branch system of some is thorny. The common hackberry with around 30 of its associate species belongs to *Euceltis* section, all live in the Northern temperate zone. The section (just as the genus too) is badly processed taxonomically and it is hard to distinguish its species from each other. In Europe two hackberry species are native, the European hackberry (is was also know earlier as common hackberry mistakenly) (*C. australis* L. incl. *C. caucasica* WILLD.) that lives in South Europe, North Africa and West Asia and can even reach the 25 m height. The oriental hackberry

TABLE 1 Comparison of the most important characteristics of European hackberry and common hackberry

Characteristic	<i>Celtis australis</i> L.	<i>Celtis occidentalis</i> L.
Height	–20 m	–25 m
Bark	smooth, grey and slightly glistening even when elder	smooth and grey when young and later grayish brown, coarse with bulges and ribs
Canopy	loose, ruptured	dense, compact
Leaf		
blade	thick	thin
tip	long acuminate	acuminate
abaxial surface	greenish grey, permanently hairy	light- or yellowish green, ± bald
Shoot axis	hairy	bald
Perianth (tepals)	usually five-parted	usually six-parted
Fruit		
diameter	8–12 mm	6–10 mm
peduncle	15–30 mm	8–15 mm
husk	slightly striated	smooth
color	violet black	off brown
taste	sweetish	austere
putamen	reticulated surface with small pits	coarse surface with small pits

(*C. tournefortii* LAM. incl. *C. glabrata* STEVEN ex PLANCHON) can be found in South East Europe and in Asia Minor, it is shrub-statured and does not grow higher than 6 meter. Seven *Celtis* species live in North America, of those *Celtis occidentalis* is the most important from sylvicultural point of view.

In the last century, but even in the present time many researchers have mixed up the European hackberry and the common hackberry, the common hackberry was often mentioned as European hackberry. The most significant morphological differences between the two are shown in Table 1. In Hungary the frost-sensitive European hackberry is planted rarely and only in the internal areas (for example Pécs, Buda), where it can escape into the wild sometimes.

Two variants of the common hackberry were described:

var. *pumila* (PURSH) GRAY – the leaf base is specifically asymmetrical, the leaf blade is at most twice longer of its width;

var. *canina* (RAF.) SARG. – the leaf base is barely asymmetrical; the leaf blade is at least twice longer of its width.

MORPHOLOGY

In its native range it can even reach the 30 m; in Hungary usually it does not overtop the 25 meters. Trunk is straight if in close standing commonly traceable even in the treetop. In free-standing the trunk is big, coarse and disintegrates into disordered branches, the lower branches and boughs bag. The boughs, rods of the regularly truncated, trimmed individuals and of the young trees are long elongated, splayed in bows. The bark is smooth and grey while young, later it is grayish brown, coarse laced with bulges and ribs, when elder the bark can crackle too. The root is richly branching, gets into deep, it gets even into 3-6 m of depth, it develops only rarely near surfaced, laterally running rope root. The lateral roots are muddled terminated, hugger-mugger, short and many of them are of downward. The branching system is sympodial. The rod is thin, brown or reddish brown, balding, the base of the leaf petiole is strongly salient, the suberous verrucae are striking and whitish. The pith is small and rounded. The buds are 5-6 mm long, brown, tapered ovoidal, tapering, flat and osculant to the stem, the edge of the bud scale is slightly hairy. Its distinctiveness is that the apex of the apical bud bends strongly sidelong. The position of buds and leaves is alternating. The shoots are of staggered growth, thin, pallid green, balding with partitional pith. The leaves are ovate, 5-10 cm long and 2.5-5 cm broad. The leaf base is rounded, slightly asymmetrical, above the broadest part of leaf the leaf margin is aristately serrated, the tooth are bent forward, the tip of leaf is acuminate. The leaf blade is thin, glistening green above, bald, smooth; the abaxial surface is pallid or yellowish green, sparsely hairy alongside the veins. The leaves are pinnately nervate, the lateral veins bend towards the apex, anastomising, and the lowest vein-pair is more developed than the others. The petiole is 1-2 cm long, sparsely hairy, its stipules drop off early. Its autumnal foliage coloration is yellow.

The flowers are polygamous, unisexuals or hermaphrodites, axillary, the male flowers are located on the lower part of young shoots, the hermaphrodite flowers can be found singly on the upper part of shoot. The peduncle of the flowers are long, the perianth is green, mostly of six \pm free tepals. The number of the stamens is equal with the number of the tepals. Stigma it have two, big, deeply segmented, back folding and thickly haired. Its drupes commonly stand solely, the fruit peduncle is talk is 8-15 mm long, the fruit is of 6-10 mm of diameter, the fruit husk is orange, then off brown when mature, the episperm is thin and of austere taste, the putamen is rounded, the ends are tapering, yellowish white colored, its surface is coarse with small pits. (Table 1.)

ORIGIN, DISTRIBUTION

Celtis occidentalis is native in the Eastern part of North America. Northern border of its distribution is traced out by the 45° of latitude, the southern border by the 35° of latitude and the western border by the 115° of longitude. More north of this, it appears on the south eastern part of Wyoming and north

eastern part of Colorado too, and on the north it spreads up nearly till Winnipeg Lake and its area spreads over the Great Lakes region too. It is much harder to determine the Southern border of its distribution, as its area overlaps with *Celtis laevigata* WILLD. (sugarberry), and from here only few unambiguous data of its occurrence is available. Within its natural distribution area it is chiefly a tree of flat countries, where on the deep top soiled alluvium of floodplains it associates with other hard leaved species (for example *Ulmus americana*, *Fraxinus pennsylvanica*, *Acer saccharinum*, *Quercus* spp.), it seldom forms unmixed stands. It can even be found on the north eastern part of the area particularly on the spur of limestone mountains, but here it is mostly of shrub form. In Central Eastern Kentucky it is one of the dominant tree species of the upper tree-layer together with the *Ulmus alata*, *U. rubra*, *Acer rubrum*, *Asimina triloba*, *Carpinus caroliniana* and *Carya ovata*, while in the lower layer the members of the *Fraxinus*, or rather of the *Ulmus* genus as well as the *Acer rubrum* occur dominantly. In the 1930's the common hackberry became a dominant tree species of the secondary forests in the State of New York, where the most important associating species are the *Prunus serotina*, *Sassafras albidum* and the *Quercus palustris*. In Illinois seedlings of the common hackberry can be found even in the lower layer of stands surmounted by the *Quercus muhlenbergii*. In parkland forests of Missouri in absence of larger disturbance (flood, overflow) *Celtis occidentalis* shows up also, together with the following species: *Fraxinus pennsylvanica*, *Carya cordiformis*.

In Europe, it was first brought in England in 1636, we have no knowledge regarding the time of its first appearance in Hungary, but at a guess it could be in the first half of the 19th century.

LIFE CYCLE

It grows fast while young. The early development of seedlings strongly depends on the environmental factors. Usually the annual height growth of a seedling developing under a dense treetop does not overtop the 2.5 cm; the average annual growth of a planted seedling in the first 6 years is 40 cm. On a suitable soil the growth in diameter of the hackberry can even be 8 mm, but commonly it is less than that. On a nutrient-poor soil it grows slowly and the individuals often remain pint-sized. Usually it is a small or medium sized tree. When full-grown, its height is 9-25 m, diameter is 45-60 cm, but on a habitat that is really favorable for the common hackberry it can reach the 39 meter of height and the 122 cm of diameter. The species roots deeply, its root can even reach the 3-6 meter of depth. On loam the lateral expansion of root is rather more remarkable; in some cases the lateral growth of roots can reach even the 12.6 meter, till the growth of depth still only 1.4 meter. The maximal age of the common hackberry is 150-200 years. It blossoms following the frondescence, usually in April or May. The fruits ripen in September-October, but remain on the tree even in winter time. Usually it yields richly, in 1 kg 8300-12 500 pieces of putamen can be found, its seed weight is 80-120 g/1000 seeds. Its germination is epigeal. According to examinations carried out in Indiana following a one year-long storage of seeds in leaf-litter 34% of them germinated, while following the storage of seeds throughout two winters the germination ratio was 20%. The fruits are dispersed by birds and small mammals, but it can be dispersed even by water. The consumption of seeds by animals can occasionally worsens the germination ratio: the germination ratio of seeds was significantly lower following the consumption of putamens by raccoons than in case of the untouched fruits. In Iowa the sedentation of seedling was observed in hardwood forests, whereas in a latter stage of the succession, in grassland communities the species was not able to settle down successfully. In Pennsylvania seedlings of the common hackberry were found even on those bushy, shady habitats, where the seeds of others species were not able to germinate.

In MCKENZIE'S (2000) opinion the common hackberry tolerates well the storm, snow, ice and wind, but contrary to this, according to the results of an examination, carried out in Urbana (Illinois), that was set up to estimate the damages caused by a hailstorm on 25 alley trees in a park, the common hackberry was between the most seriously damaged species, 8.8% of the individuals of the species were damaged in some way. The reason of damage can be originated in the type of branching system of treetop and the densely located tiny branches. The species is sensitive to the fire; many pathogens can infect the plant following the impairment.

HABITAT PREFERENCE

The common hackberry is able to adapt to a wide range of climatic factors. In North America, within its natural distribution the annual fall varies between 360 and 1520 mm. In point of temperature it also has wide ecological tolerance, it endures even the temperature oscillation of 60 °C, within its natural area the number of frost free days are 120-250 days. Thanks to its drought tolerance it can even survive the extraordinarily dry periods. The permanently high soil water level is unfavourable for the species, but the periodical inundation markedly causes no damage. It was observed in Kentucky that the 46 days-long inundation in the vegetation period did not harm the common hackberry, but following a 110 days-long inundation the symptoms of ailment started to show up on the individuals. The species often survive an inundation during the vegetation period, but usually in the second or the following one it perishes. In Illinois a permanent inundation of 90 cm of depth ruined the individuals previous to the supervention of the fourth year, in mud, or rather in paddle 70% of trees perish by the end of the sixth year. The seedlings are even more sensitive to inundation than the full-grown trees; even a short-term water cover can kill the majority of seedlings. In its native range it is chiefly a desert tree, it develops on the deep alluvial soil of river valleys, but on the north east it can even be found on the spurs of limestone mountains. It develops the best on eutrophic, humid soil, but regarding the soil's texture it subsists on many different kind of soil, on sandy, clay and loam soils too, the soil preferred by the species is varies between 6-8 pH.

We can find many references in silvicultural literature regarding the habitat requirements of the common hackberry. In Hungary the matter about the deployment of the common hackberry arose already at the beginning of the 1900's. PÉCH (1903) suggests the deployment of species in two planting zone: the first planting zone contains the North Western Plain Region and the Hungarian Great Plain, till the 200 m of elevation. The following climatic conditions are typical of the first planting zone: the annual average temperature is 9-10 °C, the average temperature of the growing season is 19 °C, the annual average precipitation is 500 mm, the relative humidity for air is 73% and the lowest temperature is -23 °C. The second planting zone is till the elevation of 300 m and contains the undulating countryside surrounding the Hungarian Great Plain. Its climatic conditions are the following: the annual average temperature is 10-12 °C, the average temperature of the growing season is 18-25 °C, the annual average precipitation is 700 mm, the relative humidity for air is 74% and the lowest temperature is -27,4 °C.

AJTAY (1931) found untouched common hackberry next to a black locust that was languishing on the low-grade sand soil in his own wood, on the border of Szentmártonkáta township, that is why he has suggested the deployment of the common hackberry into the lower level of the black locust woods of the Great Plain. He suggests planting the common hackberry chiefly at deeper positions on whitish grey colored, loamy sand soils, in his opinion the species can even be deployed onto „the most low-graded soil”. BABOS (1957) suggests planting the common hackberry also into the lower levels of the black locust woods in order to protect the soil.

KISS (1920) notes commenting the matter of the afforestation of the Hungarian Great Plain that the common hackberry is 60-80 years old, very nice specimens can be found on sand, at favorable place with excellent development. Near by elder trees, or rather in a distance of 3-4 km of them naturally renewed individuals can be observed.

SZÓNYI (1957) considers the presence of hackberry in the lower tree-layer to be indispensable in the afforestation of sand in Hungary, as in his opinion it tolerates better the poor, run-down habitats than the Hungarian species. He notes that hackberry in the lower layer of the native Grey poplar woods forms closed layer on sand soils containing some loam too. He suggests the deployment of the hackberry into the lower layer and together with the black cherry (*Prunus serotina*), onto the undulatory surfaced veil-sand of the sand ridges of the Duna-Tisza Interfluve, or maybe onto brown forest or meadow soils under a thin veil-sand overlay, or rather onto their combination. He recommends the deployment of the hackberry from seeds or seedlings into the lower level of the black locust, scotch pine and black pine plantations on the plains of the sand-ridges of the Duna-Tisza Interfluve.

MAGYAR (1960) in his „Alföldfásítás” titled study summarizes the habitat requirement of the common hackberry as follows: the tree species requires mild climate, tolerates well the warm summer, but tolerates with difficulty the too harsh winter. It develops optimally in case of sunny, warm exposure, on eutrophic, loose soil of good water regime, but subsists on dry, sandy or pebbly soil too. It tolerates quite well the shading especially while young, but at elder age it becomes light-demanding. It develops well on calcareous and acid sand, and it abides on the drier sand hillocks too.

BIOTIC INTERACTIONS

Of the diseases of common hackberry caused by viruses the so called „Island chlorosis” is well known, that appears on leaves (= yellow islands in a sea of green) as yellow spots. Beside the virus, the following fungi can cause leaf patchiness too: *Cercospora spegazzinii*, *Cylindrosporium defoliatum*, *Cercospora celtidis*, *Mycosphaerella maculiformis*, *Phleospora celtidis*, *Phyllosticta celtidis*, and *Septogloeum celtidis*. The most common disease of species caused partly by fungus is the so called witches'-brooms. The phenomenon is ascribed to the joint effect of two factors: a powdery mildew fungus (*Sphaerotheca phytophila*) and a mite (*Eriophyes celtis*). According to the observations it is quite likely that the mite induces the broom formation and then the fungus penetrates into the deformed buds, as a result of that appear the broom-like growth. On bigger trees even a few hundreds of brooms can evolve without lessening appreciably the vitality of tree. The presence of brooms chiefly busts up aesthetically the appearance of the tree, especially in winter time when the foliage is missing. The trees planted in parks, on walkways, in open areas can get damaged more often and more seriously, than the ones in forests. The *Celtis* genus is less sensitive to the Dutch elm disease (*Ophiostoma ulmi*) caused also by fungus than the *Ulmus*; and as to *Celtis occidentalis* it is fully resistant, that is why the common hackberry is commonly recommended to use in park or alley. Of the basidiomycete fungi, the occurrence of the brown rot agent *Armillariella mellea* was observed on the root of the common hackberry. The common hackberry in association with symbiotic fungi forms ectomycorrhizae.

In Hungary for a long while it had no any notable insect pest, but in the last years the occurrence of the polyphagous oystershell scale (*Lepidosaphes ulmi*) was observed on it, that among others appears on hawthorn, apple, willow, poplar, black locust, lilac, linden and sorb too. Occasionally leaf mites can harm it too; those can cause serious leaf loss already by the middle of summer. The nettle-tree butterfly (*Libythea celtis*), earlier better known only in South Europe, have been spread towards north thanks to its host plants, *Celtis occidentalis* and the *C. australis*. The butterfly species, protected in Hungary, was observed in Slovakia already from 1950. The common hackberry is a host plant of four gall-forming insects: *Pachysylla celtidismamma*, *P. celtidigemma*, *P. celtidivescula*, *P. venusta*. They cause no serious harm. The *Pachysylla celtidismamma* causes swelling, warty gall on the abaxial surface of leaves. The common hackberry is its only known host plant. The disease is very common; most of the trees are infected, although its presence usually affects only few branches, thus it does not cause serious harms in the tree's vitality, rather spoils only the aesthetical appearance of the tree. In case of serious infection the leaves can get deformed. The *Psyllaephagus pachysyllae* wasp species, parasite of *Pachysylla celtidismamma*, often sets back the population of the gall-forming insect. The gall making insect is a nourishment of many permanent and migratory bird. The *Pachysylla celtidigemma* causes the hypertrophy of the bud that pods up spherically and perishes. The *Pachysylla celtidivescula* forms small bulging blisters on the abaxial surface. Other *Pachysylla* species form small blister-like galls on the bark of the young branches. Linkage in the nourishment of three Homoptera species (*Hemiberlesia diffinis*, *Icerya purchasi*, and *Morganella cueroensis* in Texas and of one butterfly species (*Malacosoma americana*) in Virginia was observed to the common hackberry. The *Scolytus muticus* wood-beetle normally appears only on dead or dying branches. From Colorado many insect species are known that feeds upon the species of the *Celtis* genus: the undeveloped individuals of the *Chrysobothris femorata* make tunnels under the bark, on the trunk and on the bigger branches. Above the wound bigger bark parts can undergo necrosis, thus the presence of the insects weaken the tree. The lesion primarily affects the sunlit side, later it spreads on other parts too. The full-grown individuals of the *Corythucha* species, those having multiple host plant (oak and ash species) are

sucking on the abaxial surface of the leaf, by that they can turn the foliage yellow and brown. The larvae of the *Asterocampa celtis* consume the leaves too. The *Archips argyrospila* can appear on numerous hardwoods, its larvae can cause serious leaf-losses by the chewing of the leaves. They can damage the fruits too, those drops off and strains earlier so. The gathering feeding larvae of the *Nymphalis antiopa* can also cause defoliation, just as the full-grown individuals of the *Epicauta fabricii*, however both of these insects have numerous host plant aside from the common hackberry.

Of the vertebrates the presence of the common hackberry can be exceedingly important for the birds, as in winter time the species that winter in Hungary and the birds coming from the North consume the common hackberry's crops with pleasure. In Hungarian authors' opinion the crop of the common hackberry is many bird's winter nourishment, it is visited by troops of fieldfare and bohemian waxwing, just as by hawfinches, but rooks, blackbirds and tree sparrows has been observed to feed on it too, moreover the fruit of the hackberry was even found in the winter defecation of the marten. In Central Europe 16 bird species consume the fruit of the *Celtis* species, this compared to other not native tree or shrub species is a relatively high number. The harsh, coarse and early appearing bark tiles of the common hackberry protect them against the deer stripping, however the rabbits and the fawns can harm the young individuals. In the stands of plain among the nourishment plants of the red deer beside the black locust and the common elderberry, the common hackberry is listed too.

Compounds of allelopathic effect of the common hackberry are known, those belong to the tannins (triterpenoid-saponin) and to the phenoloids (tannins, phenol acids, flavonoids).

ECONOMIC IMPORTANCE

The common hackberry is the most often used tree in allies, but it can be planted as a soliter too. It is fast growing while young, tolerates well the dry, warm and polluted air of cities, sustains the salting of roads and due to its excellent regenerating capacity it tolerates the mutilation of root, the lesion of bark, the mutilation of treetop and the regular trimming. Its disadvantage is that the branches bend down disturbing the traffic, so it needs to be trimmed regularly.

Its timber is similar to *Ulmus*, its stodgy, hard and tough, the core is greenish brown, the narrow alburnum is greenish yellow. Its timber is not utilised in Hungary, at the most it is sold as firewood.

In the middle of last century because of its shading and big amount of dead fallen leaves it has been interspersed into poplar, Scots pine, black pine and black locust plantations. After the black cherry, the common hackberry is the second most important tree in the formation of the lower tree-layer. Nowadays it is only rarely planted in forest plantations, or not willingly. Partly its utilization of this purpose is forestalled by the fact, that it is not as undemanding of the habitat as it was presumed earlier.

The fruit of the species has austere flesh, it is suitable for human consumption, sweets are made from it in South Tirol. The pollen can cause allergy.

NATURE CONSERVATION SIGNIFICANCE

In UDVARDY's (1997) opinion around Budapest the common hackberry is the most common adventive species after the Tree-of-Heaven and the boxelder. The spreading of the species can primarily be observed on sites, where it was planted as park tree, alley tree or with sylvicultural purpose, and from here by birds' mediation it could easily settle down even on dry habitats, as it can be observed on the sand of the Kiskunság. The scale of its spreading on the floodplains for the time being is not so intense, as it is of the boxelder or of the desert false indigo, that is why the conservationist maintenance that concerns solely the common hackberry is not much common, moreover at many places they do not make anything against it because of the protected nettle-tree butterfly (*Libythea celtis*) that lives on the tree.

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WILD CUCUMBER

(*Echinocystis lobata* TORR. et GRAY)

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TAXONOMY

Scientific name: *Echinocystis lobata* (MICHX.) TORREY et A. GRAY, synonymous names: *Echinocystis echinata* (MUHL. ex WLLD.) BRITT., STERNS et POGGENB., *Echinocystis echinata* (MUEHL.) VASS., *Echinocystis oregana* (TORR. ex S. WATS.) COGN. Name at the time of its description: *Sicyos lobata* MICHX. Common names: wild cucumber, prickly cucumber, wild balsam apple, wild cucumber vine, mock-apple, wild mock cucumber. The names containing “burr” cucumber and with similar adjectives official concern to the *Sicyos* genus but at the same time the “wild” cucumber also means the species of the *Marah* genus. Other common name: creeping Jenny.

The wild cucumber belongs to the family of the cucurbits family (Cucurbitaceae JUSS.) which has 120 genera and 800-900 species mostly in the tropics and subtropics. In Europe only *Bryonia* and *Ecballium* genera are indigenous. The family of cucurbits in Hungary is represented by ten genera with six species living as wild – the two native *Bryonia* species and four adventives – moreover by nine cultivated species. *Echinocystis* genus inside the family belongs to the Cucurbitoideae KOSTEL. subfamily and on the base of its acinaceous, polycorporate pollens and the erecting ovule classified – with *Cyclanthera* and *Marah* – into Cyclanthereae SCHRAD. tribe. Earlier it was mentioned as member of Cyclantherinae C. JEFFREY subtribe of Sicyoeae SCHRAD. tribe. In this interpretation *Echinocystis* TORR. et A. GRAY genus is monotypic with *Echinocystis lobata* species. (Along the 19th century it was classified as member of *Micrampelis* RAF., *Hexameria* TORREY et A. GRAY, *Megarrhiza* TORR. et GRAY, *Echinopodon* NAUD., *Marah* KELLOGG genera, therefore these are reckoned as synonyms of *Echinocystis* genus in the case of *Echinocystis lobata*.)

Generally it can be accounted as well differentiated, less hybridizable, stable species with normal generative propagation. In Romania was described the hybrid of *Sicyos angulatus* and *Echinocystis lobata*, the *Echinosicyos cibiensis* KAMNER et TOPA (1952).

Similar species: most similar to the wild cucumber is the also North American originating *Sicyos angulatus* L., the star cucumber but that has barely aristate and less deep lobes on its leaves, hairy stem, the carpellate flowers standing in heads and therefore the fruits also develop in groups, further the fruits are single seeds with long spike and smaller than the fruits of the wild cucumber, the maximal length is 1.5 cm. Without comparative sample the first wild cucumber specimens of the Carpathian Basin were described as star cucumber. The star cucumber live on the same types of habitats as the wild cucumber, it is a rare alien species (Miskolc, Sopron, Kőszeg, Tiszántúl, Nyírség?). The look of the two native bryony species (*Bryonia alba*, *B. dioica*) can be similar in vegetative phase but the fruits of these are berries.

The rare, Mediterranean originating *Ecballium elaterium* (L.) RICH., squirting cucumber has a somewhat similar flower structure and shape of leaves and fruits, but it has no tendrils and it is perennial. Also a bit like is the North American perennial, hypogeically germinating species of the *Marah* KELL. genus with wide pinnae of corolla 5 (-8), which do not exist in Hungary.

MORPHOLOGY

The wild cucumber is climbing plant as high as 7–8 meters with slim stem, which is hairy only at the nodes. The 5–8 (–15) cm long leaves have long peduncule, (three-) five (-seven) long pointed lobes, cordate base, the leaf blade is palmate, thin, almost bare with entire margin. According to its growth form the plant belongs to the smilacoid group: it creeps with the mostly three-forked tendrils, growing from the leaf axils – belike originating from stipules maybe from the stem – which able to move finely. At one node are four tendrils. The creeping is explainable with the sensitivity of the tendrils for touch: at the point of the touch the growth of the tendril slow down and speed up on the opposite side and therefore the tendril convolve like a spring and ring about the touched stem. After its fixation the axis of the tendril straighten and become stronger, thereby the stem of the wild cucumber will be kept away from the supporting plant.

The plant is monoecious. The staminate flowers are small, white and standing in compound racemes at the leaf axils. One raceme is built up by 20–100 flowers. The carpellate flowers are generally alone or in small group standing at the axil of leaves or tendrils, with short peduncule.

The sepals and petals are fused to a short tube, the petals deeply five or most frequently six narrow lanceolate pinnated in both sexes, its color is green-white. The pinnae of the petals are in average 5 (3–6) mm long and 1 mm wide. The number of stamens is five, the filaments are coalescent, and the pollens are polycolporate. In the carpellate flowers are no nectaries, the ovary is densely setaceous hairy. In the ovary two placentae sit in the most cases with two seedbud in each. The fruit is juicy and fleshy when young, drying out when ripen, filled with seeds and texture of the vascular bundles. When ripe it is 3.5–5 cm long, globular-oval or lengthy- cylindrical shape. The fruit has two cells with soft and thin wall, its surface is densely soft echinate. Inside generally can be found four flattish seeds with brown or black testa. Often develop 1, 2, 3, or 5 seeds in the fruit: the proportion of the non four-seeded fruits exceed the 50%. If the number of the seeds is less than four the white, empty testa often can be found without developed tissues inside. The weight of the seeds does not differ in the non four-seeded fruits from the normal significantly on the base of our examinations. The length of the seeds is between 1.3 and 2.2 cm, the average is 1.5 cm, the width is 0.6–1.1 cm, the thickness 0.2–0.4 cm. The weight of thousand seeds is between 256.8–293.0 g, the specific gravity 1.0847–1.0979 g/cm³ that is a bit more than of the water. The fruit open irregularly, beginning near the top and the time it lose its outer wall, in winter usually only the fibrillated mesocarp (middle fruit wall) can be seen. After ripening, at the base can form a fissure and through it some of the ripe seeds can fall out. The seeds falling out make possible unspecific (gravitational) spreading as germinate near the place of the development. Some of the seeds stay in the fruit and spread by hydrochory. The fleshy cotyledons are rich in oily storing tissues. The endosperm undergoes special cytological, physiological and molecular conversions (apoptosis) along of which the nutritive tissues totally degrade.

Number of chromosomes: $2n = 32$.

ORIGIN, DISTRIBUTION

Its native range is North-East America where the distribution area lies between the 35° and 53° degrees of Northern latitude and from the coast of the Atlantic Ocean to the 110° degree of Western longitude so it is indigenous beyond the United States in the Southern part of Canada. Moreover the plant has sporadic occurrences more westward where probably ergasiophygyte (i.e. originate from gardens or other plant collections). In its original area and also in Europe only to North from the 0°C degree isotherm of January were able to produce extending populations. The first individual of the Carpathian Basin and at the same time of Europe were documented – as collected herbarium specimen – by GUSZTÁV MOESZ at 1st of August in 1904 south to Brassó, near Derestyé in the Tömös Cove. The first specimens because of the lack of comparing specimens often were identified as *Sicyos angulatus* (MOESZ's data were revised by JÁVORKA and he published it in 1937). RAPAICS found it at Debrecen-Pallag already in 1913 but defined and published it in 1916 as star cucumber too. This false *Sicyos* data were inherited by other authors (BOROS 1932, SOÓ & JÁVORKA 1951). The specimens from Pallag definitely escaped from botanical gar-

den as it was assumed by RAPAICS too (but about the star cucumber of course). The early Hungarian data for a long time were unknown to the botanists of Central Europe therefore many author thought the advent of the species to Europe happened in the first part of the 1920's on the base of the current observations (Austria, Steyermark, Fürstenfeld, willow forest along brook, with hop, A. HEINRICH's observations, from 1920, published by K. FRITSCH in 1923). The consequence of the aggressive spreading of the sporadically occurring (data from herbaria: LOVASSY: Keszthely, VERA CSAPODY: Dunaharaszti, from 1924, respectively from 1925) or not identified wild cucumber was in the end of the 1920's and in the 1930's was collected or published data about it from more and more spots: GLATZ: Keszthely-Fenékpuszta, MARGITAI: Bereg County, Déda, HÉJJAS: Somogy, Csurgó, JÁVORKA: Szentgotthárd, Rába, VERA CSAPODY: Szigetszentmiklós, SOÓ: Nyírség (Bátorliget), Mátra, etc. As a plant spreading with hydrochory, easy to follow its sweep along the rivers as one case was published by PRISZTER: along the Austrian River Lafnitz it was spread between 1920 and 1925 (maybe imported with bales of cotton). Along the River Rába occurred in 1936 at Szentgotthárd, in 1938 at Rábagyarmat and Csákánydoroszló, in 1939 Körmend and in 1949 Vasvár. On account of the fast spreading for the 50's – on the base of the more hundred floristic data collected by PRISZTER (1955, 1958) – it appears as naturalized species in the Western and South-Western part of the Transdanubia moreover in the Hungarian Mountains (listed and illustrated on maps by PRISZTER, 1958). The distribution area in this time bisected Hungary in South-West – North-East direction. Out of the about 500 km long and 50-60 km wide belt at that time only few occurrence were known (Hungarian Great Plain, Nyírség, Tiszántúl). For 1960 some new localities became known: Bükk-Torna Karst Region, around the Lake Balaton also on the southern side, Baranya County, around numerous settlements of the Mátra Mountains, on the Mezőföld and at more places in the Tolna-Baranya Hills. It was found in the Kőszeg Mountains. PRISZTER denoted it from more countries of Europe in 1955: Czechoslovakia, Romania, East Austria, Sudetenland, Germany, and Switzerland. After few years the additional spreading of the species was observed in Austria, furthermore the presence in Carpathian Ukraine and Croatia assumed by PRISZTER were proved too. The publication of SLAVÍK and LHOTSKÁ described the situation around 1967 shows it presented in Central Europe in Germany, on the areas of the former Yugoslavia and Czechoslovakia, in Austria, in Romania, in Switzerland, in the Western part of the Soviet Union and in Hungary. The centre of the distribution at that time was still in Hungary.

Nowadays it presents in all Hungary and rare only in the North-Western Plain Region and in the Southern part of the Duna-Tisza Interfluve. The large-scale distribution over Europe is determined by the climatic circumstances – as in its native land. No or only exceptionally present on areas where the average temperature of January is not between 0 and 5°C degrees below zero. (The mentioned mean temperature of January in Europe is „associated” with 500–1000 mm annual precipitation and 18–25°C average temperature in June). On the base of the analysis of the isotherms of January the Atlantic, Mediterranean, boreal and subboreal, moreover the extremely continental areas of Europe are out of the potential distribution area of the wild cucumber. Geographically this area includes „Central Europe” in its widest interpretation from Germany over Austria, Bohemia, Slovakia and Poland to Transylvania. It touches the Northern part of the Balkan and the Southern Baltic states also. The newer data with remarkable importance originate from these Northern, Southern and Eastern border areas for example from Lithuania and Ukraine. The wild cucumber can occur anywhere in its secondary European distribution area where the local conditions make it possible.

Summarizing the data, the European distribution of *Echinocystis lobata* surely began on the area of Austro-Hungary in the beginning of the 20th century. Its importation could happen by two ways: accidentally with cotton transports as well as it was planted advisedly as ornamental plant and after that by escaping. It is possible in the early phase of the invasion both of them played role. But along the 1920's and 1930's more probably it was spread over the area as ornamental plant used at numerous locations, far away from each other, in hydrologically isolated areas. From these multiplied centers started to expand by natural ways and the invasion was rapid along the streams. The limit of the distribution in the South and West is determined by the 0°C isotherm of the average temperature in January – as in its native land. Considerable spreading is calculable Northward but the centre of its distribution for the present will remain the Pannonicum flora province.

LIFE CYCLE

Its life form is summer annual, its lifetime is about 130 days in the vegetation period, generally from May to October. The growth of the plants from the germination shows sigmoid curve. The exponential phase begins about at the 60th day when the plants start to branch richly. About on the 93rd day the exponential phase is ending and the fruit forming reach its summit.

The flowering begins in a relatively late phase of the life between July and September. At first the flowers near to the apex open and the flowering extends basipetally backward. The staminate inflorescences open earlier (proterandry) and in larger numbers than the carpellate ones. The summit of the staminate flowering is about at the 79th day of the lifetime whereas in the case of the carpellate flowers it is at the 93rd day. The staminate inflorescences open alone or sometimes double at the nodes. In the inflorescence during two-three weeks possible to find opened flowers. The carpellate flowers do not form inflorescences but opens alone or double at the nodes. Seldom, the third flower may open, if earlier at that place died a flower. In the beginning of the flowering on the individuals almost exclusively only staminate inflorescences exist and at the end of the flowering the number of the staminate inflorescences and carpellate flowers are about equal. The pollination can be autogamic but the characteristic is the entomophilous type. The pollinators represent very diversified groups of insects: Bees: Apidae (Apinae): *Apis mellifera*, Anthophoridae (Eucerini): *Melissodes bimaculata*, Halictidae (Halictinae): *LasioGLOSSUM versatus*. Wasps: Sphecidae (Larrinae): *Tachytes distinctus*, Tiphiidae: *Myzinum quinquecincta*, Scoliidae: *Scolia bicincta*. Flies: Syrphidae: *Allograpta obliqua*, *Eupeodes americanus*, *Milesia virginensis*, *Syrpita pipiens*, *Syrphus ribesii*, *Toxomerus geminatus*, *T. marginatus*, Sarcophagidae: *Ravinia stimulans*, Calliphoridae: *Lucilia sericata*, *Phormia regina*, Muscidae: *Musca domestica*, *Neomyia cornicina*, Anthomyiidae: *Anthomyia acra*, *A. leucoprocta* (*A. leucostoma*). The list above have reference to the United States but – in the absence of local data – it is assumable these insects can be the primary pollinators of the wild cucumber in Hungary too. The carpellate flowers may bring full size fruit in 14 days after the end of flowering. The fruits contain one-six seeds, most often four. The seeds fall out when the fruit dries. The pericarp opens at its distal end. The seeds fall out only after four-six weeks after the end of flowering. The accidental loss of fruit – except for the effect of seed predators – may have two reasons: some nodes do not yield carpellate flowers or some of the flowers do not develop into fruit. In the case of larger plants the loss of fruit is rarer in this way.

The seeds and fruits can spread by two major ways, the seeds fall out and germinate near the mother plant (gravitational) but it can be spread by water (hydrochory) too. The latter can happen by two modes: the seeds fall out and because of their specific gravity which is close to those of water but slightly larger – in the case of a flood touching the habitat – will spread under the water or stay in the fibrous wall of the fruit and float on the water. Probably both of these hydrochor dispersal modes can reach great distances. Over the mentioned above are some notes about the dynamochor opening of the fruits, which report initial speed higher than 11.5 m/s. In this case – opposite to the squirting cucumber – the seeds leave the fruit at its distal end. Some rodents may collect the seeds as reserve.

The fresh ripe seeds are in deep dormancy. On the base of TTC tests the large proportion (85-95%) of the seeds is vital. The fail of the germination therefore can not be the result of the low vitality but the deep dormancy. The seeds of the ripe (brown colored) capsules germinate in higher proportion than seeds originating from the unripe (green colored) capsules. The after-ripening and the dormancy can extend from two weeks to six months. Coherently the seeds collected earlier (one-two year old) will germinate successfully after two weeks in moist, granulose peat but the fresh seeds need five months to start germination. Under moist conditions in low temperature (5–10 °C) the stratification loosen the dormancy of the seeds after 3-6 weeks. According to newer investigations the really low temperature – 18°C below zero or lower – under dry circumstances stabilizes the dormancy. The extraction of the testa increases the degree of germination about by 50% which – taking into consideration that the watery extract of the testa of the wild cucumber delay the germination of some test species – indicate the germination inhibiting agents at least partly localized in the testa. If the inner conditions of the germination are given, under moist conditions the germination can start already at 5–10 °C degrees so the overwintered seeds germi-

nate well under open ground places in the next spring. In moist and cool medium the enzymes necessary for the germination become active moreover the level of juvenile hormone also increases. The germination is epigeic so the cotyledons above the soil take part in the feeding of the seedling.

HABITAT PREFERENCE

It is a lowland-mountain species. Frequent primarily along rivers and streams on nutrient rich and calciferous, wet-moist soils or with variably water supply, slightly acidic, humic, alluvial, deposit, clay or loam soils. It can be observed in alluvial forests and weed associations on wetlands, along ditches, canals and roads in ruderal communities or in stoop-crop growings. Sometimes it is mass producer in badly treated gardens. Tolerate and show degradation with low or medium demand for nitrogen. Halophobic, seldom occurs on saline or alkaline soils. In the vegetation period not tolerate well the inundations; the stem can die in this case.

On its original distribution area the annual precipitation is (400–) 500–1000 (–1500) mm, the mean temperature in June is 17–25°C, in January between +1 and -21°C degrees. The low temperature in the winter is necessary to loosen the dormancy of the seeds. In its invasive distribution area these values are about similar except for the mean temperature in January what is between 0 and -5°C degrees. The wild cucumber is able to endure the temperature below 0 C° only as seeds. The seeds freshly ripe at the end of September probably are dormant because around October the temperature makes possible the coming up of the seedlings and after it the young plants would die in the hard winter. The seedlings occurring in the spring are light demanding but the bushes and trees in this time not shadow too strongly. The developed plants also do not tolerate the lack of light, and in overgrown position their growth stops.

BIOTIC INTERACTIONS

Allelopathy, competition

The extract of its seed and testa have allelopathic effect but this is short term and under natural conditions insignificant.

Because the wild cucumber is a climbing plant it can overgrow the supporting plants – primarily in developed size. In the floodplain of the Lower Tisza often occurs together with the also invasive riverbank grape (*Vitis riparia*). Despite of its similar growth form, because of the different life form the Fox-rule is not effectual, namely permanent coexistence evolves between the two species. But presumably in longer term the perennial riverbank grape could have advances against the wild cucumber which however can colonize better the accidentally, but in riverside areas often occurring gaps of the vegetation. Conceivably similar competition evolves between the wild cucumber and the indigenous wild grape (*Vitis vinifera* subsp. *sylvestris*) too. But – as it is experienced – the Fox-rule is effective in the relation of the two vine species. The growth form pretty rare in the Hungarian flora put on that question is any native homologous species, which is crowded out by the wild cucumber? Probably there is no such species (the *Bryonia* species are shadow tolerants and seldom run over the canopy) so the wild cucumber filled an “empty” niche.

Parasites

Observation of any plant-parasitic activity in relation attacking the wild cucumber is not known. In floodplains *Cuscuta lupuliformis*, *C. campestris*, or *C. europaea* are the probable candidates for this. The phytomelan content of the testa adumbrates broomrape-resistance.

Herbivores

About the pests of the wild cucumber in Hungary was published data in non-, or hardly available places. The most useful data originate from the United States but most of them concern even more to the cultivated genera of the Cucurbitaceae family. As the following pests have wide host range and primarily feed on the vegetative parts of the plants very likely feed on the wild cucumber too.

Among the insects the cucumber beetles, *Acalymma vittatum* and *Diobrotica undecimpunctata howardi* (Coleoptera: Chrysomelidae) worth to mention. The plant is not harmed primarily by chewing but because of the propagated bacterial infections (for example *Erwinia tracheiphila*, see later). The connection is so close this bacterium can overwinter only in these beetles. The indirect harm of the beetles in North America is so considerable that along the traditional chemical treatments the biological defense is also subject of intense researches. In this warfare among others the endopathogen nematodes can be good agents (for example *Steinernema riobravise* (*Rhabditus*: Steinernematidae)). Despite of that the above mentioned cucumber beetles are relatively host specific to the cucurbits, because of the vector specificities – and because infect the cultivated species too – their use in the biological control of the wild cucumber is better not to try.

The primary impairing effect of the whiteflies (Homoptera: Aleyrodidae) and plant-lice (Homoptera: Aphididae) is these pierce the leaves and suck humors there. Consequently the plants weaken, the growth rate decrease, the leaves can be chlorotic, fall early and the plant die. Secondary harms accrue from the excreted honey-dew on the surface of the plant which can be breeding-ground for bacteria and fungi and the beetles also can be vectors of viruses. *Bemisia argentifolii* and *Bemisia tabaci* whitefly species affect all of the cultivated cucurbits. The whitefly have very low host specificity: the first have more than 500 known host plant from very variable angiosperm families. *Trialeurodes vaporariorum* whitefly species mostly in greenhouses cause great economical losses. Like the above treated species this also has wide host spectrum and - beside others - all of the cultivated cucurbits are its feed plants. *Aphis gossypii* melon- or cotton leaf louse has exceptionally wide food spectrum, it affects mono- and dicotyledonous plants equally. Its exceptional proliferation and the signs of its hurt are well known. *Aphis gossypii* is known as vector of more than 50 viruses. This plant-lice is cosmopolitan and native in Hungary too. If the chance is given beyond the numerous species of the Cucurbitaceae naturally attacks the wild cucumber too.

The harm of the trips (Thysanoptera: Thripidae) soon after the occurring evolves. The larvae and the imagoes suck in groups on the leaves near the veins, on the stem mostly on or near the apex moreover on the flowers and the developing fruits. The feeding causes deformations. *Thrips palmi* widely distributed in warmer climate also feeds in *Echinocystis*.

The larvae of the leaf-miner flies (Diptera: Agromyzidae) bite long and straight holes – more or less characteristic to the species – in the leaves and young stems under the epiderm of the plant. The harm of a lonely individual is insignificant but when the infection destroys the leaves, the growth slow down and the young plants can die. The hardly affected plants are like burned by fire. The chewing of the larvae opens the way to the bacterial and fungal infections. The leaf-miner flies – for example *Liriomyza sativae* and *L. trifolii* – are not host specific, mostly affect dicotyledonous plant among those almost all important species of the cultivated Cucurbitaceae. Although the larvae of the fruit flies (Diptera: Tephritidae) to a maximum destruct the juicy pepo fruits, some species attack the plant organs with softer tissues and the seedlings too. Because of the oviposition the fruit usually deforms and falls. The hurt make possible the bacterial and fungal infections. On tropical and subtropical areas important example is *Bactrocera cucurbitae*, which affects the papaya too. The mentioned Diptera species have many parasitoids.

Among the buds (Heteroptera) despite of its subtropic-tropic distribution reach the warmer part of the temperate zones *Pycnoderes quadrimaculatus* (Heteroptera: Miridae) native in the New World. As its common name suggests (bean caspid) it harms the bean, but most often is observed on the species of the Cucurbitaceae among others on close relatives of the wild cucumber (on *Sicyos* or *Marah* species). It causes injuries on the surface of the leaves and stems and around that the plant whitening. If the species present with considerable populations the black colored debris of metabolism cover the underside of the leaves and white patches the upper side. In its native land the bugs are controlled by their natural enemies and therefore the chemical control is unnecessary. Likewise not specialist in its feeding but in the North American distribution area is often found on the wild cucumber the bud species called *Anasa armigera* (Heteroptera: Coreidae). At the places where numerous insects are feeding the leaves are destroyed but the overall surviving of the plant is not endangered considerably.

The mite species affecting the cucurbits cause spottiness with the sucking, on some plants the leaves coloring or if the infection is extended the leaves fall. Some mites like *Tetranychus neocalidonicus* (Acar: Tetranychidae) form a net extending over the all plant. These organisms are less host-specific and are important viral vectors.

It is surprising to some extent the wild cucumber despite of its relatively large seeds – which seems as ideal feeding source – has neither pre- nor post-dispersal seed predators mentioned by the literature.

Nematodes: *Rotylenchulus reniformis*, a tropic-subtropic species with wide host plant specificity which cause strong damages in cultivated plants almost independently from those taxonomical situation. It has been found in almost all cultivated plants of the Cucurbitaceae family. As consequent upon the infection the development of the root system fall behind and the upper organs weaken and the life-time decrease.

Pathogens

Viruses: The wild cucumber is a natural host of the cucumber mosaic virus (CMV), which is one of the most important plant pathogen viruses in Hungary. The virus can spread with the seeds of the wild cucumber and the infected seeds can spread by the flooding streams. The CMV is transmitted by different insect vectors from the cultivated plants to the weeds and vice versa. The wild cucumber has considerable role in the epidemiology of this multi-hostal virus causing great damages. The infected *Echinocystis lobata* plants show mosaic type leaf lightening in the summer months. The symptoms occur usually evenly on the surface of the leaves. In some cases strong leaf deformations are detectable accompanied by veiny mosaicism and lightening of the leaf veins. The infected plants show strong falling back in growth, the diameter of the stems and the seeds decrease. The seedlings grow from the seeds of the infected plants are underdeveloped and deformed with small leaves. The tendrils if not hurt mechanically do not spread the virus. The wild cucumber can be infected not only in its cotyledonal phase but in juvenility too when have few foliage leaves. The wild cucumber is also natural host of the bean yellow mosaic potyvirus (BYMV), tobacco ringspot nepovirus (TRNV), the prune dwarf ilarvirus (PDV) moreover the prunus necrotic ringspot ilarvirus (PNRSV). It can be infected by the potato X potexvirus (PVX). The wild cucumber can be host for the zucchini yellow mosaic polyvirus (ZYMV) which economically also cause great damages. Latter is not propagated by the pollen of the wild cucumber. The infection of the CMV and ZYMV do not decrease the germination potential considerably therefore the seeds help the spreading of these viruses in longer term. The role of the wild cucumber is not precluded as spreading factor for the soil borne (spreading with the soil) viruses affecting primarily the cultivated species of the Cucurbitaceae family as the cucumber fruit streak virus (CFSV), the cucumber leaf spot carnovirus (CLSV), the cucumber soil borne carnovirus (CSBV) and the melon necrotic spot leaf carnovirus (MNSV). The wild cucumber shows different resistance against the listed viruses, in vitro easily infected by the CMV.

Bacteria: The saprophyte *Pseudomonas syringae* pv. *lacrimans* also affect the species of the Cucurbitaceae family: on living plants it causes leaf spotting and later spread over the fruit. This bacterium „species” has zero host specificity. The bacterial wilt of the cucurbits is caused by *Erwinia tracheiphila*. In the first phase of the infection one or few leaves wilt and become pale green. Later the infection spreads over the whole plant and finally causes its death. Inside the transporting tissues of the affected plants milk like, gluey fluid is produced. The virus can overwinter exclusively in *Acalymma vittatum* and *Diobrotica undecimpunctata howardi* cucumber beetles (Coleoptera: Chrysomelidae), in the spring the beetles coming out from the soil with their chewing infect the host plants. Endangering bacterium causing wilt on the cucurbits too is *Erwinia carnegieana* (syn. *Pectobacterium carnegieana*).

True fungi: Sometimes possible to observe anthracnose caused by the fungus species of *Glomerella cingulata* agg. (Ascomycotina, Polystigmatales, Phyllacoraceae). The fungi classified here have the widest host spectra. More specific to the Cucurbitaceae family than the collecting species is the discriminated *Colletotrichum lagenarium* (syn. *Colletotrichum gloeosporioides*). The symptoms of the infection are the yellow, brown-yellow spotting of the leaves primarily on the veins at first than the spots grow and become brown, later cause necrosis. On the stem the spots lengthen and become black. Necrotic spots occur on the fruits too. In wet weather as signs of the produced spores the centre of the spots coloring to pink. The fungus overwinters in the dead plant organs and keeps its vitality for five years in the soil

as well as in the seeds. The infection happens through the cuticle of the host plant. The conidia forming in the acervulus is spread mainly by the splashing or flowing water but can spread with mechanical transmission too. The spores germinate 5–30 °C degrees, most optimal is the damp and warm (19–24 °C) weather. The symptoms occur after a week. *Cercospora echinocystis* native in North America causes leaf spotting and can live on the water melon too. In connection with the wild cucumber only few other fungal pathogen known as disastrous but presumably the species affect the cultivated members of the Cucurbitaceae family – many of them have wide host spectrum – infect the *Echinocystis* too. The most important are: *Rhizoctonia solani* (belly rot), the root and the stem rotting, *Pythium* species (cottony leak), cause rot of the fruits and roots, tilting of the seedlings (*Pythium aphanidermatum*), *Fusarium* species infect the seeds, if the seedlings outcome at all dies because of the rotting of the stem (see also *Rhizoctonia* and *Pythium* species), *Fusarium oxysporum* f. sp. *cucumerinum* (*Fusarium* wilt) can infect later and cause the burn-like death of the plants. *Didymella bryoniae* (syn. *Mycosphaerella melonis*) and *Phoma cucurbitacearum* (syn. *Ascochyta cucumis*) (gummy stem blight) are host specific to the cucurbits and cause the death of the cotyledons, leaf deformations, brown coloring of the stem which became white later. *Erysiphe cichoracearum* and *Sphaerotheca fulginea* powdery mildew species affect the leaves and stem produce white coat starting from the older leaves, the affected leaves and young shoots die, the spores spreading with the wind and infect extensively. As symptoms of *Cladosporium cucumerinum* (scab) infection on the leaves brown spots with yellow margins and deformations form, on the fruits dark grey spots occur and later fuse as large scab-like areas of the infection. After the infection of *Corynespora cassicola* (syn. *C. melonis*) (target spot) on the leaves form angular yellowish spots which become rounded with light brown centre and dark brown margin later. *Sclerotium rolfsii* cause variable harms depending on the host plant for example on the water melon the fruit rot.

Pseudofungi: In Hungary the first observed infection of *Pseudoperonospora cubensis* powdery mildew on wild cucumber was in 1996 in the populations beside the Kis-Balaton. This is the first data of this fungal disease with pathotypes able to infect the cucumber and pumpkin too. *Pseudoperonospora* genus belongs to the Pseudofungi (Mastigomycotina, Peronosporales, Peronosporaceae). The first symptoms usually occur on the older leaves. In the first phase of the infection on the upper side of the leaves angular, yellow spots form. Under warm and damp conditions on the underside of the leaves forming a grey downy coat and this give the common name of the fungus, downy mildew but which name is used for some similar genera also. The soft coat of the underside is formed by the furcating conidium holders at the apices with numerous spore produced by asexual reproduction. With the growth of the spots the all leaf become yellow and after it dies. In warm and damp weather the infection spread fast on the plant and between the individuals too. The spores are spread by the wind. The infection can harm the fruits too. The sexual procedures of the fungus take place in the leaves. The overwintering parts of the fungus rest in the fallen leaves. The life cycle is relatively alike to the more known peronosporae (downy mildew of the vine, potato-blight). Among the lower fungi the following *Phytophthora* species can affect the cucurbits: *Phytophthora capsici*, *Ph. drechsleri*, *Ph. nicotianae*, which cause the tilt of the seedlings, rot of the root, leaf spots, scab and leaf-fall.

Mycorrhiza

Because about the mycorrhizic relations of *Echinocystis lobata* and generally the species of the Cucurbitaceae family really few data are available we carried out our own investigations. Roots of two specimens were investigated. One from the Tisza flood area near Mindszent from the relatively shadowy border of an alluvial hardwood forest and a more opened mostly dewberry-tall herb community. The other sample grown in a garden, the seed was collected in the floodplain of the Tisza near Szentes. None of the samples showed signs of strong mycorrhization. Because only few samples were investigated which were collected at few locations it is not possible draw general conclusions. According to literature data the members of the Cucurbitaceae family can be inoculated by fungi of the “*Glomus* Group A” which form AM-type mycorrhiza – for example by *Glomus mosseae*. We would like to thank the help in the mycorrhiza investigations for dr. GÁBOR M. KOVÁCS.

ECONOMIC IMPORTANCE

Benefits

In North America the native population used the plant widely as panacea (i.e. medicinal plant which „cures everything”): the roots grinded to dust and used as warm poultice for headache. By their belief the infusion of the plant moderate the gastric disorders, the less serious nephritic problems, the rheums, cold and heat and used it as refresher too. The very bitter tea cooked from the roots was alleviator of pain. Clearly as the manifestation of the signature-theory in the ethnobotany the roots was estimated as aphrodisiac – think about its fruits often hanging double. In Indian descriptions also can be found notes about its use as abortifacient or menstruation helper. The North American native people used the seeds of the wild cucumber also as button, for some plays or to thread as beads. They also get on the juice of the fruits has narcotic effect for the fish. It is planted as ornamental plant in its native land and in Europe too.

Damages

In North America the plant is agricultural weed in corn and soya. Also can be weed at synanthropic habitats mostly in wet areas, alluvial forests and in ruderal and weed communities along ditches, channels and roads. Sometimes it can be crowded in badly treated garden cultures and can harm bushes, small trees by its dense tissue.

As reservoir for some plant viruses the wild cucumber help the continuous survival of the diseases independently from industrial crops and can prove a kind of „green corridor” for some pathogens.

NATURE CONSERVATION SIGNIFICANCE

In its secondary distribution area – mostly where form large populations – it affects the structure of the indigenous vegetation disadvantageously and at some locations it can be estimated as transformer plant. The species decrease the biodiversity of the habitats and if occurs crowded it can push down the smaller indigenous plants. Because the experienced hydrochory, it easily colonizes habitats along rivers.

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BOXELDER

(*Acer negundo* L.)

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TAXONOMY

Scientific name: *Acer negundo* L. 1753, synonyms: *Negundo aceroides* MÖNCH 1794, *Acer fraxinifolium* NUTT. 1818, common names: boxelder, ash-leaved maple.

According to recent taxonomic studies genus *Acer* consisting of 120 (~200) species, belonging to order Sapindales, family Sapindaceae and subfamily Hippocastanoideae is widespread in the North Temperate Zone. It has greatest diversity in China. Formerly the genus have been considered to make up a separate family, Aceraceae which involved one more genus, *Dipteronia* of only one or two species of which *D. sinensis* OLIVER native to Central China can be planted in Hungary as an ornamental tree.

Boxelder has fairly distinct geographic races:

- var. *negundo* – eastern United States and introduced to eastern Washington and Oregon
- var. *interior* – Rocky Mountains to Arizona and Canada
- var. *violaceum* – northeastern United States and northern Great Plains
- var. *texanum* – western Missouri, eastern Kansas and throughout the Southeast
- var. *californicum* – California
- var. *arizonicum* – Arizona and New Mexico.

MORPHOLOGY

Boxelder is a deciduous small to large tree with an irregular form. This variable-sized tree may reach 20 m in height (in native habitat), but more often medium sized (12–15 m). The trunk often divides near the ground into a few long, spreading, rather crooked limbs, which branch irregularly to support a broad, uneven crown. When growing among other trees, boxelder forms a high, open crown, with the undivided portion of the trunk much longer and usually straighter than that of an open-grown tree. Trunk diameter is 30–60 cm in common, but may reach 90 cm as well. Boxelder has a fast growth rate and a short life span; it typically lives for 75 years, with 100 years maximum longevity. Growth is rapid when young; long, smooth, green annual shoots extend 60 cm or more in a year. At maturity growth slows and brittle trunks and limbs shatter; old trunks frequently put out clusters of sprouts and sometimes develop large burls. Fertile shoots usually grow only 5–10 cm per year, individuals cut back to ground level however may bring as much as 2.5 m long shoots in the first year. Its main root is deep, while lateral ones are shallow and spreading. Lateral branches of trees cut back to ground level and regenerating as dense sprout bushes laying down the ground and root easily. The bark is light grey and smooth but becomes furrowed into narrow, firm ridges and darkens with age. Twigs are stout, light green to purplish or brownish with a polished look or are often covered with a whitish bloom that is easily rubbed off. The blunt buds are 2 to 5 mm long with one or two pairs of scales and are coated with fine white hairs. Boxelder is one of those few maples which have pinnately compound leaves. Opposite leaves consisting of 3 to 7 leaflets are from 15 to 38 cm long, light green above and grayish green below,

usually without hairs. The leaflets are shallowly lobed or coarsely toothed. Its wood is medium light and soft among maples, decaying relatively quickly in soil. This completely dioecious tree has pale green male (but in Hungary often with red anthers) and female flowers with a strongly pronounced reduction of flower parts, and contains no rudimentary parts of the opposite sex. Male flowers are on slender stalks in loose clusters, and female flowers are arranged along a separate stem. The fruit is composed of two fused, winged samaras which eventually separate upon shedding. The angle separating the two wings is less than 60 degrees. The samaras, about 4 cm long, hang in long chains on slender stalks, mature in autumn, and remain on the tree well into the winter (while they are dispersed continuously). Each contains a single seed without an endosperm. Seeds are 2 to 3 times as long as they are wide and are markedly wrinkled. Many ecotypes of this species occur. Varieties are distinguished by the morphological characteristics of glaucousness, pubescence, or color of the branches and/or samaras.

ORIGIN, DISTRIBUTION

Boxelder is widespread in riparian and marshy communities throughout most of the United States. Its range extends from New Jersey and central New York west through extreme southern Ontario, central Michigan, northern Minnesota, central Manitoba, central Saskatchewan, southern Alberta and central Montana, eastern Wyoming, Utah, and California; and south to southern Texas and central Florida. It is also local in New Hampshire, Vermont, Massachusetts, Connecticut, Idaho, and Nevada. Boxelder has been naturalized in Maine, southern Québec, New Brunswick, Nova Scotia, Prince Edward Island, and in southeastern Washington and eastern Oregon. Varieties of boxelder occur in the mountains of Mexico (Nuevo Leon, San Luis Potosi, and south to Chihuahua) and in Guatemala. Boxelder is a component of various deciduous forest plant associations in the North American Great Plains. It is associated with the following over-storey dominants: green ash (*Fraxinus pennsylvanica*), narrow leaf cottonwood (*Populus angustifolia*), plains cottonwood (*P. sargentii*), aspen (*P. tremuloides*), willow (*Salix* spp.), and bur oak (*Quercus macrocarpa*). In Arizona and New Mexico, boxelder is the over-storey dominant in several high elevation riparian forests. In much of this species' range there are no described plant communities.

Firs data of boxelder are from 1872 according to PRISZTER. PÉNZES notifies in 1942 as a mixed among huge oak trees of Újpest Island, and as a shade (road-side) tree especially on the Pest side, furthermore in private gardens and considers as established. SOÓ notifies in 1966, that it is planted in a great mass on flood areas, on sandy and slightly alkaline soils of the Great Plains of Hungary, and that it has already been escaped and established on riparian forests and black locust plantations. Seedlings of boxelder are common in weed associations. According to BARTHA & MÁTYÁS (1995) it has been planted to several kind of habitats since the 19th century, occurs o the whole territory of Hungary, mainly along rivers (lower Danube valley), marshy areas near Lake Balaton, and also on dry sandy soils of the Great Plains. An escaped mingle tree of disturbed areas, plantations, cultivated forests. It occupies 0.1% of the total forested territory.

LIFE CYCLE

Boxelder flowers before or with leaf output from March through late May. Winged fruits are ripen from September to October, and dispersed continuously from September to March. Seeds keep germination ability for long time (at least one year). It does not require great heat for germination, only some moisture, in Hungary they germinate from April through September. After heavy summer rains, in warm climate seeds germinate in large number on sandy soils of the Great Plains. Germination type is epigeic; elongated, narrow cotyledons emerge above ground and turn green. Main root penetrates deep in soil in a short time, its length may exceed half meter in the first year, while medium dense, but in dry weather not too long lateral roots develop. Its good drought tolerance is surely due to its long main root, and lateral roots are able to utilize water of short rains, which cannot penetrate into deeper soil layers. Boxelder reproduces both sexually and vegetatively. Large seed crops are produced each year. Seeds

persist through the winter; they are dispersed by wind or by birds and squirrels. Wind will carry these winged seeds up to 100 m across a snow surface. Boxelder establishes by seed under a wide range of conditions: immediately after disturbance on moist disturbed soil, along riverbanks, and in areas with heavy cover and medium to heavy competition. According to investigations made in southern Illinois reproduction of boxelder on areas with light (<1.3 cm), medium (1.3–5 cm), and heavy (>5 cm) duff (on the basis of number of 1–2 year old seedlings) has been 4:3:1, respectively. Vegetative reproduction is also common on damaged plants of this species. New shoots will appear on exposed or injured roots. After the extreme drought condition of the 1930's in the Great Plains of North America, during which nearly all boxelder trees in shelterbelts 30 years or older died back to the ground, many trees recovered by producing root sprouts, forming a dense hedge or undergrowth. In shelterbelts of the northern Great Plains (US), boxelder has a dense growing habit resulting from the plant suckering at the root collar. Seven years after timber harvest in a South Carolina bottomland, sprouts from boxelder stumps greater than half meter in diameter were reported to be dying or losing vigor. Although this species will produce abundant sprouts after disturbance, the primary method of reproduction is through seed, due to the quantity produced each year and the facility of its distribution.

HABITAT PREFERENCE

Boxelder has a wide tolerance of soil types and water conditions, therefore it tolerates well polluted urban air, it grows well both on full sun and part shade.

In North America boxelder generally grows on moist sites along lakes and streams, on floodplains, and in low-lying wet places where its shallow root system can find abundant moisture. Hardy to extremes of climate, boxelder is drought tolerant once well established and can also withstand short periods of flooding. This species is able to tolerate a wide variety of soils but shows a strong preference for well-drained, moist soils. Although boxelder will grow on soils from gravel to clay, it grows best on deep, sandy loam, loam, or clay loam soils with a medium to rocky texture and a pH of 6.5 to 7.5.

Throughout its range, boxelder is most often associated with various species of cottonwood (*Populus* spp.) and willow (*Salix* spp.). On the northern Great Plains (US), boxelder will generally outlive cottonwood and willow to become an associate in American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), mulberry (*Morus* spp.), and green ash (*Fraxinus pennsylvanica* var. *subintegerrima*) communities. In the central Great Plains and in the eastern United States, boxelder occurs with elms (*Ulmus* spp.), sugar maple (*Acer rubrum*), basswood (*Tilia* spp.), and ashes (*Fraxinus* spp.), which eventually replace boxelder in the over-storey along with other more durable and shade-tolerant species. At higher elevations on the Utah plateaus, boxelder occurs in the riparian zone with water birch (*Betula occidentalis*), narrow leaf cottonwood (*Populus angustifolia*), willows, and blue spruce (*Picea pungens*). In New Mexico and Arizona, scattered along streambeds in riparian forests at higher elevations, boxelder is a typical canopy dominant with Arizona alder (*Alnus oblongifolia*) and coyote willow (*Salix exigua*). The elevation ranges of boxelder in several states are as follows:

Arizona	from 4,450 to 8,000 feet	(1,356–2,438 m)
Colorado	4,500 to 7,870 feet	(1,372–2,400 m)
Montana	2,240 to 4,500 feet	(680–1,372 m)
Nevada	2,600 to 4,500 feet	(792–1,372 m)
New Mexico	6,350 to 6,775 feet	(1,935–2,065 m)
North Dakota	2,310 to 3,840 feet	(704–1,170 m)
South Dakota	3,000 to 3,500 feet	(914–1,067 m)
Utah	4,000 to 10,000 feet	(1,219–3,048 m)
Wyoming	3,500 to 7,700 feet	(1,067–2,347 m)
Mexico	4,600 to 5,947 feet	(1,400–1,800 m)

Boxelder occurs in a variety of forest types ranging from early to late serial, making its successional position difficult to determine. It is moderately shade tolerant but does not reproduce in its own shade. It usually establishes under pioneering species such as cottonwood and willow, particularly in the northern Great Plains (US), and is then followed by more shade-tolerant, climax species. In Arizona and New Mexico, boxelder is a dominant or co-dominant over-storey species in several high-elevation riparian communities.

BIOTIC INTERACTIONS

According to allelopathic investigations (CSISZÁR pers. com.) aqueous solution of dried boxelder leaves slightly inhibited germination of white mustard (*Sinapis alba*). On the basis of literature data, compounds responsible for allelopathic effect of boxelder are terpenoids, triterpene saponins and alkaloids.

Most important pest of boxelder in Hungary is fall webworm (*Hyphantria cunea*) of family Arctiidae. It has been introduced into Hungary from America, but circumstances and time of introduction is unknown. In the beginning it was a peculiarity of entomologists. First individuals have been caught by ZSIGMOND VELEZ in the Csepel free port: in 5th August 1940 two females and in 25th May 1941 one male. Caterpillars have been found and nursed to moth first by JÓZSEF SZŐTS on an apple tree of the Budapest Szécsényi Hill. It has been distributed from Budapest along roads and railways. In 1948 it has been found almost in the whole country. It has reached the surrounding countries in the following order: Czechoslovakia 1946, Yugoslavia 1948, Romania 1949, and Austria 1951. It has appeared as a pest first in 1946, when south from Budapest in an about 50 km zone some trees have been totally defoliated. After multiplication of larger scale fall webworm has become one of the most studied pests of Hungary within few years. It is an extremely polyphagous species. Feeding caterpillars have been observed on more than 100 species in Hungary, and on more than 200 plant species in Central Europe. Its most preferred food plants are boxelder, white mulberry (*Morus alba*), sweet cherry, apple and walnut. These plant species are so called primary food plants of it, on these development of caterpillars is the fastest, and mortality is the lowest. According to my observations in the Great Plains of Hungary the damage caused by fall webworm does not retard growth of boxelder even in case of total defoliation. Boxelder causes a much greater problem by providing multiplication space for fall webworm. Most successful protection against the webworm could be exactly destroying boxelder, as its primary food plant.

Data concerning mycorrhiza connections of boxelder are not available.

ECONOMIC IMPORTANCE

Though its wood has no technical value, after all it provides fuel, and 2–3 years after cutting back to ground level it provides a large amount of stick for grapevine, bean or tomato, and it has a great importance in planting shelterbelts. Beside basic form, varieties of colorful (e.g. yellow) and variegated foliage are planted as ornamental trees. Boxelder is not a desired timber species in North America because its wood is light, soft, close grained, and low in strength. The wood is used locally for boxes and rough construction, and is used occasionally for cheap furniture and woodenware. Boxelder was once used for posts, fencing, and fuel but the soft, spongy wood generally makes poor firewood. Riparian boxelder communities provide important habitat for many wildlife species and protect livestock from temperature extremes in summer and winter. Many species of birds and squirrels feed on the seeds of boxelder. Mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) use it in the fall as a browse species of secondary importance. This tree may be poisonous to livestock. The nutritional value of boxelder is low for livestock, with fair energy value, poor protein value, and suspected toxicity. Growth of boxelder is poor on saline, alkaline, and most acidic soils; it is not recommended for use in rehabilitation of disturbed sites. This tree's potential for erosion control and for long-term re-vegetation is low to medium. In California, Arizona, and parts of Nevada and New Mexico, boxelder is one of many native species used for re-vegetating flood control basins to provide quality wildlife habitat. In the southeastern United States where soil moisture (or inundation) is likely to be excessive for several weeks

at a time, boxelder is one of the favored flood-tolerant species recommended for recreation plantings. Boxelder is propagated by seed, first cultivated in 1688, is often held in low regard as an ornamental tree in cities. Its limbs are brittle and break easily; its trunk is susceptible to rot and infested with boxelder bugs, which make their way into houses with the arrival of cold weather. The leaves turn a dull yellow and fall untidily over a long period, as do the winged seeds, giving this species the reputation of being a "dirty tree". However, because of its fast growth and drought and cold hardiness, boxelder is popular in rural communities for street and ornamental plantings; and for shelterbelts. Boxelder's abundant sap contains a large proportion of sugar as well as mucilaginous and demulcent properties, and can be made into a "pleasant" beverage. The Plains Indians used the sap as a source of syrup, and it is still used today, but the product is not as sweet as syrup of sugar maple (*Acer saccharum*). This tree is also easily storm damaged; its weak branches often break off in the wind, but the trunk is wind firm. Boxelder is easily injured by heart rot, fire, and insects. It is often infested with boxelder bugs which feed on the tree but rarely kill it. Weedy habit appearing on different human made semi-natural habitats can be mentioned as its most important economic damage, moreover as primary food plant, therefore the main propagator of fall webworm causing serious damages in horticultural crops.

NATURE CONSERVATION SIGNIFICANCE

Due to its pioneer character, boxelder causes problems of nature conservation mainly in softwood riparian forests, where it pushes out native species of also pioneer character. I have not seen yet any damage caused by game on boxelder in Hungary; presumably until game finds other food (e.g. native species or suitable pasture) it will not touch boxelder.

Beside flood areas problem caused by boxelder appears on places, where the plant finds open ground surface, and plant competitors are absent. Such places are disturbed soils (e.g. not so long ago abandoned arable lands or horticultural areas, building sites with arranged terrain standing empty for a longer time, garbage deposits), improperly managed green urban places, and moisture retentive gaps of built environment. In such places boxelder appears as a gap inhabitant similarly to other species (such as *Ailanthus altissima*, *Populus xcanadensis*, *Paulownia tomentosa*, *Buddleja davidii*), and in lack of care and intervention in time it may cause serious damages in the structure of buildings.

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TREE OF HEAVEN

(*Ailanthus altissima* (MILL.) SWINGLE)

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TAXONOMY

Scientific name: *Ailanthus altissima* (MILL. 1786 sub *Toxicodendron*) SWINGLE 1916; synonyms: *Ailanthus peregrine* (BUC'HOZ 1783 sub *Albiona*) BARKLEY 1937, *Ailanthus glandulosa* DESF. 1786, *Pongelion cacodendron* FARWELL 1930, DEG. 1937.

Genus *Ailanthus* of family Simaroubaceae belonging to order Rutales (or according to the latest system order Sapindales) comprises some seven species distributed mainly in East and South-East India and in the Far East, the only temperate zone representative of which is *A. altissima*. According to the evidence of fossils the genus was distributed in the Tertiary from North China to the Amur region, from Japan to North America, and in the Mediterranean and in Central Europe.

MORPHOLOGY

Tree of heaven reaches 27 m height; its life form according to RAUNKIAER is MM. Its mid gray bark is mottled by short longitudinal fissures. Its wood is light and soft, decaying quickly in the earth, saprotrophic fungi (e.g. *Schizophylum commune*) decay it quickly above ground too; therefore it is not suitable for posts or stakes. Its value as a fuel is low. One year old twigs are thick, brittle, spongy pith filling up the majority of cross section is light brown. Twigs are mid brown; their surface is velvety due to minute papillae. Leaf scars are big, blunt triangular in shape, small buds are hemispherical. Fresh shoots are green or purplish may grow as much as 3 meter in a year until the first frosts. Leaf length may reach one meter, odd or rarely even pinnate, consisting of 13–41 leaflets depending on their state of development. Leaflets are oblong, pointed, smooth edged, well developed ones are somewhat lobed at base, sometimes with lateral gland like projections. Both side of leaflets are covered by microscopic glandular hairs, which emit a foul smell volatile oil somewhat resembling burnt stew. This has an important role in resistance against pests. Flowers are of two type, may be bisexual (which are proterogynous) or staminate, which develop on separate individuals, therefore the plant can be termed semi-deciduous. Flowers parts are five or rarely six, number of sepals, petals and pistils are five or six. Pistils are in two whorls, numbering 5+5 or 6+6. Fruit is a samara cluster, with five or six fruit not always all developing. Samaras are turned longitudinally, oily storage sotedonous seed is situated in the middle, revolving horizontally while falling down, hence able to move sideways in still air, in contrast with maple or ash samaras.

On dry sandy soil in close stand tree of heaven brings up a long trunk. Within dry urban environment or as a solitary shade tree along country roads its trunk branches lower. According to the identifying key developed by BAGI (1994) built on the plant growth form system of BARKMANN (1988) this two corresponds to *Quercoid* growth form. On extremely dry urban habitat it develops an umbrella like crown, branching about 1.5–3 m above ground. Since there is no such a growth form in the BAGI's key, I have named it *Pineoid*. In a fresh environment the trunk branches even lower, which corresponds *Tilio-*

Fagoid according the key, while mass of suckers (sprouts) can be identified as *Cornoid* growth form. On sandy soil these sucker colonies transform into closed, hemispherical stands in time, with impenetrable density except 1–2 m² spots with no sprouts.

ORIGIN, DISTRIBUTION

According to the Chinese literature tree of heaven is native to the lower course of river Yangtze (in provinces Hubei, Henan, Anhui, Jiangsu; Hunan, Jiangxi, and Zhejiang [1000–1800 mm annual rainfall]) and in Korea, where now its synanthropic distribution spreads from 22 to 43° Northern latitude up to 1500–1800 m above sea level. It tolerates drought and pure soil well, likes sandy soils, but does not tolerate humid habitats for long time. It survives on slightly acidic, neutral or slightly alkaline soil containing 0.6% salt. In north-east China it survives –35°C frosts. On loess highlands and mountainous areas with limey soil it behaves as a pioneer, on mine and industrial areas it is applied as reforestation and green area plant.

Its global distribution has begun in the 1740's, when its seeds have been carried into Paris during a continental tour through Siberia. According to the earlier literature its European career has begun in London in 1751 and in Paris in 1875 it was planted as a substitute of plane-trees. It was introduced into the USA also in the 18th century, where first it was planted as an ornamental tree in the northern towns, but now it is widespread in the most part of the western hemisphere. It is frequently planted in subtropical and north temperate regions, thus it has been established in whole Eastern Asia and Europe, in North America in Pennsylvania, Ohio, Wisconsin and Nebraska States. Due to its characteristics, later it has been established in all continents. For reforestation of slopes, dunes, barren areas and for wind-breaks it is planted in Austria, Italy, Yugoslavia, in dunes of the Black Sea, in dry areas of south-eastern Europe and Asia Minor, and in the former Soviet Union. It has been proved an excellent plant for industrial areas and roadsides by planting it in air polluted industrial areas and towns. Because of "good features" of its wood, among others its high cellulose content, in Austria and East Europe and in Argentina, Uruguay, India and New Zealand it is planted in plantations of forestry. Global planting of tree of heaven resulted in, that its contemporary synanthropic area consists of temperate and Mediterranean regions of five continents. It has further spontaneous occurrences in Australia, Japan, North Africa and Central Europe.

The first data of tree of heaven in Hungary are from J. BARTOSSÁGH in 1841 and 1843. He was regretting that on his own estate in Villány, young saplings of tree of heaven, planted to the southern foot of Szársomlyó hill of Nagyarsány, were damaged by frost. SOÓ & JÁVORKA (1951) indicates it as an established plant on the Great Plain. By CSAPODY *et al.* (1966) in spite of the old suggestion of Albert BEDŐ it cannot be used for reforestation of barren areas. Besides SOÓ (1966) and BARTHA & MÁTYÁS (1995), SOÓ & KÁRPÁTI (1968) also indicates its frequent naturalization, and that it is planted in plantations on the Great Plain.

LIFE CYCLE

Seeds keep germinating ability for a long time (many years). It requires warm and moist environment for germination. For this in Hungary the adequate heat outdoors is available from the end of May. Round cotyledons emerge above ground and do photosynthesis. Its elongated hypocotyl thickens quickly at the first root branch. Major part of its root system is situated close to the soil surface, branching in palm or fan shape, most commonly spreading in one direction, some of them thicken, and perform considerable storage, which is important in regeneration of cut back or frost damaged parts. If above ground parts damage, adventitious buds develop on roots near soil surface, such individuals develop into dense sprout colonies in time. On dry sandy soil in a relatively closed stand tree of heaven raises a high trunk. In dry urban environment or as solitary shade tree aside country roads its trunk branches lower. Its expected life span is estimated only 130 to 150 years, but sometimes much younger (30–50 year old) individuals die quickly for unidentified reasons so far. *Schizophylum commune* appears on dead trunks and branches in all case.

Mean time of leaf output falls on early to mid April, unfolding shoots are reddish brown. Foliage turns uniformly green in time, its growth is continuous, may last until frosts. Inflorescence is a very dense panicle, flowers open in June, emit a nauseous sweet odor, produce a lot of nectar, therefore tree of heaven is said to be good for bee browsing. Fruits develop already two weeks after blooming; they turn yellow or red (f. *erythrocarpa*) till August, later they become dry and brown. Fruits fall continuously from late autumn till next spring. Vegetative propagation is done by adventitious buds developing on roots, – similarly to *Aegopodium podagraria*, *Asclepias syriaca*, *Anemone hupehensis*, *A. sylvestris* – the result of which will be a dense colony (of root suckers) in time. Among short root suckers developing at the end of summer the phenomenon neoteny can be observed: an inflorescence consisting of few flowers appear on only 10–20 cm tall suckers. In one case I have observed one fruit of final size, but not yet ripe on a neotenic sucker, this however could not ripen before winter.

HABITAT PREFERENCE

Today in Hungary tree of heaven is widespread mainly on plane and hilly lands, only seldom seen in the mountains. If it is planted to such place, where its spreading is not hindered by biotic or abiotic factors, it spreads aggressively. Abiotic limit of its spread I think is the lower mean annual temperature; biotic limit however is deep shade. It is in harmony with my observation, by which in Transylvania it can be found only in southwestern towns sporadically (Szászsebes–Şebeş, Ópiski–Simeria Veche, Déva–Deva, Kimpényszurdok–Câmpuri Surdoc, Arad), as escaping from planted individuals, it is relatively frequent in Arad, and in Hungary in Zala and in higher regions of the mountains it is virtually absent (perhaps the 9°C mean annual isotherm is the limit).

Because of its wide ecological amplitude it has been planted, and unfortunately is still being planted, in settlements in greatest mass, escaped individuals and stands can be seen mainly in towns. Within urban environment tree of heaven prefers not too shaded, warm areas, often seen as gap inhabitant (in gaps between the pavement, roadway and house walls, among gravel and construction debris, on old walls), around ruined buildings, in factory yards, railway embankments, and in green urban areas in the protection of hedges, ornamental shrubs, where public domain maintainer can hardly access it. In such gaps, where there is a relatively larger space available for roots under the surface, settled individuals grow up and if they are bisexual, within 4–5 years they fruit profusely.

Outside settlements it has been planted by road sides and forestry plantations, from where it penetrates to all places, where adequate heat and light available. In addition to disturbed environment, tree of heaven settles in areas covered by natural vegetation without closed canopy (Buda–Sashegy, Nagyharsány–Szársomlyó, Fót Somlyó, Bölske–Gyűrűs valleys, Káli-Basin–Salföld; Pannonhalma Landscape Protection Area–Sokoró, Torna Karst). On these places in the beginning tree of heaven appeared thread by thread in the form of ½ to 1 m tall suckers, later some of these slowly grew up, and have irreversibly changed the composition of the vegetation, threatening the natural habitat of one or two rare plant species in more cases.

BIOTIC INTERACTIONS

In connection with allelopathy of tree of heaven MERGEN (1959 cit. RICE 1984) gives an account of the fact, that within stands of tree of heaven succession is conspicuously slow, and after a long term, apparently poor vegetation remains under them. MERGEN has observed a quick wilt of other plants, the cut stem surface of which has been treated by alcoholic extract of rachis and leaflets of *Ailanthus altissima*, among 35 gymnosperms and 11 angiosperms only *Fraxinus americana* has proven resistant. Hydrolyzed leaf extract of tree of heaven contains the following materials according to HEGNAUER (1973): quercetin, gallus acid, ellagic acid, 0,2 isoquercetin, kaempferol (=robigenin); p-cumaric acid, cafferic acid and 11.9% tannin. According to HEGI (1924) occurrence of diastase is characteristic to buds. Reserve material of seed is 50% oil, the principal components of which are oil acid and linolenic acid, and 12.5–27.6% protein. Seed contains no starch. On the basis of investigations of HEISEY (1990) tree of heaven contains one (or more) substances, which potentially inhibit germination and growth of seed-

lings. Extract of bark – especially root bark – has the strongest inhibition effect, that of leaflets has medium, and that of wood has low. Raw extract of root bark of tree of heaven contained 34 mg/ℓ water soluble material, leaflets contained 119 mg/ℓ, which has inhibited the growth of radicle of *Lepidium sativum* in 50%. Seeds also contained germination inhibitors, which cannot escape through the pericarp, but after the removal of which they dissolve on wet agar. Tree of heaven leaflets showed the strongest germination inhibiting effect at spring sprouting, and inhibitor content of trunk bark was highest right before leaf output. HEISEY has observed a low selectivity by testing germination inhibiting effect of root bark extract of tree of heaven on seven herbaceous plant species (*Amaranthus retroflexus*, *Lepidium sativum*, *Abutilon theophrasti*, *Setaria glauca*, *Echinochloa crus-galli*, *Pisum sativum* cv. 'Sugar Snap', *Zea mays* cv. 'Silver Queen'), however *Abutilon theophrasti* has proven a little more resistant. Root bark extract of tree of heaven has shown a strong herbicidal effect by spraying on greenhouse soil in pre- and post-emergent mode. Post-emergent spraying has shown almost total mortality even in the lowest dosage – except *Abutilon theophrasti*. HEISEY says it is realizable to develop herbicides of natural basic material from allelopathic agents of tree of heaven. LAWRENCE et al. (1991) have also showed, that young leaves and shoots of tree of heaven contain certain agents in significant quantity, which inhibit the growth of neighboring plants. Their investigations have proved, that soil around tree of heaven also contained similar toxins in considerable amount. On course of their greenhouse experiments, those plants, and their seeds that has not been exposed to the effect of tree of heaven proved to be more sensitive to toxins of tree of heaven in comparison with those, which has already treated before.

In Hungary no pest of disease of tree of heaven is known. Belonging to family Saturniidae, *Ailanthus* silk moth (*Samia synthia*) native to East and Central China is now distributed in whole South Asia: China, India, Malaysia, Indochina, Japan and the Philippines. In the framework of experiments aiming improvement of silk industry, in the middle of the 19th century this moth has been introduced to France (where there are still surviving populations), northern Italy, Switzerland, and Austria and among others to Great Britain and the United States. As an original food plant, tree of heaven has been introduced that time to the above countries. In spite of its low cost, tree of heaven silk could not compete with silk of silkworm raised on mulberry (*Morus alba*). Distribution of ailanthus moth is very restricted within the United States: it occurs only in SW-New York, Connecticut, New Jersey, E-Pennsylvania, Delaware, Maryland and Virginia.

Ailanthus moth usually has one generation in the United States, it flies from late June to early July. It does not attracted very much to light, but its cocoons often seen hanging on strong thread from stalks of compound leaves of tree of heaven in autumn after leaves fallen. Imago comes out from the cocoon in the morning, especially in warm time through a slit opening at the base of suspending thread. Larvae feeding on *Padus pennsylvanica* spin a reddish brown silk, in contrast with those feeding on tree of heaven, which spin silvery brown silk. Moths mate readily in captivity, even in a relatively cramped cage, already in the evening of the day of capture. After twilight female pushes out fragrance gland from its abdomen. The pheromone spreading in the wind attracts males from several miles distance. Mating pairs usually stay together till next evening. Differing male and female individuals is difficult, since wing shape and color is almost entirely alike, and antennae are very similar to each other. Female's abdomen is thick while that of the male is conical. One female lays some 400 small, white eggs in short rows. Eggs hatch after 8 to 12 days, young larvae stay together in the first two larval stages (L₁, L₂). Small caterpillars chew at the edge of leaflets. L₂ larvae still stay together, their head is small, black, and their body is flat, off-white, adorned by some small black bunch of hairs. L₃–L₄ larvae are creamy white, their head and legs are yellow. Larvae are thermophilous, and develop quickly in early to mid August. Last larval stage is bluish green, their body is covered by fine white powder, and there are fleshy projections on their back and side. Among food plants of moths belonging to family Saturniidae many plant taxa are listed¹, among these ailanthus moth prefers tree of heaven, and its larvae have been observed only on *Padus pennsylvanica* until now.

Hungarian authors revealed arbuscular mycorrhiza in stands on sandy soil on the Great Plains.

¹ among others *Althaea rosea*, *Apium graveolens*, *Carpinus betulus*, *Euodia fraxinifolia*, *Juglans regia*, *Lagerstroemia indica*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Padus serotina*, *Malus domsetica*, *Ricinus communis*, *Syringa vulgaris* and *Ziziphus jujuba*, and several genera: *Berberis*, *Cornus*, *Forsythia*, *Fraxinus*, *Ligustrum*, *Platanus*, *Salix*, *Tilia*.

ECONOMIC IMPORTANCE

Tree of heaven has only fictitious economic uses, to illustrate these, let's see a contemporary quotation: "It grows quickly. ... Its sprouting ability is so high, that it is difficult to destroy. Can be propagated by seed, growing of seedlings is easy. Yields profusely every year, winged seeds spread far by wind. It has an importance in reforestation of sandy soils is as mingle tree of Austrian pine (*Pinus nigra*) and black locust (*Robinia pseudoacacia*). It can be planted as road-side, pasture and shelter belt tree, game and grazing livestock does not touch because of its smell. Good honey tree. Its wood is used for making furniture, chipboard and paper." For its large scale distribution this kinds of encouraging descriptions, e.g. DANSZKY (1964), could contribute to in a large scale. Quick growth, good sprouting ability, profuse yield and easy seedling growth is not a virtue in case of an invasive plant. I have not seen any example for the processing of its wood, maybe because of its poor quality. Its twigs, suckers and trunk cannot be used for durable sticks or posts, because after a couple of years even a trunk of 10 cm diameter decays so (e.g. due to xylophagous saprotrophic fungi), that it brakes under a smaller load. Theoretically its wood can be used as fuel, provided that it could be managed to dry out completely, but its fuel value is far lower than that of black locust. Great scale town tolerance can be mentioned as its sole use. But if we consider, that fruits of individuals planted in extremely polluted urban environment are swept several miles away by windstorms, and with establishing in an environment worthy of something better, they may cause serious problems, the use mentioned above may be a question.

As its direct economic damage, one thing can be mentioned: establishing as a gap inhabitant its growing root system and bulky base may burst building covers and pavements, which result in permanent damage. Through gaps originating so, even more rain water may get in. I have seen young, sometimes several year old individuals on vertical stone walls, facades, edges and roofs of buildings, where its damaging effect is even more conspicuous. In urban green areas, and in areas covered by natural and semi-natural vegetation its aesthetical and ecological damaging effect does not need comment.

NATURE CONSERVATION SIGNIFICANCE

Vegetation of areas infected by tree of heaven degrades continuously in comparison with the state before infection. In the beginning due to allelopathic compounds dissolving from roots, later due to increasing shading more valuable species of the original vegetation are gradually pushed out. Great mass of falling leaves and decaying litter start nitrogen accumulation in the soil, which is signed by the appearance of shade tolerant nitrofrequency disturbance tolerant species.

In the crown layer of investigated stands of tree of heaven *Robinia pseudoacacia* and *Morus alba* are present as accidental elements independently of soil type. To these on soils formed on loess *Acer negundo*, on limestone *Cerasus mahaleb* are added with a relatively high abundance. In the shrub layer of stands *Crataegus monogyna* is a common element, *Robinia pseudoacacia*, *Rosa canina* and *Sambucus nigra* are also frequent but with a relatively low abundance. From accidental elements of the shrub layer *Acer negundo* is prominent with its high abundance. The herb layer is dominated by the sub-constant *Galium aparine*, other frequent species are *Ballota nigra*, *Bromus sterilis* and *Bilderdykia convolvulus*. Among accidental herbaceous plants *Lithospermum purpureo-coeruleum* and *Parietaria officinalis* are prominent with their high abundance, the reason of this may be their strong vegetative propagation, because in my opinion though metabolites of tree of heaven inhibit germination and seedling growth of some herbaceous species, however not vegetative propagation. In my opinion *Galium aparine*, *Anthriscus cerefolium* and *Bromus sterilis* appears with great abundance in stands of tree of heaven similarly to stands of black locust, because their root system is situated in a soil layer, which contains relatively low amount of allelopathic compounds dissolving from roots of tree of heaven, or they are resistant to them.

I observed in many cases, that *Asclepias syriaca* in the closest vicinity of stands were never present inside stands, even in their sparse edge. This cannot be explained by shading, because under *Robinia* and mainly under poplar (*Populus × canadensis*) plantations milkweed forms vast polycorms. The explanation can be searched probably in allelopathic effect of tree of heaven, different from that of black locust.

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HIMALAYAN BALSAM

(*Impatiens glandulifera* ROYLE)

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TAXONOMY

Scientific name: *Impatiens glandulifera* ROYLE 1835; synonyms: *I. glanduligera* LINDLEY 1840, *I. roylei* WALPERS 1842; common names: Himalayan balsam, Indian balsam, jewelweed, Policeman's helmet.

The Balsaminaceae family inside the order of Geraniales includes only two genera. The larger is the genus *Impatiens* with some 900 species which are native mostly in the tropical mountain forests of the old-world and some of them at the subtropics. The main distribution areas of the family are the tropic Africa, the islands of Eastern-Africa and India. Only few species are native in North-America and altogether 8 in the temperate part of Eurasia. Among the 6 species presents in the European flora only one is native, the others got into Europe as frequented ornamental plants and naturalized more or less over the continent. The South-African originated *I. capensis* MEERB. is not present in Hungary. In the Hungarian flora: a native (*I. noli-tangere* L. with yellow flowers), two naturalized and two casual alien *Impatiens* species known. The last two are *I. balfourii* HOOKER fil. with white and purplish-violet flowers and *I. balsamina* with red, white or dappled flowers. The naturalized *I. parviflora* DC. is a weed of wet and mesophilous forests along rivers and shady, disturbed areas with yellow flowers. The other naturalized species in Hungary is one of the most frequent invasive plants of the country, *I. glandulifera* from the section *Salpiglochilon* WARD. (Not identical with the endemic species of Sri Lanka described under the name of *I. glandulifera* ARN. which is only a far relative of this plant.)

MORPHOLOGY

Himalayan balsam is a tall grown (1–2 [–2.5] m), summer-annual plant (therophyte). The stem is erect, simple or sometimes branching, reddish transparent, sapful, cavernous, thick (0.5–5 cm Ø), wider at the nodes (at the lowest node –5 [–7] cm). The whole plant is glabrous. The roots penetrate into the soil only 10–15 cm and from the lower nodes the plant form binding/bracing collateral roots frequently, mostly after flowering or in sloping surfaces. The leaves are large (5–18 × 2.5–7 cm), 4–5 times longer than wide, opposite, the uppers are verticillate and in this case mostly by threes. (The other *Impatiens* species occurring sub-spontaneously in Europe have sparsely standing leaves.) The shape of the leaves is ovate-lanceolate, the base is cuneate and shortly decurrent, the apex is acuminate, and the margins are sharply serrate with (18) 25–50 teeth with aristate point on each side. On the base of the leaves and on the petioles claviform side-teeth sit. These are long stalked (2–3 [–5] mm), purple headed glands which – based on their extracts – are extrafloral nectaries. The leaves include naftochinon and procianidin flavonoids as chemotaxonomic character. The inflorescence is an axillary standing, clustering raceme with long axis, the number of flowers is (3–) 5–12. The flowers are hermaphrodite, strongly zygomorphic, proterandrous, calcarate, 2.5–4 cm long, sweetly scented. The peduncule is 1 mm thick and much shorter than the flower. The calyx is colored. The central sepal of the three sepals is apparently enlarged and flaring, because of the 180 degrees distorted peduncule standing opposite to the original axis of the flower. This 12–20 mm long and 9–17 mm wide central sepal is bright purple with dark spots, ended with an

abruptly narrowing, greenish, 2–5 (–7) mm long, tail-like calcar which is bent at right angle or more. The lateral sepals are small (about 10 mm long and 7 mm wide), triangular. The additional two sepals are missing. The pentamerous corolla virtually three-petaled, because of the upper and lower side petals adhered by pairs (the upper one is 7–9 mm long and 5–7 mm wide, which is almost one-third of the lower one). The central petal is widened, cucullate and forming the upper lip of the overturned flower, the color is purplish-red, the length is 12–17 mm and the width is 6–8 mm. The two lateral petals form the lower lip together which is paler (at the var. *rosea* pink, at the var. *candida* HOOK. [syn.: *lusus pallidiflora* HOOK. f. 1899] vary from white to flesh-color with red spots). The upper petal forms a characteristic hood above the stamens and the united side petals offer a prominent lip for the insects (from the viewpoint of flower biology the species is also called humble flower [Hummelblume] thanks to its most common pollinators). After flowering the whole corolla, with the nectary drop off. The androecium is reduced, with one circle (haplostemon) and pentamerous. The stamens are standing alternately with the petals and adhered at the anthers which protect the ovary as a cap. The growing ovary levels up the cap and tears the short and wide stamens at the base. The five-celled ovary developing from five carpels is inferior, the position of the placentation is axile, and the ovules are anatropous. The fruit is opening (loculicide) fleshy capsule. The shape of the fruit is lanceolate and considerably widening to the apex (claviform), slightly five-angled (15–35 × 4–15 mm) and pointed at the apex. The seeds are 4–16 pieces per fruit, without proteins, 3–4 mm long, 2–4 mm wide and 1,5–2 mm thick, the shape is oval-globose, depressed, the color is pale grey-brown, weights 20–350 mg per 1000 air-dried seeds, on the base of recent Hungarian measurements 8,28 g/1000 air-dried seeds (CSONTOS 2000). The seeds contain fatty oil and parinaric acid. The phenotypic variability show itself chiefly in the colors of the flowers (from white through rose to deep purple), in the growth of the plant and in the occurrence and type of branching. While at the last chances the phenotype can be modified by the accessible amount of water in the soil, the genetic background of the variable flower colors is unknown. Hybrids are not known. Number of chromosomes: $2n = 18, 20$.

ORIGIN, DISTRIBUTION

Impatiens glandulifera is native at the temperate and humid areas of the Western Himalayas. From Northern Pakistan (Chitral, Swat, Hazara provinces) to the East through Kashmir in North-West India (from Himachal Pradesh to the Garhwal province) it is common between 1800–3200 meters above sea level but presents till 4300 meters. The origin of its occurrence in West Nepal is not clarified. It was brought into Europe in the first half of the 19th century as ornamental and melliferous plant. The seeds of the plant were sent by dr. Royle from Kashmir to the Kew Gardens (London) in 1839. After the introduction, the first data of escape is really early (1848) and the naturalization also (1855). In the latter case it was the first plant of this behavior in England. Recently this neophyte species is distributed almost on the all area of the British Isles and is believed one of the most dangerous alien species. Himalayan balsam became well known ornamental plant from the beginning of the 20th century in the continental Europe. By the time it was escaped at many places (first data was recorded at 1897) and after it became feral plant and acclimatized in the temperate areas. Measured from this date it was a relatively long period – more decades – till it became an invasive plant. The lengths of latent period (lag phase) differ between countries, for example in Britain it was almost 80 years and in Bohemia it was only about 40 years long. In Slovakia and Bavaria the invasion began only in the 1960s and 1970s. By the opinion of WADE (1997) it seems that in Europe in the last three decades the invasion of the species fastened, independently the arrival date of the plant. For these days it is widespread over the most part of the continent to the latitude of 64° north. Its altitudinal distribution extends from colline to montane zone. In reference this absolute data is known from the British Isles (to 210 m), Switzerland (to 800 m), Bohemia (to 830 m) and Austria (to 1000 m). In mountainous regions it occurs among others in the French Pyrenees and in the Alps, but missing from the Central Alps. In North America it occurred in the state of West Washington (USA) and in the Fraser Valley of British Columbia (Canada). In the Carpathian Basin the first subs-

pontaneous occurrences on the Eastern side first in Transylvania (1892, Nagyszeben; 1917, Kolozsvár) and a bit later in Subcarpathians (1938, Latorca and Vicsa Valleys, now Ukraine) were recorded, where in few decades it spread over.

The first data from the later formed other main centre of the species originate from Vas County (1920, Felsőőr). The following data of spreading in Hungary in larger extent are known also from this county. The distribution of the plant in the last decades in Hungary was grown considerably like in the neighboring countries too. Chiefly along the larger rivers, less frequently along the brooks of the mountains and hill-countries it is still spreading in these days too. The populations of the species in smaller extent originates as escape from cultivation in the given region (e.g. Balaton Uplands) but the populations coming with water courses are much more important. It is common for example in the West (like along Rába river) and South-West Transdanubia (e.g. along Dráva river), along the Danube (multitudinous in the Szigetköz) and grows at some reaches of the Tisza and at some locations in the Zemplén Mountains.

LIFE CYCLE

Himalayan balsam is the largest herbaceous plant in Europe which at shady spots can grow as tall as two and half meters. All seeds germinate early spring (in Hungary in March), about at the same time. The smaller differences are caused by the depth of the seeds in the soil and the exposition. The measurements show that maximum density of the seedlings is 350 individuals/m², and after all 30-40 full-sized plant will persist per square meters. The type of the germination is epigeic which means the stem below the cotyledons (hipocotyl) elongates and this levels up the cotyledons. The seeds speciality is they can start their germination under water. For the breaking of the dormancy longer cold effect is needed (about + 4–5°C for 1–1.5 months), but the seeds die off at –10°C. On the base of TTC-tests the germination potential proved as 80%. The sown seeds germinate in 8 days. The roots start to develop 12 days after the start of germination and after four weeks the photosynthesis starts in the leaves. Between the germination and the beginning of the flowering is a 13 week-long period (at shady spots it can elonged by 2–3 weeks). The flowering is most intensive from July to August but it can begin in June and at the most shady habitats can lasts till end of October or beginning of November. One flower is flowering for 2–3 days; the flowers are markedly proterandrous, autogamous and entomogamous. German researches show the flowers are visited by 33 species of insects and the extrafloral nectaries by 25 species. Czech, English and German data show the most common visitors are numerous species of humble-bees (*Bombus* spp.), the bees (*Apis mellifera*), the digger- and German-wasps (*Vespa vulgaris*, *V. germanica*) among Hymenoptera, besides these the species of fruit-flies (Syrphidae, Diptera), different species of black-flies (Thysanoptera) and light-beetles (Nitidulidae, Coleoptera). The development of the seeds is completed about 13 weeks after the flowering and the semination endures from the second part of August to November. The fruit forming is complete only in the first opening (July–August) flowers but the high seed number of the fruits (6–12 per fruit) makes the propagation effective and the good potential of germination after the wintering. In Britain the average-growth plants in 20 individuals/m² populations yield 700–800 seeds per each plant which is about 15000 seeds/m². (In Germany one research of the same type showed twice of this number.) In less dense populations the seed production can be as high as 2500 seeds per plant (in England were measured 5000–6000 values!). The local spread works with a dynamic type of self-spreading (dinamochorous type of autochory) by a spinning semination of the capsules. In maturation the wall of the capsule, built from the ovary between the five longitudinal backsides at the valves, dehisce and roll up explosively and this movement throws the seeds up to 7 meters far. In WILLSON *et al.* (1990) spectrum of types the species belongs to the ballsits. The density value of the seed rain in this way can reach the number of 6000 seed/m². Measurements show with this mechanism the species is able to spread at the speed of 3–5 meters/year. As result of this strategy the dispersion of the populations are dense, cumulative or insularic. For larger distances the plant travels by humans or animals furthermore by rivers and streams. The spreading by humans (anthropochory) can happen consciously (flower seed trade, bee keeping) and accidentally by the transport of the seed-containing upper soil level. For the zoochory is mentioned as an example the seed collecting behavior of

some small rodents (like the wood mouse, *Apodemus sylvaticus*). If the spreading happens by waterways (hydrochory) the seeds are floating, later sinking down in the water, in this way they are transported mostly in the deeper section of the riverbed with the sediments (bithysohydrochory) and only in case of stronger floods reach the banks. An example for this is that along the Rhine from Basel to Karlsruhe which is farther than 200 kilometers the plant attained in 30 years which means about 7 km/year (GÖRS 1974). The species does not build up permanent seed bank but the seeds can survive more than a year. The on field surveys show that the seeds stay at the surface of the soil, the viability was 18 month and at room temperature 3 year long. Along rivers the seeds buried by the sediment can preserve their germination potential for longer times. Because of this if a newer flood clear down the upper layer of sediment the population can revive from the buried seeds "suddenly". In the case of this annual plant the asexual or vegetative propagation is not characteristic but some circumstances can make it possibly. The stems pushed down by flood from the nodes start to develop additional roots to strengthen themselves. The still lying specimens' side branches can erect and later possible to develop flowers and fruits. The broke-down parts of the stem can work as special propagule type and in the case of strong floods can travel very long distances like other waterside plants do it too. The species is very sensitive to frost as plantlet and as mature plant. Following the autumn frosts the plants die. The holocellulose content of the plant is high therefore the remnants of died plants in the next spring still covering the soil and delay the germination of other species by this.

HABITAT PREFERENCE

Himalayan balsam is native to the humid-moist part of the subtropical climate zone at mountain areas with moderate monsoon effects (PET [potential evapotranspiration]: 0.25–1, precipitation: 100–2000<, annual average temperature: 18–24°C). The plant grows in alluvial rainforests and clearings, at higher altitudes in tall herb fringe communities along mountain-brooks, along dikes and borders of roads. Its presence is characteristic in the scrublands and pastures of the Himalayan cedar (*Cedrus deodara*) mixed forest zone. The European range of *I. glandulifera* covers temperate areas (PET: <0.25–2, precipitation: 250–1000, annual average temperature: 6–12°C). It has competitive-ruderal strategy. The plant is thermofrequent but in direct sunlight it is rare to grow so mostly lives in half-shade. In direct sunlight it can grow only that places where it is possible to take up water abundantly. Because of its higromorphic structure the presence is limited almost exclusively to the wet habitats (the pauperitic specimens of drier habitats has short internodes and small leaves). The plant likes the rich, humic clay, loam and alluvial soils. It needs more or less bare soil surfaces. The most of the authors thinks the soil acidity is indifferent, but SOÓ (1966) says it is calcifrequent. It was not found on salty and alkaline soils. As water and half shade demanding plant with uneven water balance (hydrolabile) the ideal habitat is rich in water and nutritives all year long and regularly opens up because of the removing the plant coverage by flood. (By hypothesis of VALENTINE [1971], the plant occupy an ecological niche, which is almost unused, or at least the competition is small in it.) It resists the short flooding but can not endure longer water coverage. (COOMBE [1956] observed in England if the plant occurs together with *I. parviflora* the latter grows farther from the level of the water and the *I. glandulifera* closer, at the lower grounds.) The late spring frosts can harm or kill the young plants. In this case the plantlets rising from the later germinating seeds will follow. The intense frost-tenderness limits the geographical distribution of the species. After all *I. glandulifera* likes the atlantic/suboceanic climate. The spectrum of habitats is really wide but centered to the habitats with large productivity and moderate disturbance. The species does not exist in habitats with very low productivity and strong disturbance.

I. glandulifera is most frequent along brooks and rivers and in flood plain vegetation, mostly in the willow bushes and alluvial willow-poplar forests and in tall herb fringe communities. The stands can be dense below the characteristically opened canopy of different alluvial forests, along the ox-bows with altering water levels and also in artificial forests (for example plantations of poplar hybrids). Less frequently it occurs in alluvial mixed oak-elm-ash (*Quercus-Fraxinus-Ulmus*) and alder forests and in the mesic forests of hills and mountains where the antropogenous disturbance is high and it can propagate

from these sites. In numerous cases the plant occurs on damp fallows and ruderal areas near the water. Investigating the neophytes in wetlands along the Rur river (western Germany), extreme fluctuations were recorded in the population size of *I. glandulifera*, with temporary colonization of reed communities in large quantities in some years, and total regression in other years. These processes are influenced by ground-water tables and river floodings.

BIOTIC INTERACTIONS

The solution made from the leaves of the allied *I. parviflora* in vitro watering slightly decreased the germination ability of mustard seeds to the control (CSISZÁR 2005). On the British Isles the sheep and cattle graze the leaf, stem and flower of *I. glandulifera* without any selecting. In Germany (near Bonn) SCHMITZ (1991) found the following consumers and pests (the most important species mentioned only): snails (Gastropoda): *Arion rufus*, *Succinea putris*. Homoptera: Aphididae (*Impatiens asiaticum*, *Aphis fabae*), Cercopidae (*Aphrophora alni*), Cicadidae, Ortheziidae, Psyllidae, Aleurodidae (?). True bugs (Heteroptera): Miridae, Lygaeidae (*Lygus* spp.), Pentatomidae. Flies (Diptera): Agromyzidae (*Liriomyza impatientis*), Cecidomyidae (?). Springtails (Collembola): Sminthuridae. Butterflies, moths (Lepidoptera): Sphingidae, Tortricidae, Geometridae (?). ALLEN (1949) mentions the larvae of *Deilephila elpenor* (Sphingidae, Lepid.). By SCHMITZ (2001) in Central-Europe the guild of 21 aphidophagous insect species (not included parasitoids and ectoparasites) and 5 ant species (as trophobionts) can be conjunct with the *I. glandulifera*. Parasites and diseases of the plant are not known in Europe. In British samples few cases of vesicular-arbuscular mycorrhiza, while many epiphytic fungi were found.

ECONOMIC IMPORTANCE

The nut-flavored seeds and cooked young leaves and shoots said to be edible. The oil of seeds can be used as aliment and it is good for lamp oil too. In its native area it is used for nail and skin painting. In the Oriental medicine it is known as a balm plant. Recently the Bach's flower therapy uses the plant in the natural healing. In Europe not really frequent, it became more known from the 1920's as easy spreading ornamental plant of moist habitats. Together with other *Impatiens* species it could be nectar and pollen giving pasture for bees in summer and autumn but not considerable because the bee keepers (and bees) visit the flood areas only rarely. *I. glandulifera*'s direct damage is the retardation of spontaneous renewing in the forests of the flood areas and of the artificial rehabilitation of regulated water courses. Because of its shallow roots easily turn out from the soil and therefore the large stands can endanger the stability of riverbanks.

NATURE CONSERVATION SIGNIFICANCE

Although in Central Europe the plant means not so high risk as for example on the British Isles with moister climate but it has to be considered as potentially important invader because of its increasing spread in Hungary. In terms of nature conservation *I. glandulifera* is a typical ecological weed. With its dense stands overgrow and repress the native plant species (the perennials also) and the associations of the habitats. In the alluvial and the near-to-water forests it retards the natural renewing. The plant intrudes to the backwaters of the rivers and in the case of longer drought can crowd whole channels. Because of its strong invasive and transformer character it endangers the presenting native species and decreasing habitat diversity. The mass of the numerous and simultaneously germinating and developing, fast growing plants guarantee the competitive success over the native species and not only at the opened sites as it normally affirmable in the case of annuals. In this competition only few native species can stand which has really strong vegetative propagation strategy (too) like *Urtica dioica*, *Phalaris arundinacea*, *Calystegia sepium* and *Poa trivialis*. Himalayan balsam is a migrant plant, the renewing of the populations needs continuous seed supply. The seed supply of the stands along the rivers generally originates from the upper reaches. The spreading is related to the human destruction of the natural alluvial

plant associations. In the places of waterway-regulations, clear felling and hybrid poplar plantations the ability of its spreading is increasing. This progress antagonizes the natural regeneration and the man-made reconstruction of the close-natural ecosystems along the partly artificial water courses. PROTS *et al.* (2004) found that the high resistance to herbivory and high invasion abilities of *I. glandulifera* may lead to a decrease of biodiversity of native herbivores within invaded sites and may have serious ecological and conservation consequences.

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SMALL BALSAM

(*Impatiens parviflora* DC.)

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TAXONOMY

In the *Impatiens* genus belonging to the Balsaminaceae family are about 850 species, most of them native in the tropics of the Old-World. Eight species of *Impatiens* live in the temperate zone of the Northern hemisphere: two of these in North America, four in Japan and Korea, one in Eurasia (*I. noli-tangere* L.) as well as one native in Eastern Siberia (*I. parviflora* DC.). In Europe present five *Impatiens* species beyond the native *Impatiens noli-tangere* L.: *I. balsamina* L., *I. capensis* MEERB., *I. balfourii* HOOK., *I. glandulifera* ROYLE and *I. parviflora* DC. *Impatiens parviflora* belongs to the *Brachycentron* section and *Micropetalae* series inside the *Cauliimpatiens* subgenus. The European population shows little degree of genetic variability, JØRGENSEN (1927) described the white flowered variety *albiflora* with yellow spotted corolla and the forma *albescens* which has white flowers with orange spotted flower throat. Despite of these the native population in Central Asia is very polymorphic.

MORPHOLOGY

It is annual, bare, generally 20-60 cm tall plant which can be as low as 10 cm or as high as 150 cm sometimes. The rootage is shallow with small extent, the side roots grow stronger than the main root and the stem forms additional roots frequently. The stem is straight, bare, translucent and widening at the nodes. The free standing plants can branch richly but the plants in crowded populations usually not branching. The lower part of the stem usually leafless, the upper part is branching, with leaves, pale green colored or at sunny places maybe tempered with red. The leaves are helically but the two lowest leaves standing opposite. The leaves has petiole and the length of the petioles decrease gradually toward the apex of the stem, on the lowest ones it can be as long as 4 cm but on the upper ones only about 0.5 cm. The leaves are 3-17 cm long and 4-8 cm wide, ovate, elliptic or wide-lanceolate. The base of the leaves is cuneate, the tip acuminate or acute, the margins are serrate, the number of the serrations is 13-35 pieces on both sides. On the margin at the base petiolate glands (extrafloral nectaries) are sitting. The inflorescence is apical raceme which generally bears 4-15 flowers. The flowers are zygomorphic, 7-15 mm long, the corolla is pale yellow, sometimes white, and the throat is darker yellow with thin red patterns. Among the five sepals the two frontal are reduced, the two laterals are rudimentary, green and about 3 mm long. The back sepal has the same color as the petals, it forms straight spur with 5-10 mm length. The corolla is five-parted, the lateral and back petals are coalescing by pairs, and the frontal petal is large, it can be 10 mm long. The five stamens stand alternately with the petals, the filaments are freely standing, and the anthers grow together. The pistil is formed by five carpels, the ovary is superior, and the capsules are 15-25 mm long, bare and long claviform. The fruits are dynamochor with (1-) 2-3 (-5) seeds, the seeds are brown colored, 3-5 mm long and lengthwise finely striated.

ORIGIN, DISTRIBUTION

The native area of the small balsam is Central Asia, although the exact distribution of the species inside this area and at the borderlands of Central Asia is not clarified adequately. TREPL (1984) analyzed the works about the flora and collected the possible data of occurrences but denotes that in the botanical literature the original distribution area of the species is false in many cases. The “Flora Altaica”, the “Flora Sibiriae Occidentalis” and the “Flora Usbekistana” note the small balsam from the country of the Altai, River Irtis and from Western Siberia. The species is probably native in Mongolia, on the country of the Altai-Irtis, in Sinkiang in the Thiensan and in the Jungarian Altai. According to the “Flora Usbekistana” the Pamir Altai and the Himalaya also belong to the distribution area of *Impatiens parviflora* and in the latter mountains live in height between 2100–3000 m above sea level. Over the native range the small balsam presents almost in all countries of Europe: it is introduced into Austria, Belgium, Bohemia, Croatia, Denmark, Estonia, Finland, France, Germany, Great Britain, Holland, Hungary, Italy, Liechtenstein, Luxembourg, Norway, Poland, Romania, Switzerland, Slovakia, Slovenia, Ukraine and into Canada also. The western border of the actual European distribution is Great Britain except of the extremely oceanic areas of Scotland; the eastern border is Transylvania, Estonia and Lithuania. On the south the area does not reach the submediterranean zone but dispersedly occurs in some valleys of the South Alps; on the north it can be found till the southern part of Finland and central areas of Sweden but the occurrence in Norway is very rare.

The introduction of the small balsam in Europe is probably the result of accidental import by trading activities. GRAEBNER and JØRGENSEN have found small balsam plants in 1831 escaped from the botanical garden of Geneva but they did not publish this data. By the notification of DE CANDOLLE the 1837th year became the official time of the escape which is also the first date of the European subspontaneous occurrence. The earliest German data originates from 1838 Dresden and after this the species spread fast in Germany. After the occurrence in Switzerland and Germany the small balsam turned up in 1848 in Great Britain too, where in 1930 it was known at 45 locations. It reached North Europe in the 1850s: in 1850 occurred in Finland, in 1960 in Denmark, in 1876 already presented in Sweden. In Norway the occurrence of the species is only dispersed, in 1952 it was known only at three locations. In the Netherlands relatively late occurred comparing to the countries above, the first record originates from 1895. The first appearance in Poland happened about in 1850 and two years after this the small balsam appeared also in Estonia. In 1861 it was noted from the Austrian Graz, in 1868 from the Ukrainian Lemberg and in 1869 from the Belgian Zegelsam too. In 1871 ČELAKOVSKÝ described stands of the small balsam on the isles of Prague and by his opinion the plant escaped from the city botanical garden with the flooding river. From France the first data of occurrence originates from Alsace and 1872. In Hungary and Slovakia the first data of the small balsam were observed in 1890. In the Romanian works of flora the plant is discussed as cultivated garden plant and subspontaneous in Transylvania, although for example on the Hargita it spreads spontaneously as it seems (ex verb BÍBORKA KUI). Outside Europe the small balsam is known as alien only in Canada.

In the beginning phase of its invasion the small balsam mostly occurred in botanical gardens, parks, cemeteries then after the conquest of ruderal habitats it reached the near natural forests too. HEGI wrote in 1925 that the species has large populations especially in the parks, gardens, along roads and only seldom occurs in more shadowy broad leaved or pine forests and bushes, although occasionally in these habitats also can be abundant. Moreover he noted the small balsam may settle on riversides, railway-embankments and cauliflower fields. An extending research carried out in Westfalia in 1977 the analysis of 800 phytosociological relevés showed that in this time the small balsam had no role in the forest ecosystems, the plant presented only in four samples, once in alluvial forest along a brook and three times in submontaneous beech forests. Opposing to this in 1978 CWILINSKI experienced its presence in natural communities at many locations. In 1984 by the analysis of more than 1500 phytosociological relevés TREPL classified the communities in which *I. parviflora* were presenting. According to this analysis the species presents in seven classes and twenty orders that implies the wide ecological range of the small balsam. In Hungary VINCE BORBÁS found firstly the small balsam in 1890 on the Isle

of Margit beside the ruins of the Chapel of Margit. SÁNDOR POLGÁR found the plant between Ásvány and Lipót on the isles of the Danube in 1913 and BÁLINT ZÓLYOMI found the species in 1928 at Dunacsun (today belongs to Slovakia). The early data of the plant originates from the Bakony Mountains: in 1933 a departmental excursion led by GÉZA LENGYEL found the species in the Burok Valley, moreover in 1942 REZSŐ RÉDL mentioned the presence of the plant beside Várpalota in the Valley of the Séd. REZSŐ SOÓ noted the species in Debrecen and JÓZSEF JEANPLONG in Szombathely, ÁDÁM BOROS collected it in 1943 beside Szigetújfalu, then in 1949 beside Ráckeve. The following data of the presence also originates from the areas along the Danube: by IMRE TÓTH, Lower Floodplains of the Danube; by ISTVÁN KÁRPÁTI beside Göd from oak-ash-elm alluvial forests; by ISTVÁN GONDOLA between Dunakiliti and Bezenye from white poplar alluvial forest moreover he found the small balsam along the River Lajta and Stream Gyöngyös in Himalayan balsam-bindweed community. SZANISZLÓ PRISZTER when in 1965 summarized the Hungarian data about the small balsam established that „the Central Asian originated *I. parviflora* L. appeared around 1890 in the country at more and more locations but – despite of the situation on the areas to north and to west from us – in our country it did not become common weed and today frequent or facies forming only in some locations (mostly in the Floodplains of the Danube)”. Five years later beyond the alluvial forest Soó notes the presence of the species in Turkey oak-sessile oak forests of the Hungarian mountains, in the mesic oak forest of the Nyírség and in weed associations of forests and floodplains.

LIFE CYCLE

The seed production of the plant is variable in wide range. In some forest populations may be individuals which bring only few capsules with only one seed inside and present non fertile plants too. Despite of this under suitable conditions, in the case of enough light, water and nutrients the well developed, tall plants can reach four-five seeds per fruit, and the thousand or two thousand seeds per plant neither rare, which means on a hectare about 30 million seeds in a year. Alone standing plants under favorable conditions can bring as many as ten thousand seeds in the three months of the fruit growing.

TREPL (1984) observed in alder forest averagely 90 seeds on a single plant and in hornbeam-oak forests about 10-30 seeds. Different data can occur under the mentioned conditions too if the counting happen in different times. The main fruit ripening period of the small balsam is in August. In Hungary the investigated individuals in the Sopron Mountains yielded 123 fruits in average and the average seed number per fruit was three.

KINZEL (1927) in his germination experiments got 0% result with the seeds stored at room temperature but with the seeds stored before the treatment at -5°C degrees the germination was 100%. COOMBE (1956) stored the seeds at +5°C among wet circumstances and on the 3rd day after starting the experiment he booked 100% germination and proved that the germination not absolutely necessary the effect of frost. In BAUER'S (1951) the experiment from 136 seeds treated with the cold of winter 5 germinated and 35 were destroyed by fungal diseases, in an other experiment of the author bring 9 germinated seedlings from 39 seeds but the repeating of the experiment was unsuccessful. JOURET (1974) analyzed the needs of the germination under standard and changing thermal circumstances too and found the range between 0°C and +5°C degrees as ideal from the viewpoint of the germination. In the course of the germinating experiments the authors got different results, the reason of this can be the different storing conditions before the stratification of the seeds. TREPL enlightened the length of the stratification necessary to release the dormancy depends on the ripeness of the seeds, the moisture, the substrate and the length of the storing before the stratification. The ripeness of the seeds, the moist conditions and the shorter previous storing decreased considerably the needed stratification time and the earlier occurrence of the seedling was helped by the storing in heavily acidic soil or in pine needle. In his collateral open ground and laboratory experiments he made detailed investigation about the effects of the substrate, the seed size, the ripeness, the cover, the storing time and depth and the compactness of the soil to the developing seedlings. Seeds treated with low temperature directly after the collecting and stored for two and half years reached low percentage of germination. The small, midsized and large seeds did

not show notable differences in germination, corresponding to the prediction the smaller seeds germinated in lower percentage. The open ground germination of seeds with different ripeness varied considerably, the seeds collected as unripe showed delay in the germination and the six time larger proportion of the ripen seeds germinated in March. Other determinants like the substrate, the depth of the sowing and the coverage of the seeds or the compactness of the soil did not cause significant differences. The number of seedlings were hardly reduced by the early spring frosts but despite of that the hardiness of the seedlings were dependent on the phase of the developing as the later germinated seedlings proved more hardy against the effects of the frosts. As a summary TREPL stated the large quantity of the seedlings occur in spring is not interpretable with the sudden end of the dormancy but it is the aggregate result of numerous factors. The most of the seeds start to germinate in January namely the radicle penetrate the epispERM in this time, but the seedlings occur only after a longer mild period. The earliest detected seedlings shooted out on 15th of January. According to observations carried out in Germany the most of the seedlings brake through the surface of the soil in the first half of April which is similar to our experiences from the Sopron Mountains. The germination of the small balsam usually more or less ends until the beginning of May. The growth in length is most intense from the middle of May to middle of June. With the appearance of the fruits the growth slowing down, sometimes stop absolutely but at shady habitats and in case of adequate water supply it can be continuing until the end of the summer. The flowers generally show up in the last week of May or in shade in the first week of June, the ripening of the first seeds follows this by 3-4 weeks. The flowering and the ripening of the fruits is continuous until the end of September or beginning of October but in case of favorable weather conditions possible to see flowering plant in April or November too. The early, diseased or not so vital flowers are frequently self pollinating – in opened or closed position (chasmogamous or cleistogamous) – and the later flowers are geitonogamous (pollinated by other flowers of the same plant) or xenogamous (pollinated by flowers of other individuals). The flowering of a single flower expands 1-2 days from the opening of the flower bud to the falling of the corolla. The reciprocally pollinating flowers are proterandric. The female period of the flowering namely that time when the stigma is ready to accept the pollen is judged differently by each author. The size, shape, structure of the seeds and fruits and the seed production does not differ by the actual pollination types. The flowering expands about to 4 months but the seed yielding period is barely shorter than this. None of the herb species of forests presenting together with the small balsam flower longer than two months therefore this characteristic in its production biology promote its success. The species can spread with autochory along the anthropochory because of the different turgor of the inner and outer fruit wall: the carpels segregate at the peduncle and fast roll up towards the apex of the fruit which movement shoot out the seeds. With this mechanism the seeds can fly as far as 3-4 meters from the parent plant.

HABITAT PREFERENCE

Soó (1970) described *I. parviflora* rather acidofrequent, nitrogen demanding species which presents on moist, loose, nutrient rich, lightly acidic loam, alluvial or sand soils. According to the ecological indicator values by BORHIDI the small balsam is plant of moist, moderately nutrient rich, slightly calcareous habitats and on the base of light demand is a shade or half-shade plant. The Hungarian investigations proved the presence of the small balsam in the Kőszeg Mountains on acidic (average pH: 4.5) soil with good content of nitrogen (total nitrogen content was 0.45%), on the sandstone of the Hárshegy on acidic (pH: 4.6) and heavy acidic (pH: 4.15-4.2) soils. Accordingly the small balsam can occur on soils of wide range from the strongly acidic through the acidic to the slightly calcareous soils. At the habitats of the plant in the Sopron Mountains the characteristics of the soil on the base of instrumental measurements show neutrality and most of the presenting species also have neutral soil reaction ecological indicator values or indifferent species with wide ecological tolerance. In the investigation of the nitrogen demand and total nitrogen content the ecological indicator values were dominant in the range of the mesotrophic and nutrient rich soils, the instrumental measurement showed humus rich soil.

In England in the presence areas of the small balsam the annual average precipitation is between 630-890 mm. Most of the habitats are sheltered against the wind and are partly (5-40%) in shady positions. The small balsam can live on more type of soils, if that is loose, well aerated, with good supply of water but it is not flooded, and contains in moderate or high amount of base but not necessary calciferous, the pH ranges between 4.5 and 7.6. The subsoil is alluvial (mud, deposit, sand, gravel) or loess. In England the species primarily lives on rendzinas, brown forest soils or alluvial soils.

ELIAS (1999) researched the invasion of the small balsam in the Central European forests and mentioned the lower demand of nutrients and better adaptation to the shadow moreover among the limiting factors emphasized the summer drought, the low temperature in the early spring and the high temperature in the end of spring and summer.

BIOTIC INTERACTIONS

The watery extract of the shoots proved slightly allelopathic to the seeds of the white mustard (*Sinapis alba*) If the mustard seeds watered with the extract of the small balsam, the rate of germination fall behind the control and differences were shown between the effects of the extract depending on its degree of concentration. In the case of using extract of 1 g/100 ml degree of concentration the rate of germination was 94.66% and with 3 g/100 ml 93%. The rate differed only in small proportion from the control group, the difference is not considered as significant. The mustard seeds treated with 5 g/100 ml concentration extract differed considerably from the control, only 86.66% of the seeds germinated and on the base of the χ^2 -test it is significant. The extract of the small balsam decreased only to a small degree, although the effect of the 5 g/100 ml degree of concentration was proved as significant to the germination of the control group and this can confirm slight allelopathic potential. But the existence or missing of this effect necessary to prove by open-ground experiments.

On the wild and cultivated *Impatiens* species live 19 species of phytopathogen fungi, five of them found also on *I. parviflora*: one species of powdery mildew (*Shaerotheca balsaminae*, Erysiphales), two Sphaeropsidales species (*Ascochyta impatiensis*, *Phyllosticta impatientis*) and two rust fungus (Uredinales) species (*Puccinia argentata*, *Puccinia komarovii*). The listed species are Central European except of the *P. komarovii*, which followed the host plant about with a century long delay from Central Asia to Central and East Europe. The fast spreading of the *P. komarovii* is well illustrated by that fact in two decades after its first occurrence in Europe was found almost in all of the Central and East European countries. In Hungary GUSZTÁV MOESZ (1940) found it firstly at Budapest in the Hűvös Valley but in the next year he could not find the fungus again. All of the generations of the fungus live on *I. parviflora*. The ecidiospores infect the stem, mostly on the lower and middle part, moreover the seedlings or the cotyledons too. The infected parts of the plant swell and bent, some of the plants die because the infected parts of the stem start to rot. Other plants survive with decreased vitality and yield flowers and fruits. The uredospores occur on the underside of the leaves about from June until September and teleutospores also occur on the leaves in the autumn. As it is experienced in the Kaniv Nature Reserve at the middle section of the River Dneper the sporophore of the *P. komarovii* and the seeds of *I. parviflora* ripen simultaneously. The number of the infected plants is variable between populations but occasionally it can be very high: according to the observations carried out by TREPL (1984) in the early spring of the year 1976 at numerous locations near Berlin the infection was 10-40%, COOMBE (1956) in August and June of 1951 hardly found healthy leaves for his experiments in the forests beside Heidelberg. BLUMER experienced the strong invasion of the *P. komarovii* and the death of the infected plants in 1938 in Switzerland. ELIAS noted the 65-90% infection of the small balsam plants in the April of 1987 and 1994 moreover later in May 100% mortality of the infected plants in West Slovakia. CSISZÁR (2004) in the Sopron Mountains by the examination of 100 individuals found on 21 the uredo- and teleutospores of the *P. komarovii*. Although by the time of the observing in the beginning of May 21% of the plants were infected considerable, damage and loss of vitality on the plants was not detectable. The actual damage caused by *P. komarovii* difficult to judge because some of the plants infected by the ecidiospores die, the surviving plants bring flowers and yield seeds maybe with less vitality.

Among the parasitic plants most species of the *Cuscuta* genus can occur on the small balsam but the arm usually is inconsiderable.

VOGEL (1943) and COOMBE (1956) reported the tunnels of the larva of the *Phytoliriomyza melampyga* (the authors mention the species as *Liriomyza impatiensis* by its previous name) leaf-mining fly on both epiderm of the leaves. According to SCHMUCKER's and DRUDE's (1934) opinion the individuals of the plant were considerably harmed by a bug called *Lygus pabulinus* but it can not be found on *Impatiens noli-tangere*. MINNION and GOODBAN (in COOMBE 1956) found the larva of the *Xanthorhoe birivata* (Geometridae) on the small balsam, and DAUMANN (1967) emphasized the ants looking for the extrafloral nectaries of the plant. SCHMITZ in his work published in 1999 scanned in details the organisms connecting to the small balsam: herbivorous mammals, phytophagous insects, flower visitors, the visitors of the extrafloral nectaries, the phytopathogenous fungi, parasitic vascular plants, the aphidophagous animals moreover compared the herbivore diversity of *I. parviflora* and its surrounding herbal neighbors. He lists as consumers of the small balsam 13 phytophagous insect species and one snail feeding on the leaves (*Cepaea* sp.). Nine species of the phytophagous insects are polyphagous and three of them earlier were known only in large numbers or exclusively as pest of the native touch-me-not balsam (*Impatiens noli-tangere*), and one is an introduced species originating from the native land of the small balsam. The last species, the Central Asian aphid, the *Impatiendum asiaticum* followed its host plant later than that naturalized in Europe and settled also on the Himalayan balsam but until these days it is not found on the touch-me-not balsam. SCHMITZ (1995) experienced in the case of the *Impatiendum asiaticum* 52.1% concernment among the plants.

The weakly developed extrafloral nectaries can bear only inconsiderable food source. Among the flower visitors the most important species belong to the hoverflies ("Schwebfliegenblume" = "hoverfly-flower"), which collect nectar and pollen from the flowers. Until recently 19 species of hoverflies were observed and the larvae mostly develop on the small balsam. The representatives of other insect families play only secondary role in the pollination. Except of the arachnids forty aphidophagous (plant-louse eating) species exist on the small balsam among them the hoverflies have prominent importance with 21 species. The latter group of insects are linked closely because both of the flower visitor imago and the aphidophagous larva too. The rich aphidophagous fauna is owing to the colonies of the *Impatiendum asiaticum* with large number of plants. STARY and LASKA (1999) observed ants too collecting honey-dew on the aphids and the presence of the small balsam – although it is a vigorously spreading species – judged as positive at some locations because of its aphid what increase the hoverfly populations. SCHMITZ (1995) compared the fauna of the small balsam to two other *Impatiens* species, the fauna of *Impatiens glandulifera* and *Impatiens noli-tangere*. He experienced essential differences by the three species and found that the reasons beyond the origin (native or alien) caused primarily by the different morphological characteristics. He observed the most phytophagous species on the native touch-me-not balsam, the most aphidophagous on the small balsam which is frequently infected by aphids and the most flower and extrafloral nectary visitors on the Himalayan balsam because among the three species it has the most developed extrafloral nectaries and the largest, most aromatic flowers with the richest nectaries. The author also compared the phytophagous fauna of the small balsam to plants of the same habitats but belonging to other genera. As result he got comparatively low number of species in the case of the small balsam, but higher abundance than at the phytophagous species of the other plant species. The reasons of the lower species number can be the shorter lifetime, the structure and that at the location of the research only one species of the *Impatiens* genus lives which mean some handicap comparing to the species rich genera.

CSISZÁR (2004) investigated 100 individuals of small balsam in the Sopron Mountains and noted the number of insect species in the following groups: phytophagous, phloem suckers, aphidophagous, predators, parasitoids and flower visitors. The research proved 17 insect species and 1528 individuals (among these 1442 aphids) as directly or indirectly linked by feeding to the small balsam. The most considerable phytophagous insects of the small balsam were the leaf-mining flies, presented on 34 leaves of 20 plants. Except of these two other phytophagous species were found with one individual each, belonging to the leaf beetles (Chrysomelidae). Considering the number of infected plants and

number of insects the most important group in the insect fauna of the small balsam is the phloem suckers. On 74% of the investigated plants were presenting aphids (Aphididae). From the two identified species (*Impatiens asiaticum*, *Aphis fabae*), *Impatiens asiaticum* is a new species for the Hungarian fauna and the first representative of that genus (RIPKA & CSISZÁR 2008). Beyond this group only one individual of the plant bugs (Miridae) enriched the group of the phloem suckers. On the rich colonies of the aphids were based the next level of feeding: 22% of the plants were visited by ants (Formicidae) probably because of the honey-dew. In the role of predators beside the assassin bugs (Reduviidae) lived spiders, 15 individuals of 4 families (Linyphiidae, Agelenidae, Thomisidae, Clubionidae) which probably fed on ants. In the course of this research only very poor flower visitor fauna was observed with forest cockroaches (Ectobiidae), darkling beetles (Lagriidae) and tumbling flower beetles (Mordellidae) but in the following year numerous hoverflies were observed. Among the leaves of the small balsam often live spiders although in forest ecosystems the frequency of the spiders is about 50-200 individual/ m² in which relation the arachnid fauna of the small balsam may be not so considerable. SCHMITZ (1999) compared the balsam populations and the neighboring native herb associations and found that the arachnid fauna has no characteristic differences either in species number or in abundance. But he noted that in the case of settling at earlier herbless habitats the spiders can find more favorable conditions. The small balsam as food plant for herbivorous mammals is less known. The only known is that the roe sometimes feed on the shoots of the plant. The touch-me-not balsam containing similar compounds can be good hay for cattle.

ECONOMIC IMPORTANCE

The economical and primarily forest economical implication of the small balsam on the base of the current knowledge hard to judge, many investigation should be done before. In some afforestation where large dominance of *I. parviflora* arrested the growth of oak seedling, using herbicides the germination of small balsam was successfully hindered. For example the effect of distribution of the small balsam on the soil fauna, on microclimate or on the renewal of the forest hardly known today.

NATURE CONSERVATION SIGNIFICANCE

The estimation about the nature conservation significance of the small balsam changed many in the course of time. HEGI (1925) mentioned the species as alien plant of near natural forests which outgrow its native relative, the touch-me-not balsam. Later on the base of the different ecological demand of the species SUKOPP (1962) contradicted this statement. TREPL's (1984) observations proved that the touch-me-not balsam only at the suboptimal, bit drier habitats fall back against the small balsam and in optimal position, at moist habitats it keeps its area and dominance. Until these days we have no evidence of absolute suppression of any native species by the small balsam in any habitats. In the most cases similar to other annual plants occur only at bare surfaces and form large colonies only here. Its strong penetration was observed primarily into nitrophilous, in light relatively rich border communities. In these habitats along favorable conditions for germination and growth it became dominant species of the summer aspect and it was the concurrent mostly of the *Geranium robertianum*, *Geum urbanum*, *Chaerophyllum temulum*, *Alliaria petiolata* and the *Chelidonium majus*. OBIDZINSKI & SYMONIDES (2000) researched the expansion of the small balsam in alluvial forests and moist forests and experimented significant negative correlation between the species richness and cover of the herb layer moreover the frequency and abundance of the small balsam. Farther they stated the small balsam can penetrate into floristically impoverished, degraded communities but the natural stands with dense herb layer can work as effective blockage against the expansion of the species. The spreading of *I. parviflora* is helped by every disturbance that form favorable habitats and ensure conditions for the germination and seedling growth.

SCHMITZ (1999) in the valuation of the ecological consequence of the small balsam denotes that the effect of the invasion is not uniform to the native animal and plant associations but locally different. He detach three possibilities on the base of the effects: 1. The expansion of *I. parviflora* narrow down the

native species, the cover decrease or these plants vanish from the area; 2. the role of the species is “Lückenfüller” (“leak filler”), it co-exists with other species without narrowing down the others; 3. the species settles habitats in which the native species do not flourish.

During the early phase of the settling in Europe the small balsam lived primarily in botanical gardens, parks, fences, gardens, cemeteries and the other synantropic habitats like the ruderal habitats, railway surroundings, factories and loading station start to play considerable role in the spreading of the species. After its first occurrence only 50 years have to gone while the small balsam from the disturbed areas near settlements penetrated to the near natural vegetation and spreading explosively in the adjacent forests. According to the Hungarian experiences for the spreading of the species the disturbance is favorable, the plant often occurs along forest roads, loading stations or in the case of too high number of big games. But the presence of the small balsam is not limited to the disturbed parts of the forests, it spread fast in the near natural forests also. Naturally the ecological importance of the species is locally different in Hungary. On the base of the investigations in the Sopron Mountains the plant primarily fills the „empty gaps” where other plants do not thrive. Despite of this the plant year after year occurs on disturbed areas or bare surfaces and go ahead in wide belt colonizing new areas, so its effect is enduring and presenting year after year therefore the other plant species maybe not disappear but can be narrowed down at the given habitats.

Based on the low level of variability of the phytophagous organisms connected to *I. parviflora* compared to the native species, it is possible to imagine that the expanding, continuous populations cause the decreasing of the faunistic richness locally. But it is not true under all circumstances because the effect upon the fauna also depends on the habitat conquered by *I. parviflora* and the consumer organisms. As it was mentioned before some authors judge the spreading of the small balsam at some location positively from the viewpoint of hoverflies and spiders. Among the native insects the *Phytoliriomyza melampyga* leaf-mining fly which originally live on the touch-me-not balsam was successful in the settling on the two neophyte *Impatiens* species and by this conquered the river banks and the relatively drier habitats of the forests.

Among the negative effects of the alien species, it has to be mentioned the imported pests or consumers which can be endangering to the native species too. In the case of the small balsam two of this type of organisms is known, the phytopathogen fungus *Puccinia komarovii* and the aphid *Impatientinum asiaticum* which settled successfully on the other alien balsam species *Impatiens glandulifera* but until these days is not found on the native *Impatiens noli-tangere*.

The alien species also have virus spreader effect which can endanger the native species too. The polyphagous *Aphis fabae* plant louse can spread the cucumber mosaic virus which has wide host plant spectrum but because the virus and the plant louse seldom present on the species together its role in the spreading of the virus is negligible.

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COMMON MILKWEED

(*Asclepias syriaca* L.)

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TAXONOMY

Asclepias syriaca belongs to the family of Apocynaceae, subfamily Asclepiadoideae, whose members' number is about 2700, mostly with tropical and subtropical ranges. In Hungary there is only one genus representing the Asclepiadoideae subfamily, i.e. two native species of *Vincetoxicum*: the common swallowwort (*V. officinale* = *V. hirundinaria*) is common in arid grasslands and sandy shrub communities, whereas the Hungarian swallowwort (*Vincetoxicum pannonicum*) has hybrid origin, and is strictly protected. These two species cannot be confused with the milkweed.

There are about 140 species belonging to the *Asclepias* genus, most of them having tropical distribution. The 108 subtropical-temperate zone species living together in North-America (some are rare and protected) hardly hybridize among each other under natural conditions; moreover, it is difficult to cause hybridization artificially. Because of the fact that they are almost exclusively allogamic, the possible resulting hybrids are unable to permanently sustain their populations. In Hungary only *A. syriaca* is a weed, and even in Europe only *A. curassavica* is known to have naturalized in the south of Spain, thus the permanent presence or invasive appearance of other *Asclepias* species or hybrids is not expected. However, it is important to emphasize the responsibility of botanical gardens and ornamental plant nurseries – and also of legislators –, because it might become possible that some American species could show invasive behavior under the conditions prevailing in Hungary.

English vernacular names include milkweed (from the high milky sap content), cotton weed, wild cotton, blood flower.

MORPHOLOGY

The milkweed is an 80–150 cm high perennial plant with robust growth, somewhat resembling tobacco. Its thick roots are plagiotropic, usually traveling laterally, about 10–40 cm below the soil surface, but sometimes they do penetrate the soil as deep as even reaching 1–1.2(–3.8!) meter. Their roots are rhizomatic, but the “rhizomes” do not originate from shoots, thus we thereafter will refer to them as rhizomatic roots, as suggested by Ujvárosi. These roots are especially effective in vegetative propagation of the plant, during which extensive clones can form comprising solitary or small groups (2–5) of shoots. Leaves on the stems are positioned oppositely, have short stalks, and are broad lanceolate. Their length is 15–25 cm, breadth 5–9 cm, margins entire. Leaves are thick and are not lobed, have stiff venation, their undersides are covered in white down. The flowers are arranged in 5–10 cm long cymae situated terminally and/or under the leaves. They are androgynous and pentamerous (the pistil, however, is made up of two, almost loose carpels), their color varying from off-white through pinkish to red. Flower structure is extremely sophisticated: the calyx is small and green, the corolla is pentamerous (the petals being 3×3–4 mm), folding back when the flowers open. Calyx and corolla fuse at their base only. The most striking component of the flowers are the 4 mm long, accessory corolla (crown) looking ahead, its fused tubular centre enclosing the ovary. The accessory corolla forms five sacculles

at the front, with one horn-shaped nectar-producing structure located in each. Nectar accumulates in the saccules. The style of the pistil is sessile, widening and pentangular, located at the height of the saccules, and has five pistil furrows (pistil chambers) on its side. Staminae fuse with the pistil surface above the furrows, and are strongly modified: pollen produced in the anther hemispheres agglutinate to pollinia, and the pollinium pairs are connected by a twin-armed translator. The two arms join at the part called corpuscule, and this is the part which fuses with the pistil (legs of pollinating insects can be caught here). In each of the chambers of the pistil there are many ovules, with marginal placentation. The fruit has slightly curved, oval-cylindrical horn shape. It is an 8–11 cm long, 2–3 cm wide follicle, opening on its ventral joining (alternatively, it is understood as a follicle-like capsule). The twin fruit type is rarer, because usually only the ovule of one of the carpels get fertilized. The surface of fruits is covered in soft spines or dawn. Seeds are flat, measure 7×5 mm, and their weight is 7–8 g per 1000 seeds. They have high oil content, bear long (2–2.5 cm) hair on their top side, and are carried far away by wind. All parts of the plant contain white, milky sap which is toxic (symptoms are: diarrhea, heavy breathing, spasms, and balance problems).

ORIGIN, DISTRIBUTION

Asclepias syriaca originates from the eastern lowlands of North-America, between northern latitudes 35–50°, and western longitudes 60–103°, including moist as well as dry (cold and warm) temperate zone forests. It was introduced to Europe in 1629. Its spontaneous expansion started probably in the Mediterranean region. In his book published in 1719 TOURNEFORT mentioned that in 1665 a plant described with the phrase “*Apocynum majus Syriacum rectum etc...*”, later found to be identical with *Asclepias syriaca*, could be found among the plants of the Paris Botanical Garden. Almost 100 years later LINNAEUS also thought it to have eastern origins. The centers of its current distribution include Canada and the United States in America, Iraq and the neighboring countries in Asia, whereas in Europe it is centered on France, Switzerland, Germany, Poland, Ukraine, the Caucasus and the Baltic region, as well as the Carpathian Basin.

The first piece of data, seeming reliable enough to be considered as the first Hungarian occurrence is from the British traveler ПОКОКЕ who mentioned it from Transdanubia during his journey in 1736–37. It must be noted, however, that nothing suggests the presence of *Asclepias syriaca* in Hungary in the floral research data books of КИТАЙБЕЛ, published around 1800 and covering a period of a quarter of a century. (On the other hand, it is not possible that ПОКОКЕ confused *Asclepias syriaca* with *Vincetoxicum officinale*, because in that case he would not have included the latter separately in his list, under the name *Asclepias latifolia*.) The spreading of milkweed in Hungary later on was assisted by the fact that in addition to being a decorative plant, a number of different uses were attributed to it. When these finally did not prove to be true, its cultivation in agricultural lands was discontinued, but its wild-growing populations having survived from cultivation continued to serve as centers of invasion, with plants spreading from there later causing severe damage. Its expansion was assisted also by the development of roads and railway system, because low-intensity tillage and later the application of pre-emergent herbicides which were quite ineffective against milkweed and thus removed competing species only, meant that suitable expansion routes were opened up for milkweed. It was especially on sandy soils that milkweed could spread very fast. According to the Nation-wide Weed Survey in 1988, about 16 thousand hectares of agricultural lands were infested (meaning a ranking of 113 in the list of weeds), and in addition to such lands, it causes damage on much larger areas in orchards, vineyards, forestry areas (poplar plantations, locust-stands, sandy pine stands). The highest degree of infestation today is recorded in the counties Bács-Kiskun, Tolna, Jász-Nagykun-Szolnok, Somogy, Csongrád and Pest. Further strong invasion is expected to occur in the Nyírség region. During the weed survey in 1997, it was ranked as 76th. Growing it as an ornamental means another type of danger, because that way it can spread in any part of the country, provided that suitable habitats are available locally.

LIFE CYCLE

Their germination taking place at temperatures above 15 °C, *A. syriaca* seeds germinate from the middle of April to the middle of May. Another condition is that seeds are situated at a soil depth of about 0.5–1(–5) cm, because if lying on the surface, they will refuse to germinate. Under optimal, conditioned circumstances (at 27°C, after cold treatment lasting for at least 15 days at 5°C) the success rate of germination can be as high as 99%. Buried seeds sustain their germination ability for a long time: the proportion of seeds capable of germinating remains as high as around 90% even after five years. Under suitable conditions, seeds will germinate with a dramatic speed (disturbance-broken type). Very soon after germination – after about three weeks – milkweed reaches its perennial status, i.e. it is from then on able to regenerate shoots from the root system, owing to the induction of new buds in the upper one-third of the main root. These buds start to grow only around the end of the first growing season. The plants will not develop flowers in the year of germination; only their rhizomatic roots develop. Next spring one bud starts to develop on each laterally growing rhizomatic root. New shoots developing from these will grow from late April to mid-June, and in the case of plants that are several years old, newer ones will grow also from where shoots used to be in the former year (1–3[–6] pieces). Shoots (ramets) will remain in physiological contact for several years. Plants flower from June to August. Insect pollination being most typical, the major pollinator in Hungary is the honey bee (*Apis mellifera*) (extensive *Asclepias* stands can even detract bees from pollinating sunflower), but just like in the native range of milkweed, other wild bees (about 20–30 genera in America) and especially bumblebees (*Bombus*, e.g.: *B. vagans*, *B. terricola*) can also have importance. Moths and butterflies (Lepidoptera) probably have less importance here than in the USA, and flies (Diptera) as well as beetles (Coleoptera) are even rarer pollinators. The effectiveness of pollination and fertilization is very low, however (<5%). Fruits ripen by late August, early September. Seeds are able to germinate after just a few weeks of dormancy. In the meantime, the intensive development of rhizomatic roots starts again during July and August, to last until mid-September. The buds forming on them remain dormant throughout the winter. Having lost their foliage in autumn, stems die off. It is difficult to estimate the possible lifespan of such vegetative clones, but under favorable conditions it could be well in excess of a hundred years.

HABITAT PREFERENCE

Milkweed appears mostly on less heavy soils, especially on sand or sandy loess. If soils used by milkweed in sandy grasslands are compared with those of undisturbed open grassland habitats it is found that in the former there is higher organic matter, free phosphorus and nitrate-nitrogen content, and under dense milkweed clones the pH is more in the acidic range, and also, the amount of calcium-carbonate is locally reduced. However, soils dominated by milkweed do not actually differ from secondary sandy grassland soils. *A. syriaca* is primarily a plant of disturbed habitats where soil characteristics have much less importance than other environmental factors such as the absence of natural competitors and the disturbed nature of the habitat. Thus, it is not surprising that there are huge amounts in abandoned agricultural fields in flood plains, especially along the south-Hungarian Danube section.

Asclepias adapts to different habitat types primarily by the high degree of flexibility of its clone structure: in more favorable habitats it forms thicker ramet structures more of a phalanx type, whereas in less suitable habitats it explores and invades the area by sending out longer rhizomatic roots, following a guerilla-type behavior. The radius of root system expansion can reach as much as 3 m within one year.

BIOTIC INTERACTIONS

The root extract of milkweed has an allelopathic effect on the most typical grain crops as well as on the common weed species. However, the physical effects of the presence of milkweed (such as shading and space occupation) have greater importance under natural conditions.

Milkweed disappears from vegetation with closed herb layer and and/or high canopy coverage. For example, with adequate management and cutting, it can disappear from alfalfa fields in three years. Milkweed is a natural host plant for the cucumber mosaic virus (CMV). It also hosts the Californian western flower trips *Frankliniella occidentalis*, Thysanoptera, the most dangerous virus vector, thus it can indirectly assist infection by tomato spotted wilt virus (TSWV) in weed-infested vegetable-producing areas. A variety of fungal plant diseases can appear on milkweed such as rust *Uromyces asclepiadis* Cke, *Puccinia bartholomaei*, mildew *Erysiphe cichoracearum*, botrytis *Botrytis hypophylla*, fusarium *Fusarium roseum*, cercosporos and alternariae, but these are generally not suitable for being used in biological control; moreover there may even be a risk of milkweed acting as a vector. Micro-organisms can accumulate in its nectar, among which it is especially the yeast fungi *Metschnikowia reukauffi* that can inhibit the functioning of the pollen tube. Its root system is damaged by nematodes (*Meloidogyne incognita*, *Pratylenchus penetrans*) and wireworms i.e. the larvae of click beetles (Elateridae). Its stems are the main food for a number of insects. Where it is cultivated, insecticides need to be used against the milkweed longhorn beetle (*Tetraopes tetraphthalmus*).

In sandy areas in Hungary, its young shoots are eaten almost bare by the weevil *Peritelus familiaris*, but this insect is strongly polyphagous. Its foliage is often consumed by the adults of the alleculid beetle *Omophlus proteus*, adults and larvae of the dwarf bush-cricket (*Phaneroptera nana*), as well as very rarely by adults of the leaf beetle *Galeruca tanacetii*. Some of its consumers (e.g. in its native range caterpillars of the butterflies *Danaus plexippus* and *D. chrysipus*, Danaeidae) in certain cases utilize the toxic cardenolide agents of the milkweed (aspeciozide, syriobiozide, calactine, calotropine) as a way of protecting themselves against predatory birds. *A. syriaca* is attacked by a variety of aphid species, some of them causing the dying back of shoot tips in Hungarian populations too. The most striking of them is the vivid orange *Aphis nerii* known from Hungary since 1983, which mostly damages members of family Apocynaceae, but the CMV-vector role of this species has also been proved. Under Hungarian conditions, the expansion of *Asclepias* is probably most strongly limited by the hemipteran *Lygaeus (Spilosthetus) equestris* (in America, by the large milkweed bug *Oncopeltus fasciatus*). The main damage caused by these hemipterans is that they suck sap from flower buds and young fruits which will fall off some days later, whereas more ripe fruits remain small and disproportioned. The weight and germination rate of seeds that have been sucked in their ripening stage through the coat of the closed or just opening fruit will be considerably reduced. This hemipteran sucks sap from the leaf blade as well as from the primary leaf veins of *Asclepias*, the result usually being that these parts die back. It may attack ripening achenes of the sunflower too, and its vector role in transferring bacteria, fungi and viruses is also proved.

Milkweed is hardly eaten by livestock due to its bitter-tasting milky sap and toxicity, although sheep flocks that have been trained so may graze on it in Hungarian sandy areas, if nothing else is provided.

On *Asclepias* populations in the Hungarian plain region between rivers Danube and Tisza, endotropic mycorrhizal as well as ectotropic associations created by septate hyphae are shown to exist. Endotropic mycorrhizal function is a medium degree association.

ECONOMIC IMPORTANCE

Initially, milkweed was thought to have many ways of economic utilization. Its young shoots and buds soaked in warm water were eaten as a substitute for asparagus (it is less toxic at that stage), juice, wine and volatile oils were made from its flowers, silk and insulating material from the seed hair, oil was pressed from the seeds, and even its milky gum was considered as raw material for natural rubber production. Its intensive cultivation was launched in the 1870s–1880s, but was soon discontinued due to economical reasons, until the middle of the 20th century. Today it is important only in honey-production: its honey is nice and aromatic, making *Asclepias*-honey a true Hungarian speciality. Its fruits that sometimes have peculiar shapes are used in Ikebana. Its steroid glycosides affecting heart functions are studied from pharmacological aspects.

Milkweed causes direct damage by infesting plough lands, vineyards and young forestations. Its removal from railway line sides and other linear objects is very costly. It can detract bees from pollinating sunflower, therefore it causes crop loss.

NATURE CONSERVATION SIGNIFICANCE

Primary problems caused by milkweed in natural sites are that in the occupied areas it can inhibit the regeneration of near-natural plant communities. *A. syriaca* does not threaten or only hardly affects natural or semi-natural communities (not even open sandy grassland areas!), since in such areas its colonization strategy is strongly restricted, and its vegetative propagation (which is otherwise very effective) towards the inner parts of these sites is also limited by the prevailing vegetation. Its invasion is significant in plant communities that have been degraded due to some anthropogenic effects. Such are abandoned plough lands, poplar plantations, and clear-cut or burnt down forests, secondary annual sandy grasslands. Its appearance is almost always related with the disturbance of the upper soil layers (treading, ploughing, over-grazing, erosion, etc.), or with the accumulation of nutrients (due to the use of fertilizers, forest burning, mineralization of organic matter, caused by the drying moist habitats). (In this respect, the behaviors of the alien *A. syriaca* and that of the native *Calamagrostis epigeios* are very similar to each other.) Because the extent of degraded areas grows rapidly, *A. syriaca* occupying these expands with similar intensity. The problem is even more serious when the aim is to facilitate the regeneration of areas already infested by *Asclepias*, although this aim can be often important, because *Asclepias* stabilizes the degraded status of grasslands effectively and for an extended period, and when degradation occurs in near-natural habitats, milkweed can immediately enter there due to its effective propagul-transfer. It is a source of contradiction that in order to remove milkweed from an area, the methods to be used create conditions highly suitable for its colonization (e.g. soil disturbance). This implies that areas can be cleared of milkweed permanently only if the activities are well harmonized and if resources to cover the extremely high costs are available.

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GREEN ASH

(*Fraxinus pennsylvanica* MARSH.)

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TAXONOMY

The genus *Fraxinus* of the Oleaceae family comprises mostly deciduous trees and some shrubs. The number of species is around 65, most of them growing in the temperate zones of East-Asia and North-America. There is considerable taxonomic differentiation within the genus, therefore the species are classified into two sections (*Ornus* = manna ashes and *Fraxinaster* = true ashes).

American ash belongs to the latter category. There are 4 ash species native to Europe (*F. ornus*, *F. excelsior*, *F. angustifolia*, *F. pallisiae*), and in addition to these, sometimes the North-American *F. americana* is also planted (this one is not known to have naturalized). (It is important to note that in earlier – mostly forestry – literature, the name *F. americana* was often erroneously used for green ash, too.)

There are no hybrids between species of the different sections and between European and North-American species, but within one section or one continent, hybridization does occur.

MORPHOLOGY

Green ash is a tree generally not growing higher than 25 m. In ash stands it has straight, spiring trunk up to its crest; bifurcation is not usual. The crown in such conditions is narrow, its branches are slim. In an open, solitary position, however, the trunk is short and cylindrical, the crown is wide, and the branches are mostly weeping. Unlike for common ash (*Fraxinus excelsior*) and Hungarian ash (*Fraxinus angustifolia* ssp. *pannonica*), its bark becomes crackled soon. Fissures of the longitudinally crackled, brown rhytidome are narrow, and the bark platelets have flat backs. Initially, the green ash has tap root, and later it develops a shallow, extensive root system. Its stems are thick and light grey, only slightly flattening at the buds, whereas in the case of common ash and Hungarian ash, flattening is significant. Accordingly, the pulvinus is less protuberant in green ash, whereas in the other two species it strongly protrudes. Its axillary buds are oval and larger than the hemispheric axillary buds of common ash and Hungarian ash. Bud scales are rusty brown and downy, but even so, the color of bud scales cannot be used as the only determining feature in the identification of ashes, because Hungarian ash – and also manna ash sometimes – can have buds similarly colored to that described above. It is typical for the green ash that the endings of the transporting tufts on the narrow, crescent-shaped cicatrices are more or less angular in shape. The shoots are dull; the odd-pinnate leaves are 20–25 cm long, made up of normally 7, sometimes 9 leaflets. The ovate or lanceolate leaflets are 7–10 cm long and 3–5 cm wide, apparently larger than the leaflets of the native ash species. The leaflets have short petiolules, a feature typical of manna ash only, among ashes native to Hungary. Leaflet blade is thin, paper-like, and the midvein on the underside is not covered in rusty hair, unlike in the similar manna ash in which leaf blade is thick and leathery, the midvein on the underside has rust-brown hair at its base. Foliage is loose but high, and is somewhat more compact than in the common ash, due to the larger size of leaflets.

It is dioecious, whereas native ashes are polygamous. The axillary panicles of male inflorescences are tight, whereas the females are elongated. Only common ash has axillary panicle inflorescences among native ashes, but it is easy to distinguish this species and Hungarian ash (with its axillary raceme) from green ash, because the latter has bell-shaped, 4-lobed, fused calyx (this is absent in common ash and in Hungarian ash, too). It has no corolla.

Its fruits are samaras arranged in pendulous panicles, making female specimens easy to recognize. The fruit is 35–70 mm long, narrowing steadily towards its base; its tip is rounded or obcordate, yellow colored. There is a residual calyx part at the base of the seed. The seed itself is cylindrical – just like in manna ash –, but twice as long (15–25 mm). In Hungarian and common ash the wing continues down to the base of the seed, and the seed itself is flattened, whereas in green ash (and manna ash) the wing extends not further down than to half the height of the seed. The fruit of manna ash is similar, with reddish-brown coloration and half the size of that of green ash.

Variability

It is mostly varieties originating from the northern margin of its distribution that have spread in Hungary, which readily hybridize. With the various types having been interbred, an almost complete series of hybrids exists, ranging from bald leaf types to entirely hairy ones. It results partly from the fact that seeds were collected mainly from trees found in parks where hybridization is more likely than in stands of planted forests.

Varieties occurring in Hungary are as follows:

Northern green ash (*F. pennsylvanica* var. *austini*)

Its stems and shoots are thinner and hairy just like the rachis. Leaflets are ovate-lanceolate, light green, hardly shiny at all, with long hair on their undersides. The terminal leaflet is not strikingly larger than the others. The foliage turns yellow in autumn, and falls early in the season.

Green ash (*F. pennsylvanica* var. *subintegerrima*)

Its stems and shoots are thicker, and are bald, just like the rachis. Leaflets are ovate, vivid green, shiny and bald. The terminal leaflet is strikingly larger than the others. The foliage turns yellow-brown in autumn, but is lost somewhat later in the season.

ORIGIN, DISTRIBUTION

Green ash is native to North-America, where its distribution extends from New-Brunswick and South-Ontario to the Mexican Gulf, and to the Rocky Mountains in the west. Among North-American ashes this species has its range extending the most to the north. Its largest populations grow in river valleys of lowlands and mountains, and in coastal areas of lakes. Several varieties and climatic types have evolved in its extensive range.

F. americana was the first North-American ash species to have been imported to Europe (1724), followed by *F. pennsylvanica* var. *austini* around 1780, and *F. pennsylvanica* var. *subintegerrima* around 1820.

In Hungary around the early 1900s, attempts were made to convert softwood (willow-poplar) gallery forests to hardwood stands, using the green ash. From the 1950s, green ash was used for creating second canopy layer in floodplain poplar plantations. The first report of green ash in scientific literature was in 1950.

In Hungary it is common everywhere, except for the western country border region and the mid-altitude hilly (mountain) regions. It is concentrated in river valleys and marshy or saline areas. Its proportion in forests is 0.4%, meaning almost 6000 hectares within forest-covered areas. (It must be noted however, that these data are from forestry planning, where the statistics cover only species with values more than 5%.)

Green ash occurrence with proportions more than 1% are recorded in the following Hungarian regions: Szigetköz, Hanság, Rábaköz, Muraköz, Kis-Balaton, Ormánság, Mohács-island, Sárköz, Gemenc, Solti-sík, Sárrét, surroundings of Velence Lake, Zámoly-Basin, Tiszazug, Bodrogeköz, Tiszahát, Maros-Körös Lowland, Kis-Sárrét.

LIFE CYCLE

Green ash shifts its life cycle very early: it produces fruits as early as at the age of 6–7 years in solitary position, and at 10–15 years of age if growing in a closed stand. Later on it has abundant crop every year. When young, it grows fast, easily forcing out other tree species. Its seedlings reach a height of 30–35 cm by the very first autumn, and from then on the trees grow about 1 m annually. Their height increase slows down at the age of about 20 years, to be totally finished at 30–35 years of age. Trunk width grows less intensely than that of Hungarian ash or common ash. In a habitat with average conditions, its height is about 15–20 m, or in areas with good water supply, even as much as 30 m. It is a relatively short-lived tree: specimens older than 80 years are very rare.

Green ash normally starts flowering when its trunk width reaches about 18–20 cm. Flower buds start swelling some days earlier on male plants than on female ones. Pollen release lasting for about three days, the pollen is transported by the wind within a range of 60–90 m from the parent plant. As soon as emerging from the bud, the pistil immediately becomes mature, and this lasts for about a week. Pistillate flowers and young fruits are very sensitive to frosts in late spring. Flowers that remained unpollinated or were pollinated with incompatible pollen will fall from the tree within one month. About one month after pollination, fruits developing from fertile flowers reach the size typical of ripe fruits, although the growth and development of the embryo comes to an end only in late September or early October. The color change of the ash keys (from green to yellow and then brown) continues until the fruit is completely ripe. As soon as the fruits are ripe, they begin falling from the tree. They are usually dispersed by the wind but can be dispersed by the water too.

The green ash flowers in April, before frondescence. Its fruits ripen in September, fall in the beginning of winter, as of November. Seeds maintain their germination ability for a period of 2–3 years. Seed weight is 25–30 g per 1000 seeds. Its leaves unfolding in the first half of May only, green ash shoots later in the season than common ash and Hungarian ash. The seedlings raise their cotyledons above ground level (epigeous germination). Cotyledons are lanceolate, have one midvein, and the lateral veins are pinnate. Cotyledons normally survive for all the summer. The first true leaves are single with serrate margin and barbed base, whereas the second foliage leaves have three leaflets, and all the rest are already odd pinnate.

Green ash readily develops offshoots from its base, but there are no root suckers. It is able to reproduce through vegetative as well as generative ways of reproduction; after its soil is disturbed, it produces offshoots and seeds abundantly. It has lot of fruit each year, which can be dispersed to great distances by wind and water. If the top of the tree is removed, it reacts to this damage by rapidly producing offshoots, especially if it is a smaller tree. The ability to produce offshoots depends on the age of the tree and the width of its trunk. Following such damage, the tree readily produces shoots from the crown of the root system and from the stump. In isolated environment, it spreads by offshoots rather than by seeds. Green ash grows offshoots easily in its sapling age and when its trunk is already arm-thick, producing bunches that comprise several offshoots.

Green ash is quite tolerant of fires: it can adapt to fire, and regenerate itself after fires. If the fire is intensive, it can burn younger trees, because their rhytidome is still quite thin. If the main stem is damaged, the plant rapidly brings up shoots from accessory buds on the upper roots. After a minor fire, its population will regenerate from seeds in the canopy and carried there by wind and water. Reaction to fire and the time required for regeneration depends on the intensity and frequency of fires, as well as on the age of the tree and on the prevailing season.

HABITAT PREFERENCE

Being a thermofrequent species, green ash, in the northern part of its native distribution area, prefers lowlands that warm up in the summer. Due to its temperature demand, in Hungary it is found primarily in lowland areas, and avoids regions with colder climate. Here, it tolerates the extremities of continen-

tal climate very well; it resists both early and late frosts. The northern types (var. *austini*) are adapted to shorter vegetation season; therefore they lose their foliage earlier in the autumn. It has been found that the green ash variety (var. *subintegerrima*) has better tolerance of extreme habitats.

As to soil nutrient content, green ash is not specially demanding. It avoids the dry and nutrient-depleted soils of the Hungarian Plain region. On saline soils – due to its salt tolerance – it establishes itself well, but its initially rapid growth comes to a halt after a while, and later it starts to dry out. It avoids very heavy, clay soils.

Being a water-demanding tree, it does well in semi-wet or wet habitats. Its optimal growing areas are in the thick alluvial soils of floodplains. It has excellent water tolerance, even tolerating prolonged flooding in summer, provided that the water is moving. It easily survives floods (such as the great flood on Danube in 1965). In its younger age, its tolerance of habitat conditions is especially good, making use of even nutrient-depleted habitats with changing hydrological conditions. However, its shallow root system cannot ensure the required amount of water in such habitats; therefore its growth is limited there. It is a light-demanding species, but its shade tolerance typical in the young age of trees lasts longer than in common ash and Hungarian ash.

BIOTIC INTERACTIONS

The possible allelopathic effects of green ash have been tested by CSISZÁR, using germinating white mustard seeds. Applying the watery extract of the two green ash varieties occurring in Hungary (*F. pennsylvanica* var. *austini*, *F. pennsylvanica* var. *subintegerrima*), seeds were germinated on room temperature and watered with the extract. Germination rate was evaluated on the sixth day. Among the experimental seeds, 98% of those watered with pure water (control group) germinated, whereas in the case of seeds treated with extract from *F. pennsylvanica* var. *austini* 76%, and in the group treated with *F. pennsylvanica* var. *subintegerrima* 67% of the seeds germinated. This suggests an allelopathic effect of green ash, but this needs to be confirmed under field conditions, too.

The leaves and green shoots of the green ash have even higher amounts of coumarin-containing matter than in common ash and Hungarian ash; therefore foliage-eating insects almost completely avoid this species. However, the saw-fly *Tomostethus nigrinus* and the blister beetle (*Lytta vesicatoria*) can cause even entire foliage loss occasionally. Holes or intervascular sections are eaten from the leaves by the ash-weevil (*Stereonychus fraxini*) appearing sometimes in masses. Brownish, “cauliflower-like” galls are created in the inflorescence by ash gall-mite (*Eriophyes fraxinivorus*). Larvae of the moth *Pseudargyrotoza conwagana* develops in the fruit, but it is not common. The trunk of tree specimens growing mostly in dry habitats is damaged by wood leopard moth (*Zeuzera pyrina*), or sometimes by common goat moth (*Cossus cossus*). Common wood-beetles are *Lepersinus fraxini* and *Hylesinus crenatus* both of which are thought by some researchers to have an effect in the induction of ash-cancer. The direct inducer of ash-cancer is the bacterial pest *Pseudomonas syringae*, often damaging the trunks. Among timber species, *Ganoderma applanatum* and *Perenniporia fraxinea* can occur.

Its sapling stands that often grow up spontaneously are favored by red deer, especially at wintertime. Bark stripping, however, occurs only in its younger age, because its bark becomes crusty earlier than in the case of common ash and Hungarian ash. In areas over-populated by large game animals, the stems of young green ash are sometimes stripped white (e.g. Lower-Danube floodplain), and young specimens are damaged by hares as well.

In America, green ash serves as food for many insect species, among which *Lepidosaphes ulmi*, is one of the most important ones, greatly damaging seedlings and young specimens. *Prionoxystus robiniae* penetrates the alburnum of trunks and thicker branches, assisting the establishment of fungi. Occasionally, *Tomostethus multicinctus* and *Tethida barda* can also cause serious damage. *Podosesia syringae* can damage the woody structure of trees of any size, thus increasing mortality. The fungus *Mycosphaerella fraxinicola* causes leaf spot, leading to premature defoliation. *Gloeosporium aridum* also can have the same effect. Rust caused by *Puccinia peridermiopora* leads to the formation of distorted flowers and aborted branches.

Green ash has vesiculo-arbuscular mycorrhiza.

ECONOMIC IMPORTANCE

The wood of green ash in America is hard, strong, solid and elastic; its color is yellowish, with broad white alburnum. Its density is moderately high; its water content is low. Its wood is less valuable and less marketable than that of common ash or Hungarian ash. Some users therefore separate the two types of wood, whereas others process them together.

In America, green ash is utilized in a number of fields: furniture industry produces bent chair parts, kitchen furniture and seating surfaces. In the production of sporting goods it is used mainly because of its flexibility: baseball-bats, paddles, tennis rackets, hockey sticks, skis and ski-poles are manufactured. It is also used in vehicle industry, for example for producing the wooden skeletons for cars and aircraft, and also in the case of railway wagons, propellers, ships and boats. Green ash is used also in milk-, poultry and toy production, for producing boxes, palettes and flooring, and also as industrial wood (fencing, pens, tool handles).

Owing to its golden yellow autumn coloration and good tolerance of the urban environment (nutrient-depleted soil, use of salt in winter), its cultivated varieties are planted in cities and parks. However, older specimens may cause problems by making tarmac surfaces bumpy.

In the year 2002 a total of 42 500 saplings were produced for forestry purposes in Hungary. Based on data from the National Institute for Agricultural Qualification (2001), the 13 entities are producing green ash to be used in horticulture.

Amerindian people made use of every part of green ash. Yellow stain was made from its roots and red from its bark. The bark was widely used for medicinal purposes, too: internally against depression, exhaustion and gastrospasm, and as anti-aedematic, antibilious and anacathartic agent. Externally it was applied as treatment of wounds, injuries, punctures, inflammation, insect attack and snakebite. Its seeds were considered to be an aphrodisiac. Its wood was used for making furniture, fencing, poles, boxes, scaffolding, canoes, pipes, bows and arrows, wedges and drums. Sioux Indians used green ash for cultic purposes as well.

The initial enthusiasm expressed towards the green ash in Hungary soon tapered off. It was experienced after it had been planted in floodplains and under poplar plantations that its initial rapid growth slows down in its young age, and its wood production remains lower than that of other valuable deciduous hardwood species (e.g. pedunculate oak, common ash, Hungarian ash, common elm). As shown in Hungary, its wood quality is poorer than that of ash species native to Hungary; hence its industrial utilization is restricted to producing tool handles.

Earlier it was planted in windbreaks too, because its fast growth and large foliage mass made it effective in providing protection against winds. Since its nursery management is easy, and it tolerates transplantation in its first three years (better than common ash and Hungarian ash), it became more widespread in non-forest uses.

NATURE CONSERVATION SIGNIFICANCE

Along Hungarian rivers and in floodplains, green ash appears everywhere in the country, accompanying other alien plants such as false indigo and box elder. Its numbers and the damage caused to nature conservation differ from one area to the other. The most abundant populations are found in places where it used to exist in planted stands.

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GIANT AND CANADIAN GOLDENROD

(*Solidago gigantea* AIT., *S. canadensis* L.)

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TAXONOMY

Approximately 100 species belong to the genus *Solidago* L. worldwide. It is practically impossible to determine the exact species number of the genus due to its unclarified taxonomical situation. The genetic center of the genus situates is North America, where the most species are found. Flora Europaea indicates the presence of 6 species (8 varieties) in Europe; however these numbers are also questionable due to taxonomical problems (see hereinafter). Valid scientific names and synonym names of *Solidago* species and infraspecific categories that occur in the wild in Europe are found in Table 1.

S. virga-aurea L. (common goldenrod) is a native species in whole Europe. *S. sempervirens* is found in several locations in North America along the Gulf of Mexico and the Atlantic Ocean. In Europe, it only occurs on the Azores, where it might be native.

S. canadensis agg. (common name: Canadian goldenrod), *S. gigantea* (common names: giant goldenrod, late goldenrod, smooth goldenrod,) and *S. graminifolia* are North American origin species that introduced in Europe.

Some authors consider *S. canadensis* agg. as a single species with several infraspecific taxa, while others distinguish *S. altissima* as a separate species. *S. altissima* does not figure in the identification guide of Flora Europaea (1990 edition), but is mentioned as a cultivated species that incidentally occurs in the wild as well. European *S. canadensis* agg. populations are rather uniform morphologically, but differ in several characteristics from the North American populations of both *S. canadensis* s. str., and *S. altissima*, being more similar to the latter. For this reason some authors consider it a separate species as *S. anthropogena*, while others classify it to *S. altissima*. Research regarding this issue cannot yet be considered as finalized, its results do not yet appear in identification guides (for example the new Hungarian identification guide still mentions the species as *S. canadensis*), therefore we will hereinafter use the name *S. canadensis*. However, it is imperative to draw attention to that the American *S. canadensis* s. str. species and *S. altissima* have several morphological and consequently ecological differences (see in chapter Life cycle and life history). Thus, albeit these species are the favorite experimental subjects of American ecologists, due to the unclarity of taxonomical questions it is not evident which results apply to European populations and which do not. (The situation is even more complicated by that species nomination is not always clarified in publications, and hence it cannot be determined from the name *S. canadensis* if it refers to *S. canadensis* s. str. or *S. altissima* as an experimental subject.)

TABLE 1 Accepted scientific names (based on *Flora Europaea*)
and synonyms of *Solidago* species present in Europe

Accepted taxon names		Synonyms
Species	Infraspecific categories	
<i>Solidago altissima</i> L.		<i>Solidago canadensis</i> L. var. <i>scabra</i> TORR. & A. GRAY ³ <i>Solidago altissima</i> L. var. <i>pluricephala</i> M. C. JOHNSTON ⁴ <i>Solidago altissima</i> L. var. <i>procera</i> (AIT.) FERN. ⁴ <i>Solidago hirsutissima</i> P. MILL. ⁴ <i>Solidago lunellii</i> RYDB. ⁴
<i>Solidago canadensis</i> L.	var. <i>canadensis</i> ¹	
<i>Solidago canadensis</i> L.	var. <i>gilvocanescens</i> RYDB.	<i>Solidago altissima</i> L. var. <i>gilvocanescens</i> (RYDB.) SEMPLE ⁴ <i>Solidago gilvocanescens</i> (RYDB.) SMYTH ⁴ <i>Solidago pruinosa</i> GREENE ⁴
<i>Solidago canadensis</i> L.	var. <i>hargerii</i> FERN.	
<i>Solidago canadensis</i> L.	var. <i>lepida</i> (DC.) CRONQ.	<i>Solidago canadensis</i> L. var. <i>subserrata</i> (DC.) CRONQ. ⁴ <i>Solidago lepida</i> DC. ⁴ <i>Solidago lepida</i> DC. var. <i>molina</i> FERN. ⁴
<i>Solidago canadensis</i> L.	var. <i>salebrosa</i> (PIPER) M. E. JONES	<i>Solidago canadensis</i> L. ssp. <i>elongata</i> (NUTT.) KECK ⁴ <i>Solidago canadensis</i> L. var. <i>elongata</i> (NUTT.) M. E. PECK ⁴ <i>Solidago canadensis</i> L. ssp. <i>salebrosa</i> (PIPER) KECK ⁴ <i>Solidago dumetorum</i> LUNELL ⁴ <i>Solidago elongata</i> NUTT. ⁴ <i>Solidago lepida</i> DC. var. <i>elongata</i> (NUTT.) FERN. ⁴ <i>Solidago lepida</i> DC. var. <i>fallax</i> FERN. ⁴
<i>Solidago gigantea</i> AITON		<i>Solidago gigantea</i> AITON subsp. <i>gigantea</i> var. <i>leilophylla</i> FERNALD ³ <i>Solidago gigantea</i> AITON var. <i>gigantea</i> ⁴ <i>Solidago gigantea</i> AITON var. <i>pitcheri</i> (NUTT.) SHINNERS ⁴ <i>Solidago gigantea</i> AITON var. <i>shinnersii</i> BEAUDRY ⁴ <i>Solidago glabra</i> DESF., non MILL. ³ <i>Solidago</i> × <i>leiophallax</i> FRIESNER ⁴ <i>Solidago pitcheri</i> NUTT. ⁴ <i>Solidago serotina</i> AITON, non RETZ. ³ <i>Solidago serotina</i> AITON var. <i>gigantea</i> (AITON) A. GRAY ⁴ <i>Solidago serotinoidea</i> A. & D. LÖVE ⁴ <i>Solidago shinnersii</i> (BEAUDRY) BEAUDRY ⁴
<i>Solidago gigantea</i> AITON	subsp. <i>gigantea</i>	
<i>Solidago gigantea</i> AITON	subsp. <i>serotina</i> (KUNTZE) McNEILL	<i>Aster latissimifolius</i> (P. MILL.) KUNTZE var. <i>serotinus</i> KUNTZE ⁵ <i>Solidago gigantea</i> AITON subsp. <i>gigantea</i> var. <i>serotina</i> (KUNTZE) CRONQUIST ³
<i>Solidago graminifolia</i> (L.) SALISB. ²		<i>Euthamia graminifolia</i> (L.) NUTT. var. <i>graminifolia</i> ⁴ <i>Euthamia graminifolia</i> (L.) NUTT. var. <i>major</i> (MICHX.) MOLDENKE ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>major</i> (MICHX.) FERN. ⁴
<i>Solidago graminifolia</i> (L.) SALISB. ²	???	<i>Euthamia graminifolia</i> (L.) NUTT. var. <i>nuttallii</i> (GREENE) W. STONE ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>nuttallii</i> (GREENE) FERN. ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>polycephala</i> (FERN.) FERN. ⁴

Accepted taxon names		Synonyms
<i>Solidago graminifolia</i> (L.) SALISB. ²	???	<i>Euthamia gymnospermoides</i> GREENE ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>gymnospermoides</i> (GREENE) CROAT ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>media</i> (GREENE) S. K. HARRIS ⁴
<i>Solidago graminifolia</i> (L.) SALISB. ²	???	<i>Euthamia tenuifolia</i> (PURSH) NUTT. var. <i>pycnocephala</i> (FERN.) C. & J. TAYLOR ⁴ <i>Solidago graminifolia</i> (L.) SALISB. var. <i>galetorum</i> (GREENE) HOUSE ⁴
<i>Solidago sempervirens</i> L.	var. <i>sempervirens</i>	
<i>Solidago sempervirens</i> L.	var. <i>azorica</i> (HOCHST.) H. ST. JOHN	
<i>Solidago virgaurea</i> L.		<i>Solidago taurica</i> JUZ. ³ <i>Solidago lapponica</i> WITH. subsp. <i>stenophylla</i> G. E. SCHULTZ ³
<i>Solidago virgaurea</i> L.	subsp. <i>minuta</i> (L.) ARCANG.	<i>Solidago alpestris</i> WALDST. & KIT. ex WILLD. ³ <i>Solidago lapponica</i> WITH. ³ <i>Solidago lapponica</i> WITH. subsp. <i>lapponica</i> ³ <i>Solidago jailarum</i> JUZ. ³ <i>Solidago minuta</i> L. ³ <i>Solidago virgaurea</i> L. subsp. <i>alpestris</i> (WALDST. & KIT. ex WILLD.) HAYEK ³

Remarks:

1. Taxonomical situation of *S. canadensis* s. l. populations is strongly disputed. According to WEBER (1997) they are rather closer to *S. altissima*, while Flora Europaea mentions both *S. altissima* and *S. canadensis* as occurring species. American authors distinguish 5 (or 6, including *S. altissima*) varieties, while Flora Europaea only mentions one, var. *canadensis*. For the sake of completeness we put here the synonyms of the other 4 varieties as well.
2. In the case of *S. graminifolia* Flora Europaea does not mention any infraspecific taxa. Contrarily, USA NRCS database, which accepts this name only as a synonym, mentions several varieties. We have included the taxa distinguished by the American database in our list, but we could not decide on the valid infraspecific taxonomical classification. Question marks under „accepted taxon names” refer to this uncertainty.
3. Source: Flora Europaea digital version: <<http://www.rbge.org.uk/forms/fe.html>>
4. Source: USA NRCS database: <<http://plants.usda.gov>>
5. Source: Soó 1970

We face less taxonomical difficulties in the case of *S. gigantea*, the other introduced *Solidago* species originating from North America. The species has three different ploidy-level genotypes: diploid ($2n = 18$), tetraploid ($2n = 36$) and hexaploid ($2n = 54$). The various ploidy-level populations are classified at the species level by some authors and at the infraspecific level by others, but no obvious morphological differences can be identified among them. European populations belong to the tetraploid genotype.

The occurrence of *S. graminifolia* has been reported first in Hungary in 2007 from the Bükk Mountains, near to Eger.

MORPHOLOGY

Solidago canadensis and *S. gigantea* are tall and erected. The stem does not branch below the synflorescence. Shoots are 25–250 cm tall. A distinctive characteristic of both species from other North American species is that basal leaves fall off early. Leaves on the upper stem are alternate, triple-nerved and spear shaped or lance-like, margins are toothed on their upper third and smooth on their base. The synflorescence is terminal, and consists of main and collateral inflorescences, however these latter can be absent as well. Yellow-colored composite flowers knit in panicles in both the main and collateral inflorescences.

Both species are rhizomatous. Rhizomes origin from the hypocotyls, close to the soil surface; they are placed at 10–20 cm deep in the soil. They grow sympodially, i.e. aerial shoots develop from the terminal bud of the rhizome. Lateral buds usually do not sprout in, occasionally new rootstocks develop from them (but the number of these is insignificant compared to rootstocks from the hypocotyl). The rhizomes of *Solidago gigantea* live only for two years, while those of *S. canadensis* for longer periods. Root system is formed by the roots that grow on the rhizomes except for the first year seedlings that come up from achenes. Distinctive characters between two species are summarized in Table 2. Both species show considerable variation between populations in size related characters.

TABLE 2 The most important distinctive characteristics of *Solidago canadensis* and *S. gigantea*

	<i>S. gigantea</i>	<i>S. canadensis</i>
stem	glabrous (pubescent only in the inflorescence), often glaucous	pubescent, later glabrous on bottom
corymb	petals of ray florets overhang those of disc florets	petals of ray florets are not longer than those of disc florets

ORIGIN, DISTRIBUTION

Solidago canadensis is native in the United States and Canada from 26°N to 45°N, while the range of the species extends 65°N in the territory of Alaska. *S. gigantea* is distributed along the US East Coast from 30°N to 47°N and from 36°N to 55°N on the West Coast. According to a recent phylogeographic analysis, European *Solidago gigantea* populations originated from Suothern Appalachian Mountains or New England (the Hungarian ones from the later), and there were only few introduction events.

S. canadensis and *S. gigantea* were first introduced in European botanical gardens as ornamental plants in the 17th century. Their first naturalized population appeared in the mid 19th century. Few decades later, after the first successful establishment they became rapidly expanding invasive species in Europe. Data from herbaria suggest that the expansion rate of both species can be considered linear: European range of *S. gigantea* increased by 910 km² yearly on average, while the range of *S. canadensis* grew by 741 km² per year. Currently both species are widely distributed in Europe.

The expansion of *Solidago* species is first reported in Hungary in 1902 by GUSZTÁV MOESZ. Unfortunately, some of his records are based on misidentification (e.g. MOESZ considered the first specimen of *S. gigantea* in the Carpathian Basin a plant collected in 1863, which was actually the first specimen of *S. canadensis*). The first herbarium record of the giant goldenrod unfortunately lacks exact site indication, but was probably collected on one of the islands of the river Danube (probably from the Danube bend) in 1848.

Based on 113 *S. gigantea* and 19 *S. canadensis* herbarium sheets, which are found at the Department of Botany of the Natural History Museum of Budapest (revised by EWALD WEBER in 1992) both species appeared in Hungary more or less at the same time, but the number of *S. canadensis* sheets increased much slower than the exponentially growing number of *S. gigantea* sheets. Hence, it is assumed that *S. canadensis* had a slower expansion rate.

The first mass presence of *S. gigantea* in Hungary was reported from the Danube valley (1865 Csallóköz, 1873 Csepel Island). Its expansion probably started from more than one point, *S. gigantea* escaped from cultivation in several places coincidentally. Its appearance was recorded in the 1880s at several locations of Transdanubia, while east from the Danube it was only detected in 1902 near Szolnok, and records were rather rare further on as well.

S. gigantea is common on the main part of Transdanubia. Nowadays its huge stocks are part of the Transdanubian landscape. It occurs mainly in the valley of rivers and streams in the Hungarian Mountain Ranges and the Great Hungarian Plain, but occasionally (e.g. in the Kiskunság) it expands outside these as well. Currently it occurs scarcely on the eastern-southeastern part of the Great Plains. According to the predictive modeling of its distribution in Hungary, annual precipitation proved to be the most important climatic factor, however April's precipitation and annual and aestival semiannual climatic water deficit sum is important as well. Annual, April and July average temperature, however, did not prove to be significant, and interestingly, neither did July precipitation. This latter corresponds well with our observations on that water supply of the first half of the vegetation period affects the plant's growth substantially. The model prognosticates absence of *S. gigantea* below 650 mm of precipitation, and its mass presence above this level.

S. canadensis is rarer than *S. gigantea* in the country, it is found mostly along the Transdanubian and Northern Mountain Ranges and around main cities (Budapest, Gödöllő, Miskolc, Veszprém, Székesfehérvár). Interestingly, this species is very scarce in Southwestern Hungary, where the other species is abundant.

LIFE CYCLE

Sexual reproduction by achenes is only significant for the colonization of new areas. Achenes, produced in large quantities, germinate well under laboratory conditions, notwithstanding germination in the wild is relatively rare. One of its reasons is that part of the achenes are destroyed by pathogens, while the other main reason is that they only germinate in light, which means that they need free soil surface, while any vegetation or litter impedes germination. Therefore, in established *Solidago* stands, sexual reproduction never observed. The most optimal circumstances for the germination of achenes are found on abandoned arable land. In grasslands, achenes can germinate if they fall on bare surfaces (which can form for example by the devastation of tufts as a consequence of drought or long flooding, overgrazing or inadequate mowing). Achenes do not get into dormancy in autumn, but the germination is impeded by low temperatures.

S. gigantea seedlings develop 2–3 rhizomes, whose length is 1–10 cm by the end of the vegetation period. Rhizomes of *S. canadensis* are shorter than *S. gigantea*'s, therefore its clones are more compact and the development of largely extent stocks is slower¹. Rhizome length varies with shoot size within a population: larger shoots usually develop more and longer rhizomes. On the other hand, shoots sprouting from longer rhizome grow taller in general. New rhizomes most often angle at 180 degrees with older one (i.e. they continue growing in the same direction), though variation of ramification angles is high. This high variation is the reason why fairy-rings are not formed, as new specimens develop in the center of clone as well.

In closed stocks sympodial buds overwinter close to the soil surface in the litter. Superficial sprouting of buds is observed in early spring (March), and intensive growing of shoots begins only by late March, early April. Dry mass of shoots reach their maximum by mid to late August, while leaf area a bit earlier, in mid to late July. Subsequently, leaf area decreases dramatically, while shoot mass in a small compass. The reason of the decrease is that lower leaves continuously die due to self-shading, and the size of newly formed leaves decrease throughout the vegetation period. Carbohydrates of perishing leaves are

¹ American comparative studies have shown that rootstocks of *S. canadensis* s.str. are shorter (0–5 cm), while those of *S. altissima* and *S. gigantea* are rather long (0–20 cm) and there is no difference among these two latter species in this respect. There is no data on rootstock length of European *S. canadensis* populations, however it is more likely that they are closer to the species *S. canadensis* s.str.

mobilized and serve as resource for the development of new rhizomes. Specific leaf area also decreases throughout the vegetation period, i.e. the leaf mass per leaf area ratio increases. This is probably an adaptation to the decreased summer water availability.

Flowerheads start developing from early June, while flowering lasts from mid July to October. Only those shoots develop flowers that have reached a critical height. This height varies among sites and is most probably affected by genetic and environmental factors. Synflorescence size (and hence the number of corymbs per shoot) positively correlate with the size of the shoot's vegetative part. Plants developing from achenes first blossom in the second year the earliest, but first flowering usually occurs later. After flowering and the ripening of achenes, aboveground parts of the plant die. Non-flowering shoots however can live up to the first frosts, and only die because of the cold. Minerals from the shoots that die in autumn do not translocate to underground organs, as in the case of many plants with low nutrient requirements.

Nutrient exchange takes place through the rhizomes between interconnected shoots by means of which individuals (genets) level out (equalize) the spatial inequalities in abiotic factors and competition from neighboring plants.

Interannual dynamics of the development and growth of the two species do not differ significantly. There are, however, some morphological differences between these species, which are not identification keys, but are important from the point of view of the plants' life history. The difference in rhizome length has already been mentioned. A consequence of this is slower clonal dispersal of *S. canadensis*, and another is stronger integration within the clone. Energy allocation for vegetative reproduction is also differing: according to American studies *S. canadensis* turns only 5% of its organic matter production to vegetative reproduction, in contrast to the 25% allocated by *S. altissima* and *S. gigantea*.²

The most important difference in terms of aerial shoots is that those of *S. canadensis* are leaved more densely, hence have higher number of leaves per shoot and higher overall leaf area (leaf size does not differ significantly between the two species). Studies carried out in the US showed that photosynthetic rate and evapotranspiration of the leaves of *S. canadensis* are higher than those of *S. gigantea* or *S. altissima* leaves (as a consequence of the root of these two effects is that the efficiency of water utilization of the three species is nearly similar).²

HABITAT PREFERENCE

Solidago species of North-American origin have rather wide ecological plasticity, and are highly tolerant in respect of water and nutrient supply. They are capable of forming extent, closed clonal stands in various soil types, from calcareous soils to peat soils and are only absent from highly saline licks. They scarcely tolerate shading, and might occur in disturbed humid forests; however their vitality in these is usually lower.

Habitat preference of the two species differs: while *S. gigantea* occurs on humid, occasionally heavy soils, and usually in close to natural habitats, *S. canadensis* occurs on rather loose, easily warming soils in the vicinity of settlements. This concurs to their behavior in their natural habitats (the North American prairies), where *S. gigantea* prefers slightly more humid habitats than *S. canadensis*.

According to our observations the size and structure of *S. gigantea* shoots depend highly on the water availability of the habitat: in drier areas shoots are shorter, the proportion of flowering shoots is lower, the size of inflorescences is smaller and the occurrence of shoots bearing collateral inflorescence (con-florescence) is also lower. Less evident, but at least as important for the life history of the plants are the responses of the rhizome system to water availability: in drier habitats plants develop more, but shorter rhizomes. Model studies predict the opposite, because in favorable (i.e. more humid in this case) patches it is worth growing more rhizomes, because in this case the progenies also fall to the same favorable humid patch. On the other hand, in an unfavorable patch it is worth developing longer rhizomes thus increasing the possibility of that the progeny gets to another (more favorable) patch. Due to the trade-

² We may not be certain however that these findings apply to Hungarian populations as well.

off between the length and number of rhizomes, plants are only able to grow less from the longer ones, so the number of rhizomes in an unfavorable patch is expected to be lower. An explanation of the observed results is that in dry habitats the dense root system of the grass that live together with *S. gigantea* inhibits the growth of rhizomes, while in humid habitats *S. gigantea* forms monodominant clonal stocks in which no other species is present.

We have not carried out studies on the morphological plasticity of *S. canadensis* and have not found any corresponding data in the literature either. According to our observations however, apparently there are no significant differences in the size and morphology of shoots among habitats in this species.

BIOTIC INTERACTIONS

Under suitable environmental conditions, without mowing or tilling established clonal stocks can inhibit the establishment of seedlings and overcompete other herbs. In this regard key factors are the plants' intensive growth and dense shoot development, as a consequence of which light scarcely reaches the soil surface. Along with shading, allelopathic effect increases the competitive vantage of *Solidago* species. Allelopathic potential of *S. gigantea* is moderately strong, its juglone index is 0,9³. Literature also gives account of the presence of allelopathically effective (and insect repellent) diterpen derivatives (e.g. kolavenol, kolavenic acid, 6-oxokolavenic acid, 7-acetoxykolavenic acid) and polyacetylenes in *S. canadensis* agg. as well. They do not only affect directly other plant species with their allelopathic substances, but also indirectly through the inhibition of the activity of the soil's nitrifying bacteria.

In North America *Solidago* species follow after the short-lived, well-colonizing grass species in the secondary (old-field) succession. In woody landscapes they are followed by trees and bushes. *Solidago* species are able to inhibit the settlement of these latter, but tolerate badly the subsequent shading of settled arboreal plants. In drier habitats, where a forest cannot form due to climatic or pedological reasons, prairie-forming perennial grass species follow *Solidago* species.

In experimental settings perennial grass had significant negative effect on the size of *Solidago* individuals (ramets), and the number and size of their vegetative and generative reproductive organs. Apart from the competition for water and nutrients, their dense root system likely inhibits mechanically the development of *Solidago* rhizomes.

A rich insect fauna is linked to *S. canadensis* in its natural habitat: all together there are 314 phytophag insect species detected on the plant. A proportion of these is mono- or oligophagous, i.e. consumes only *S. canadensis* or other *Solidago* species. Its most thoroughly studied (though not necessarily the most important) pest is *Eurosta solidaginis* (Diptera: Tephritidae), the larvae of which develop in galls on the stem. The species has separate races that live on *S. canadensis* and *S. gigantea*. *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae), *Epiblema scudderiana* (Lepidoptera: Tortricidae) and *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae) also form galls on the plant. Leaves are consumed by *Trirhabda* species (*T. canadensis*, *T. borealis*, *T. virgata*; Coleoptera: Chrysomelidae) and *Microrhopala vittata* (Coleoptera: Chrysomelidae). The plants' saps are sucked by several cicada and aphid species, from which the following Homoptera (Aphididae) species are *Solidago*-specific: *Uroleucon caligatum*, *U. tissoti*, *U. canadensis*, *U. nigrotuberculatus*, *U. pieloui*. Herbivores strongly affect the plants. Energy allocated for generative reproduction already decreases at low herbivore pressure, while the shoot growth also slows down at higher herbivore density, and the number, length and relative mass of rootstocks decrease as well. Certain insects – e.g. *Epicauta pennsylvanica* (Coleoptera: Meloidae) and caterpillars of *Coleophora* spp. (Lepidoptera: Coleophoridae) – directly consume generative parts, thus decreasing significantly the number of achenes produced. The effect of insects cannot only be observed on the level of individuals, but also have influence on the competitive and colonizing ability of the species, and through this, the speed of succession processes.

3 Juglone index is an index determined by germinating biotest to measure allelopathic potential. If its value is below 0,5, it is basically unlikely to find allelopathic reaction, while values above 1 show strong allelopathic potential. For more details see: SZABÓ L. Gy. 2000. Juglone index – a possibility for expressing allelopathic potential of plant taxa with various life strategies. Acta Bot. Hung. 42: 295-305.

North American specialist insects that feed on *Solidago* species are absent from Europe. Some generalist insect species do consume *Solidago* species, the effect of these on the plants however is not significant, which is probably a key item in the invasive ability of these species. Probably the absence of specialized herbivores is the reason of that European populations are denser and grow taller than American one.

In Hungary the presence of 25 phytophag insect species has been confirmed on *S. gigantea* during a 2-year-long study, among which *Oecanthus pellucens* (Orthoptera: Oecanthidae), *Calocoris norvegicus* (Heteroptera: Miridae), *Nysius senecionis* (Heteroptera: Lygaeidae) and *Cicadella viridis* (Homoptera: Cicadellidae) were the most frequent. There were no food specialists among the collected species.

For European fungi pests of *Solidago* species, the literature mentions *Erysiphe cichoracearum* and some other unidentified fungi species that attack achenes in the soil. Infection by *Pseudomonas syringae* pv. *solidagae* (a new pathovar) was reported from Japan. The disease was named "bacterial leaf spot". It is characterized by angular or round, dark brown necrotic spots on leaves. This disease resulted in defoliation and terminal dieback of the plants in severe cases.

ECONOMIC IMPORTANCE

Both species yield much honey in late summer, although their nectar production is highly variable with the weather and habitat. Both species are considered as medicinal plant, their dried shoots collected immediately before blossoming is sold as *Solidaginis herba*. Their chemical composition and secondary metabolic products have been extensively studied from this aspect. Hungarian data apply mostly to the more common *S. gigantea*. This plant contains approx. 9% triterpen-saponine, approx. 4% phenoloids (flavonoids, phenol-carbonic acids and polyphenols), as well as approx. 0.5% volatile oils (γ -kadin and 14 more mono- and sesquiterpenes).

They appear as weeds in forestry nurseries and fresh plantations, waste lands, clear cuts and under high voltage powerlines. Their pollen is produced in large quantities and may induce allergic reactions in susceptible individuals.

NATURE CONSERVATION SIGNIFICANCE

The establishment of large *Solidago* stocks is an indirect result of the improper management of natural and close to natural habitats. The lack of regular mowing and/or grazing that is necessary to maintain grassland vegetation makes it possible for non-native species from this genus to invade these areas.

The formation of closed stocks goes hand in hand with the devastation of the original vegetation, and also affects negatively the vertebrate fauna: nesting birds leave their nests, and stocks can form impassable barriers for mammals. Parallel to the decrease of plant diversity decreases the species richness of phytophag and subsequently that of predator invertebrates as well.

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ASTER SPECIES FROM NORTH AMERICA

(*Aster novi-belgii* agg.)

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TAXONOMY

In Central Europe the most important aster species originating from North America are mentioned under the collective name of *Aster novi-belgii* agg., therefore in this work we use this name also. The following species and hybrids belong to this taxon: *A. laevis* L., *A. lanceolatus* WILLD., *A. novi-belgii* L., *A. tradescantii* NEES, *A. ×salignus* WILLD. and *A. ×versicolor* WILLD. Other authors differentiate three main species which are: *A. lanceolatus* agg. (*A. lanceolatus*, *A. tradescantii*), *A. novi-belgii* agg. (*A. novi-belgii*, *A. ×salignus*) and *A. laevis* agg. (*A. laevis*, *A. ×versicolor*). Take the importance into consideration the species *A. novae-angliae* L. will be discussed also. Other hybrids to be mentioned are *A. dumosus* × *A. novi-belgii* which could have the same distribution area to *A. novi-belgii* according to the monograph edited by TUTIN (1976) and in this case it can be present in Hungary too. Taking the diversity of the determination keys into consideration the determination of the actual taxa could be problematic. In the determining of the escaped species of Central Europe it is often difficult – and sometimes impossible – find connections with the species characteristics described in North America. According to the USDA classification the discussed aster species have been included in the genus *Symphotrichum* NEES.

As Soó (1924–1925) has written the North American asters has no „well-defined, constant species and the gaps between the individuals of the developmental series with infinite diversity is almost absent.” In this way the genus brings on taxonomical difficulties in North America too and in addition some species can interbreed (often in horticultural process) and therefore the limits among the species can be absolutely fuzzy.

The newest Austrian list of alien species contains *A. laevis* var. *concinus* (*A. salicifolius* auct., *A. concinns*) and *A. pilosus* species, therefore they are worthy of attention as potential new invaders in Hungary. The alien plant list of the Czech Republic complements with more naturalized species: *A. cordifolius*, *A. divaricatus*, *A. dumosus* × *A. novi-belgii* and *A. macrophyllus*. Sometimes some additional non-native ornamental species can escape: *A. dumosus* L., *A. ericoides* L. (*A. multiflorus* AITON), *A. foliaceus* LINDL., *A. lateriflorus* (L.) BRITTON, *A. longifolius* LAM., *A. patulus* LAM., *A. puniceus* L., *A. riparius* NEES, etc. In horticultures can be presenting *A. schreberi* NEES, *A. shortii* LIND., *A. grandiflorus* L., *A. spectabilis* AITON, *A. vimineus* LAM., *A. umbellatus* MILLER [*Dollingeria umbellata* (MILLER) NEES] and *A. ptarmicoides* (NEES) TORREY et GRAY [*A. albus* (NUTTALL) EATON et WRIGHT]. However some Central European works about the invasive plants almost completely disregard the asters of North America.

As it was afore-mentioned the *Aster* species of North America interbreed relative easily and form hybridogenous clusters which has no comprehensive taxonomical estimation. Soó (1964–1980) distinguished numerous variations of the North American asters but some of these could become eliminated by the revisions in the future. To avoid the causeless misconceptions this work will not deal with these variations.

Also alien sometimes escapee species is the sub-alpine *A. bellidiastrum* (L.) SCOP. (*Bellidiastrum michelii* CASS.), which has European origin and differs from the examined North American asters in characteristics and biology. In rock gardens also planted the European alpine aster (*A. alpinus* L.) which can escape too but this work does not cover these species.

Most important examined species:

1. *Aster laevis* L. – smooth blue aster, glaucous Michaelmas-daisy. Synonymous names: *Symphotrichum laeve* (L.) Á. LÖVE et D. LÖVE, *A. rubricaulis* LAMK., *A. cyaneus* G. F. HOFF.

Intraspecific taxa:

- var. *laevis*
- var. *concinus* WILLD.
- var. *geyeri* GRAY
- var. *purpuratus* NEES

2. *Aster lanceolatus* WILLD. – white panicle aster, narrow-leaved Michaelmas-daisy. Synonymous names: *Symphotrichum lanceolatum* (WILLD.) NESOM, *A. bellidiflorus* WILLD., *A. salicifolius* LAMK. non SCHOLLER, *A. frutetorum* WIMM. ex WEISS, *A. lamarckianus* ASCHERS. et GRAEBN. non NEES; *A. paniculatus* auct. LAMARCK, non MILLER, *A. simplex* WILLD.

Intraspecific taxa:

- subsp. *hesperius* (GRAY) SEMPLE et CHMIELEWSKI
- var. *hesperius*
- subsp. *lanceolatus*
- var. *lanceolatus*
- var. *hirsuticaulis* SEMPLE et CHMIELEWSKI
- var. *interior* (WIEGAND) SEMPLE et CHMIELEWSKI
- var. *latifolius* SEMPLE et CHMIELEWSKI

(The European distribution of the currently described subspecies and varieties up to the present unknown.)

3. *Aster novae-angliae* L. – New England aster, hairy Michaelmas-daisy. Synonymous name: *Symphotrichum novae-angliae* (L.) NESOM, *Lasalea novae-angliae* (L.) SEMPLE et BROUILLET

Intraspecific taxa:

- var. *novae-angliae*
- var. *roseus* DC. (invalid?)

4. *Aster novi-belgii* L. – New York aster, confused Michaelmas-daisy. Synonymous name: *Symphotrichum novi-belgii* (L.) NESOM, *A. longifolius* auct. non LAMK.

Intraspecific taxa:

- subsp. *novi-belgii* (*A. floribundis* WILLD., *A. tardiflorus* WILLD. auct. non L., *A. adulterinus* WILLD.)
- subsp. *laevigatus* (LAMK.) THELL. [*A. laevigatus* LAMK., *A. novi-belgii* var. *laevigatus* (LAMK.) A. GRAY, *A. brumalis* NEES]
- subsp. *stenolepis* THELL.

[Two additional subspecies are probably invalid: subsp. *floribundus* (WILLD.) THELLUNG, subsp. *subprenanthoides* THELL. GRAY (1888) notes four feasible variety: var. *laevigatus*, var. *litoreus*, var. *elodes*, and var. *thyrsiflorus*; J. LABRECQUE & L. BROUILLET reviewed var. *villicaulis* (GRAY).]

5. *Aster tradescantii* L. – shore aster, small Michaelmas-daisy. Synonymous names: *Symphotrichum tradescantii* (L.) NESOM, *A. parviflorus* NEES, *A. fragilis* WILLD., *A. artemisiflorus* POIR., *A. leucanthemus* DESFONTAINES, *A. saxatilis* (FERNALD) BLANCHARD, *A. vimineus* LAM. var. *saxatilis* FERNALD. [The valid name according to some new species lists (e.g. MARHOLD & HINDÁK 1998): *A. parviflorus* NEES, which is then again identical with the species *A. tradescantii* auct. non L.]

6. *Aster* ×*salignus* WILLD. – common Michaelmas-daisy. Synonymous names: *A. salicifolius* SCHOLLER non LAMK., *A. hungaricus* POIR., *A. lanceolatus* × *A. novi-belgii*.
7. *Aster* ×*versicolor* WILLD. – late Michaelmas-daisy. Synonymous name: *A. novi-belgii* subsp. *laevigatus* (LAMK.) THELL., *A. laevis* × *A. novi-belgii*.

MORPHOLOGY

The North American *Aster* species have smaller and more flower heads than their European relatives. The following descriptions compiled with the merging and comparison of determination keys can help the determination of each taxa:

Aster laevis L.

30–100(120) cm high, rhizomatous perennial plant. The grey-green (sometimes reddish) stem is lignescent, straight, more or less bare, sometimes with more rows of small hairs under the leaves. The leaves are various, thickening, the basal leaves are inverse egg-shaped and narrowing to the leaf-stem, the leaves of the stem are lanceolate or oval, 8–15 cm long and 1,5–4 cm wide with entire or sometimes serrated margins, amplexicaul, and on the branches small. The flower cluster is thyrsus formed by flowerheads; the diameter of the flowerhead is (15–)25(30) mm. The yellow tubulous florets are about 2 mm wide, the ray flowers are bluish-lilac or whitish. The scales of the flowerhead grow in 4–6 rows and are imbricated, the inners are about 5–7 mm long, the outer shorter. The outer flower bracts fit close, with light colored dry skin at the margins and green zone at the middle. The fruit is 2,5 mm long achene which is bare or sometimes hairy. The somatic chromosome numbers: $2n = 18, 48-50, 54$.

Aster lanceolatus WILLD.

Rhizomatous perennial plant. The straight stem is 50–120 (130) cm high, mostly bare with row of up-running small hairs. The leaves on the stem are inverse egg-shaped – lanceolate, the narrowing leaf blade is sessile, 3–15 cm long and 0,5–2 cm wide, bare or sometimes with small hairs and not auriculate (in the Hungarian literature sometimes: with rounded auriculate shoulders), with entire margins, rarely pointed; the basal leaves are pedunculate and the leaves on the side branches are smaller. The diameter of the flowerhead is 15 mm (sometimes may be 20–25 mm), the more or less one-sided flower clusters form thyrsus (as many 1000 flowerheads); the length of the flower bracts is 4–5,5 mm, the inners are 2–3 times longer than the outers and fit close. The disk flowers are yellow, the rays white or bluish-lilac, maximum 1 mm wide and short. The fruit is 1,5–2 mm long achene, with small hairs, the umbrella is 3,2–6,4 mm long. The somatic chromosome number: $2n = 64$.

Aster novae-angliae L.

The plant is 30–100 (200) cm high, rhizomatous, the stem is rough-hirsute or with rigid hairs, at the upper part glandulous. The leaves are narrow, lanceolate, the leaves of the stem are 6–10 mm wide and 5–8 cm long, generally with cordate or auriculate shoulders, hairy, more or less amplexicaul. The clusters of flowerheads form thyrsus, the all flower cluster is sticky glandulous, and the diameter of the flowerheads is 20–40 mm. The disk flowers are yellow, the ray flowers dark blue, dark lilac, blue, bluish violet or bluish lilac colored, occasionally changing between pink and dark red. The flower bracts are generally narrower than 1 mm, pointed and sitting in three rows, even length, and sometimes the outers sticking out. Its characteristic attribute is calendula smell of the fresh flower cluster when crumbed. The achene is densely hairy. The somatic chromosome number: $2n = 10$.

Aster novi-belgii L.

60–140 cm high perennial with branching rhizomes. The stem is straight, except of few row of small hairs bare (occasionally under the flowerhead can be hairy), sometimes umbellately branching. The

lower leaves are lanceolate-elliptic which narrowing cuneally to the short peduncule, the uppers are narrow lanceolate, 4–10 times longer than wide, at the base auriculately amplexicaul (till half of the stem), the margin sometimes serrated or entire, the leaves are 4–17 cm long and 0,4–2,5 cm wide, on the side branches smaller. The thyrsus is formed by many flowerheads which has about 30 mm (25–40 mm) diameter, the size of the flower bracts are about $5,5\text{--}7 \times 1$ mm, the inners and outers are equal (in some determination keys the outer ones can be shorter by half or two-third) green, freely close fitting or sticking out at the point. The 1,5 mm wide tubular flowers are yellow, the ray flowers are lilac, bluish lilac, in culture sometimes pink, purple or even white. The fruit is 2 mm long achene which is occasionally hairy. The somatic chromosome number: $2n = 18, 48, 50, 54$.

Aster tradescantii L.

(50) 60–100 (120) cm high plant with long rhizomes. The stem is straight with soft hairs. The leaves of the stem are narrow, inverse narrow-lanceolate, sessile, not amplexicaul, without auricles, with entire but rough margins, pointing at the end, and the leaves of the side branches are little. The underside of the leaves is continuously hairy. The diameter of the thyrsus forming flowerheads is 12–15 mm. The flower bracts are only 4 mm long, at the central area green part, overlapping, the inners are 2–3 times, by some authors 3–4 times longer than the outers, at the point sticking out. The tubular flowers are yellow, the ray ones whitish or light lilac, after flowering with reddish color. The achene fruit is 1,5–2 mm long and hairy.

Aster \times *salignus* WILLD.

Consolidated horticultural hybrid with parent species of *A. lanceolatus* and *A. novi-belgii*. It differs from *A. lanceolatus* by its lower leaves with short peduncules, sharply serrated margins (by the opinion of some with entire margins), the stem-leaves not so auriculate (narrower than the leaves of *A. novi-belgii*), the flowerheads are larger, those diameter is 25–35 mm. The somatic chromosome number: $2n = 18(?)$.

Aster \times *versicolor* WILLD.

It is a hybrid of *A. laevis* and *A. novi-belgii*. The stem and leaves nearest approaches to *A. laevis*. The leaves are sessile, barely amplexicaul, may be auriculate, the leaves of the side branches are a bit larger than the similar leaves of *A. laevis*, and the length of these are 2–3 larger than width. The flower bracts fitting close, the outers are shorter with widely skin-like margins and green point, and opposite to *A. novi-belgii* not overlapping and the length can differ.

ORIGIN, DISTRIBUTION

The examined neophyte taxa of the genus originate from North America, mostly from the North-Eastern states of the USA and from Canada (in North America 68 species belonging to the aggregate are known).

A. lanceolatus originates from the eastern part of North America, the distribution area spreads from the western part of Newfoundland to Saskatchewan and to the South to North Carolina, West Virginia, Kentucky and Missouri and Kansas states. *A. novi-belgii* also originates from the East coast and it is native from Newfoundland through the southern part of Quebec till Georgia. *A. laevis* spreads from Maine to the south till Georgia and Alabama, and to the west to British Columbia, Oregon, Utah and New Mexico. *A. novae-angliae* originates from South Canada and the central an eastern part of the USA: it spreads over west to Alberta, Wyoming, New Mexico, to the south till Alabama and North Carolina. The area of *A. tradescantii* lies from the Southern part of Newfoundland and Quebec to the Great Lakes and it is native to the Northern part of New York State.

The first known planted species in Europe could be *A. tradescantii* which arrived in 1637. Belike it escaped fast because in 1718 in Germany naturalized populations were recorded. In 1754 spontaneous populations were described near Verona. For a long time botanists did not pay enough attention to the populations of *A. \times salignus* spreading along the rivers that first recorded in 1787 at the banks of the Elbe.

In the second half of the 18th century and the first third of the 19th century more new species arrived to the gardens. It can be mentioned as a curiosity that the occurrence of hybrid *A. ×salignus* is not known from North America until now. The same applies to the other variants of *A. novi-belgii*. *A. ×versicolor* is extremely rare in North America. *A. lanceolatus* spread over Europe in the 19th century and in the present days it lives all over Central Europe maybe except Switzerland. The appearance of *A. lanceolatus* and *A. ×salignus* in Hungary has been given to the end of the 18th century and beginning of the 19th century (1793-1825). The first European data about *A. novi-belgii* comes from the 18th century and one of the centers of the spreading along of the Danube was Bratislava. From the 19th century two data is known around the city (1825, 1890), maybe it came before *A. ×salignus* around Bratislava (1871, 1883). *A. novi-belgii* agg. is common along the Danube, the bulk presence of the plant is known from the 60's-70's of the 20th century. In this region nowadays *A. lanceolatus* is the most common. The frequency ratio of the different species depends on the environmental factors and can be differing. For example in Poland the most pervasive is *A. lanceolatus* (it presents in 260 pieces 10×10 km sized quadrates), followed by *A. novae-angliae* (155 quadrates), *A. ×salignus* (139 quadrates), *A. tradescantii* (94 quadrates). The habitat requirements are reflected by that fact that in the Polish part of the Carpathian Mountains only one species *A. novi-belgii* is accounted as successful invasive species and the others (*A. lanceolatus*, *A. novae-angliae*, *A. ×salignus* and *A. tradescantii*) are rare.

BALOGH *et al.* (2003) account only *A. lanceolatus* and *A. ×salignus* as invasive species presenting at natural and/or semi natural habitats among the North American *Aster* species, while *A. novae-angliae*, *A. novi-belgii* and *A. ×versicolor* are mentioned as non-invasive naturalized species. It was tried to compare the more important and authentic presence data and compilations of *Aster* species but what was emerged the most data is recurring and the new data are almost missing. *A. novi-angliae* presents mostly in alluvial tall-herb communities but it is recorded also for example at Budapest. *A. novi-belgii* is also the plant of the tall herb communities but it is much more dispersed: known at Budapest, North-Western Plain Region, Győr, Western Transdanubia, Gyöngyös, Sopron, Kőszeg, Órség, Vas, Kalocsa, Debrecen; occurrent subspecies and varieties: at Debrecen, Győr, Kőszeg presenting. *A. lanceolatus* spread mostly along rivers: the Danube, Drava, Hármas-Körös and Rába. *A. tradescantii* is more frequent along the Danube, it can be found on the North-Western Plain Region, in the Csepel Island, at Nagykanizsa. *A. ×salignus* spreads in the flood areas and alluvial forests along the Danube, presents in the North-Western Plain Region, along the Rába, in the Szigetköz, at Gyöngyös, Székesfehérvár, on the Mezőföld, at Alcsút, around Velence, at Kőszeg, Pécs, in the Órség and other places. Finally *A. ×versicolor* also presents in many locations: for example at Budapest, Eger, Sátor Hill., Debrecen, Pécs, Órség, Vas, Zala, and countryside of Győr. The data connected to *A. laevis* are missing but we can give a guess about its presence on the base of distribution in the surrounding countries. Soó (1924-1925) wrote in the first quarter of the 20th century it was not observed in Hungary till those days. The actual distributions of each species pretend comprehensive revision.

LIFE CYCLE

The plant forms perennial polycormons growing with rhizomes and above-ground shoots re-growing every year. In the early spring phase of the shoot growing often the biomass of the leaves is larger than the shoots. Later after the first fourth or fifth of the growing cycle this ratio will be reciprocal. The biomass of the dead leaves can be standard or with slightly growing rate. The biomass of the side branches is growing too, and in the last triad of the growth season, the biomass of the generative organs appears. At the northern part of the North-Western Plain Region the average height of the plants is 100–120 cm (max. 160 cm), which is largest when the plant has unopened flower-buds. In the higher regions in forest stands the plants are smaller (90–100 cm). The differences in growth can be detected in the same species by the location on the two continents state interesting questions. For example *A. novi-belgii* is lower (rarely grow to 200 cm), in North America live 250 cm high individuals. Similarly *A. novae-angliae* at the original growing spots can be 240 cm tall but in Hungary generally it is only a bit more than half of it. The distribution of the biomass is also very altering, in the case of *A. lanceolatus* it depends on the cytotype of the specimen (chromosome number).

The phenological optimum of the North American asters is in the beginning of the autumn therefore the ripening of the fruits is very late. *A. laevis*, *A. novi-belgii* and *A. tradescantii* flowers from September (sometimes from August) to October, *A. lanceolatus* instead from September to November. The flowers of *A. novae-angliae* open from July to October.

A. lanceolatus forms generative organs only if the shoot reaches a critical size. The achene of the *Aster* species spread by its plumose seed (anemochory) but the flowing water also can be important spreading factor because of the achenes floating in the surface of the water (hydrochory) and therefore the central part of the dispersal area is mostly in the flooded areas (over the flood control dams is much more rare). The epizoochory also can be very effective. The investigated North American species (for example *A. laevis*, *A. novae-angliae* és *A. novi-belgii*) are not autogamic and the fruits of *A. tradescantii* are frequently sterile. In the most species the seeds ripen after the successful fertilization till November (but it depends on the actual species) and the long and warm autumn can be important. On 1 m² can evolve as many as half million achenes. Data from the Czech Republic show a single plant can develop 4000 flowerheads with 250.000 achenes. In more dense populations (350 flowering shoots) it can produce more than one million achenes. In more closed forest associations sometimes ripen „only” 70.000 achenes. For the germination not needed previous cold effects, the seed can germinate immediately. The germination potential is around 70% but sometimes it can be as low as 10% mostly in the case of hybrids.

A. lanceolatus can reproduce itself by vegetative way and the rhizomes can be one meter long. It has begun to develop the new leaf rosettes already in the flowering period. It is recorded that the vegetatively propagated plants develop more biomass for the aim of vegetative reproduction than the generative ones. For the vegetative reproduction one plant can produce 12 new rhizomes which have 12.3 cm average length and 3.5 mm average diameter – but it depends on the actual species too. There is no critical size for developing the rhizomes. In optimal case one basal leaf rosette can form more than hundred new rosettes

According to the clonal growth form of the plants in catchment area of the River Nitra 91% of the populations is small and compact but 9% is large and discontinuous (it depends apparently on the age of the polycormon and the ecological characteristics of the habitat). Independent and isolated shoots are not presenting (maybe as seedlings only) because with the rhizomes the polycormon become dense quickly. The population can grow about 30 centimeters at the edge but it may depend on the actual species, too. The reaction to the floods worth extra mention. The inundation decreases the density of the population and after the flood only few leaves stay on the stem (the new leaves develop after 3 to 4 weeks). The flooding water can lay down the stem. The *Asters* growing in frequently inundated willow woods rarely develop flowers.

HABITAT PREFERENCE

All the investigated species are nitro- and heliofrequent. They are demanding for the moist but avoid the continuously watered soils. They prefer the loose soil types but have relative broad ecological tolerance according to the soil type. Some species can survive even the longer inundations. They present both at disturbed areas and natural-seminatural habitats. They are very characteristic in alluvial forests, in tall-herb communities along water courses, at abandoned areas, at the side of roads and so on. They prefer the sunny spots but can occur at more shaded habitats too. *A. novi-belgii* agg. can be dominant in the herb layer of some alluvial woodland. *A. laevis* has different demands than the all other species because it likes the most continental habitats and can appear on drier places: on fields, opened forests, along roads and on railway-embankments. On mountains it can grow as high as 2700 m above sea level. According to our researches the populations of *A. novi-belgii* agg. were found in 50% of the cases next to flowing water, 33% along roads and the remnant at other locations as abandoned mines, railway-embankments and abandoned fields of the water catchment area.

The North American *Aster* species are frequent in the herb layer of poplar, ash and alder forests, these spread successfully in the associations of *Salicion albae* (alluvial willow-poplar forests), but sometimes can be found in the open varieties of *Fraxino pannonicae-Ulmetum*. *A. lanceolatus* is common in the weed communities of wet habitats (especially associations of *Senecionion fluviatilis* [syn.: *Calystegion sepil*] and *Arction* alliances).

BIOTIC INTERACTIONS

In numerous *Aster*-species are well known allelopathic effects. The alien species of the *Aster* genus are characterized with the high-level competition capability (C-strategy). In the case of the joint occurrence of *A. novi-belgii* and *Urtica dioica* because of the strong competition the species richness hardly reducing and the existing accompanying species has low level of abundance and vitality. The proportion of the two species is affected by the moisture of the soil (the frequent inundations are favorable to the *Asters*) and the amount of light. If the *Aster* grows in a *Polygonum amphibium* dominated patch it can out-compete the previous dominant species. Over the strong competition with some species it can form a kind of „symbiotic relation” (hybrid poplar – green ash – boxelder – American aster). The *Calystegia sepium* sometimes use the *Asters* as support and runs on it. The experiments about the competitive relations between the *Solidago gigantea* and *A. lanceolatus* show interesting results. The height of the two species is about the same but the first out-compete the later in the course of time and the possible reason can be the different morphology, i.e. the *Aster* has lower abundance but forms more side branches (BAZZAZ 1996).

As mentioned above the success of the plant is due to its long rhizomes and wide spreading polycormons. As it is measured in the northern part of the North-Western Plain Region along the Danube the population density of *A. novi-belgii* agg. is between 95 and 209 shoots/m², and along the River Morava this is 64.8–192.6 plants/m². The lowest population density (33 shoots/m²) of *A. novi-belgii* agg. near the Morava was measured in *Fraxino pannonicae-Ulmetum* association. According to the observations the inundation lowered the density of *Aster* while the density of other species' (*Glechoma hederacea*, *Galium aparine*, *Urtica dioica*, *Fraxinus* sp., *Stellaria media*, *Cardamine impatiens*, *Rubus caesius*) seedlings increased (this state can only be transitional because the inundation help the strengthening of the *Aster* in longer term). The species richness was the highest when the *Aster* density was the lowest (10,6 shoots/m²), and lowest (4,2–4,6 shoots/m²) when density of the *Asters* were high (132,4–211 individual/m² density). In other populations in the Hungarian North-Western Plain Region (FEHÉR 1998, 2000) the population density was 175 shoots/m² (in tall herb community at water side) and 185 individual/m² (at border of ash forest). The extremely dense population of *A. lanceolatus* can form a ring (in cases like this the density can achieve 719 and 743 shoots/m² values). The central ramets at the beginning of autumn can easily lean or completely lie down. The diameter of the population can be 5 meters or much more (sometimes more ten meters) but the outer lip of the patch in only an about 80 cm wide belt in the margin of patches with 5(–10) m in diameter stay standing, where the density can reach the 165–322 shoots/m² values. In the following year the centre of the patch regenerates much later and slower but the density and height can equalize in the second half of the growing season. The ring-forming populations can occur in other species too, but the total necrosis of the central area is more characteristic there.

In Hungary on the neophyte *Aster* species rarely occurs consumers and pathogens. The species belonging to *A. novi-belgii* agg. can be affected by the *Erysiphe cichoracearum* mildew fungus. It forms well developed mycelium on the surface of the leaves and shoots which can cover the all surface of the infected organs. The *Verticillium alboatrum* fungus species can occur on the cultivated *Asters*. In this case the affected plant will be yellow first and later can die. Other infections, for example by *Fusarium* species also can appear. The diverse rust fungi are not so characteristics on the North American species but for example the *Puccinia steris* were detected on *A. novae-angliae* and *A. salignus*, too.

ECONOMIC IMPORTANCE

The economical use of the covered species mainly inheres in the planting as ornamental plants. The occurrence first hundred years before was not accidental in the gardens of the nobility than because of the easy propagating (mainly by vegetative way by clone segments or rhizomes) in the rural gardens. There is almost no larger ornamental garden or settlement without them. Naturally the number of the cultivated species is much higher than the listed species here but fortunately not all of them tend to escape. The horticulture is responsible for the formation of hybrids like *A. ×salignus* and *A. ×versicolor* which are almost missing in North America. These are generally perennial garden plants and rarely used as cut flowers.

Less considerable but worth to mention that the investigated species can be interesting as melliferous plants: they give average field for bees.

NATURE CONSERVATION SIGNIFICANCE

The non-native *Aster* species cause problems mainly in alluvial vegetation: in the nitrorequent tall-herb communities often form monodominant stands. The populations growing on the floodplains sometimes make impossible the re-colonization of the original woody vegetation. They can over-compete the native species (including the endangered and protected taxa) and change the physiognomy of the associations. Although due to the clonal growth the polycormons usually successfully enlarge, sometimes the changing abiotic conditions can eliminate them (but it is a rare phenomenon). They can disappear in about 5 years due to absence of floods.

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COMMON RAGWEED

(*Ambrosia elatior* L.)

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TAXONOMY

The genus of ragweeds (*Ambrosia* L.) belongs to the Daisy or Aster family (Asteraceae). If the current perception that *Ambrosia* includes the formerly separate genera of *Franseria* and *Hymenoclea* is accepted, then this genus native to the American continent has approximately 46 species of which 4 are naturalized in Europe. Within the same family the closest relatives of *Ambrosia* are the genera *Iva* and *Xanthium* – both represented in Hungary by other invasive species –, and also the genus *Parthenium* expanding in other parts of the world. The closest cultivated plant relative of *Ambrosia* is the sunflower. The genus includes a number of similar and not easily separable species.

The currently accepted scientific name of the common (small) ragweed imported from North-America and having become widespread in Hungary is *Ambrosia artemisiifolia* L. As a consequence of former nomenclatural views (considering the name *A. artemisiifolia* either as a synonym only or as a separate species), it is the species name *A. elatior* that has become commonly used in Hungarian scientific language. Currently there are three varieties differentiated within the species, all of them having different geographic distribution in their native ranges: the typical form (var. *artemisiifolia*), and var. *paniculata* (MICHX.) BLANKIN are known to occur in Hungary only sporadically or to be missing completely. Hungarian populations almost uniformly belong to var. *elatior* (L.) DESCOURTILS. Based on cytological studies, $2n = 36$ diploid chromosome number was revealed in Canadian populations, whereas haploid chromosome number ($n = 18$) was reported from the United States. Its common names are "common ragweed" or "annual ragweed."

A. maritima L., one of the species of the genus *Ambrosia* is thought to be native to Mediterranean Europe and Africa, although certain researchers refer to it as having been introduced to these areas in earlier times, and as practically being identical with *A. psilostachya* DC., more precisely with its annual form. Others think of it as a variety of *A. ambrosiifolia*. *A. psilostachya* or perennial ragweed is another species introduced to Hungary from North-America. This name is considered to be a synonym by the last edition of *Flora Europea* and by all of the editions of the identification handbook by T. SIMON, where *A. coronopifolia* TORR. et GRAY is reported to be the valid name. Sources in the United States either treat *A. psilostachya* and *A. coronopifolia* as different species or (just like information published on the internet including the homepage of the US Ministry of Agriculture) consider *A. psilostachya* to be the valid name and regard var. *coronopifolia* only as a variety within that species. In the present study, the authors avoid submerging into the depth of taxonomic issues and use the name *A. psilostachya* instead. Cytological studies revealed different chromosome numbers for various areas of North-America ($2n = 72$ and $2n = 36$ for diploid and $n = 36$, $n = 54$, $n = 72$ for haploid numbers). The fourth species of the genus in our continent is *A. trifida* L., also introduced from North-America. Called giant ragweed in English and "three-leafed ragweed" in Hungarian, it has not been reported to occur in Hungary so far.

When using the term "ragweed" in this study thereafter, it will denote the common ragweed (*A. artemisiifolia*).

MORPHOLOGY

The ragweed is an annual plant, generally growing to a height of 20–150 cm (it can even exceed 2 m in well-fertilized soils), with wide and dense ramification. Its color is light green (lighter than the similar mugwort (*Artemisia vulgaris*), its specimens late in the season have reddish coloration. When rubbed, its leaves have a nice (mugwort-like) scent. Its upright stem has pressed-down hair or rough touch, and is rounded-quadrangular. Its lower leaves grow opposite each other, whereas the upper ones are alternately placed. The peduncle is short, the leaf blade has 1–2–3 sections. The sections are oval, the underside bearing pressed-down hair. Its small male and female flowers grow in separate inflorescences. Staminate (male) inflorescences are located terminally in racemes, with about 10–100 (–200) yellow florets in each of the conically shaped, weeping heads that have short and hairy peduncles (about the same length as the head itself. Pistillate (female) inflorescences bear a single floret, and are either single or grow in small clusters located under the peduncles of the upper leaves. The pistil is surrounded by the hairy receptacle bearing 4–6 dentations and scales. After ripening, the seed holds on to the head, creating a 3–5 mm long, cup-shaped, single-seed propagule that bears 4–6 pointed dentations in its upper part, slightly longer than 1 mm. The achene is lemon-shaped, dark olive green or maroon brown, the seed is oval and has high oil content. The weight of the receptacles is 2,3–2,7 g, that of the achene is 2,0–2,3 g per 1000 seeds.

The elliptic leaves of the seedlings have short peduncles, bear no hair, their tip is rounded. The stem below the leaves is reddish or rusty brown. The first leaves are covered with small hair, and are deeply lobed. The plant has tap roots, its secondary roots penetrate quite deep into the soil.

Hungarian populations with the morphology described above belong uniformly to *A. artemisiifolia* var. *elatior* form. In the case of var. *artemisiifolia* the other variety found in its native land, the leaves of the upper ramifications are entire, the male receptacles are larger (4–5 mm in diameter), their peduncle are strikingly longer (2–3 times) than the receptacle which has flat bowl shape. In the latter variety the entire male inflorescence is more loosely packed. Although specimens meeting some or all of the above morphological criteria may occur in the country, the only proof specimen of *A. artemisiifolia* var. *artemisiifolia* occurrence in the Hungary is regarded in literature to be the example found near the city of Szigetvár (southwest Hungary).

The perennial ragweed (*A. psyllostachya*) that has been found in Hungary already is pretty similar to the common ragweed, but it is somewhat shorter and less densely ramified. Its major morphological distinctions are that it does not have tap roots, instead it has horizontally spreading rhizomatous roots, and that the teeth on the upper side of the seed-bearing heads are rounded and shorter than 1 mm. It is expected that the giant ragweed (*A. trifida*) will also appear in Hungary. A secure distinctive feature of this annual species sometimes reaching heights of a couple of meters is that its leaves are not divided but digitate, comprising 3–5 leaf segments.

The morphological variability of the common ragweed is quite high, with several ecotypes having been described. Leaf shape and the degree of leaf division, hairiness, color and dimensions show great variance under different conditions. As to sexual variability in this species, the section on reproduction contains the relevant information.

ORIGIN, DISTRIBUTION

The genus *Ambrosia* evolved in the very dry Sonoran region located north and east of the Gulf of California from where it spread first to the surrounding less arid areas and then to the north and the east. However, the species that were later introduced to Europe evolved further off the centre of origin of the genus, more to the north in the American continent. The pollen of *Ambrosia* have been found in sediments older than 60 000 years in Canada, and the pollen grains of the common ragweed have been present since the last glacial period, i.e. for 12 000 years. Although this species was widely distributed in its homeland, it was quite rare: the amount of pollen in peat sediments is low, except for the last 200 years. As the western civilization took over in America to chop down forests and transform the landscapes, this amount grew to more than 100 times more. Today the common ragweed has a continuous range in North-America, extending to the southern part of Canada.

The common ragweed has been introduced to all parts of the world, giving it a chance to establish itself and to start spreading in temperate and subtropical zones of every continent. It has even entered the Russian far-East characterized with strongly continental climate. During the course of history, it has been imported to Europe several times, with cargoes of clover, grains and potato. Its identification in the initial times was problematic due to the fact that it was first mistaken with the morphologically very similar *A. maritima* which was already present in Europe at that time. According to the first reliable data, it appeared in France in 1846, in Germany in 1863, in Switzerland in 1878, and in Austria (Innsbruck) in 1883. Later it appeared in other West-European countries as well, but initially it was not able to establish itself, because its seeds – probably due to climatic reasons – did not ripen. Its true establishment and the start of the invasion started around the time of World War I, with ragweed-infested grain shipments from harbors of the Austro-Hungarian Monarchy. The real boom in its spreading then occurred after World War II. The European invasion had two centers: the smaller one in the south-western part of France, near Lyon, and the other one in the adjoining regions of Southwest-Hungary and Croatia (although the existence of yet another centre of origin, more to the east in Ukraine, is also possible). From Hungary, it then rapidly spread towards the neighboring countries, especially into the late socialist states. By today it has established itself in the states of South- and Central-Europe, but as an occasional species it also occurs in other countries as well. In Europe the common ragweed can complete its life-cycle in areas extending to 55° northern latitude. The northern border of its continuous range is around the latitude of South-Poland and South-Germany. *A. psilostachya* and *A. trifida* appeared around the same time, and has probably become established in Europe, yet these two species do not constitute extensive populations anywhere. Also *A. maritima*, a species with unclear status and with wide distribution in European and African Mediterranean areas have occurrence data in Central Europe. The occasional appearance of a number of other ragweed species is also possible.

In Hungary, the common ragweed appeared temporarily among cultivated plants in 1888, then several occurrences were reported in the southern areas in the early years of the 20th century. The time of the ultimate introduction from the direction of Yugoslavia, is estimated around 1922 when it was recorded in several localities in the regions of Lake Balaton, river Drava and Mura. The spreading started from Somogy county, and as early as by 1926, another centre of dispersion appeared near Budapest. Before World War II it became totally established in Transdanubia, except for the northern and western areas. The speedy invasion is said to have occurred in the period after the war, when it spread along the transportation routes of agricultural products: on roadsides and along railway embankments. By the year 1960 it had crossed the Danube and another centre of dispersion had appeared near the city of Szeged. In not more than ten years' time, the entire region between the rivers Danube and Tisza became infested, and other extensive, continuous areas have formed in the Nyírség and Hajdúság areas too. Spreading then started out from the eastern margin of Békés county. By 1981 practically the entire area of Transdanubia had become infested, and only the Northern Hilly Region and the central and northern parts of the area beyond river Tisza remained intact. By today the entire country has been invaded, but the degree of infestation is quite different among regions.

The perennial ragweed (*A. psilostachya*) was found in Hungary in 1962 in Csepel (near Budapest). Only scarce data have arose since then (the plant identification manual by SIMON signifies uncertain data from regions of the Danube and Drava), which can be explained by the fact that this plant is easily confused with *A. artemisiifolia*. The appearance of the easily identifiable giant ragweed (*A. trifida*) is also expected, as this species has been reported from neighboring countries.

LIFE CYCLE

Life phases of the ragweed have been studied in many ways in several parts of the world, both in open fields and under laboratory circumstances, unfortunately yielding opposing results in many cases, and contradicting Hungarian experiences. An obvious cause of this is the high variability and adaptivity of the species, but the effects of artificial products can not be excluded either.

The germination of ragweed seeds is a highly complex process influenced primarily by the status and history of the seed itself, and by temperature, light, soil water potential, the interaction of all these, and other factors. As TTC tests have revealed, about 70-79% of the newly ripened seeds are viable in Hungarian populations. Seeds of the ragweed are not able to germinate right after ripening, instead they are in the status of primary dormancy. In the open field this status is broken during the cold late autumn and winter months. Under laboratory conditions, 4 °C stratification for at least 6 weeks (optimally 12 weeks) was found to be the most effective treatment. Following this effect (meaning early January in Hungarian climate) the seeds are able to germinate; it is only cold weather that restricts the launching of the process (forced dormancy). Following that, a certain combination of environmental conditions (see specified below) allows high rate of seed germination. However, the alteration of these factors in seeds that, for some reason, could not germinate (due to drought, low O₂, and high CO₂-tension, high temperature, lack of light, etc.), can induce secondary seed dormancy period. Secondary dormancy can be broken the same way as primary dormancy, meaning that under natural circumstances seeds will become able to germinate again in the next year. In line with the description above, ragweed seeds that have not germinated will regain and loose the ability to germinate in cycles during successive years. Seeds remain viable for a long period: in two unrelated experiments it was possible to germinate seeds preserved in greater soil depths after a maximum of 39 and 40 years, respectively.

In seeds that have been stratified for a longer time, germination can start even at lower temperatures, i.e. slightly below 4 °C. As temperature raises, the rate of germinating seeds increases; various laboratory investigations have found that the highest values were obtained at 31 °C or at alternating temperatures simulating 15/30 °C day/night regimes. Based on findings in open fields, the first seedlings in Hungary are observed in late March, to be followed by germination maxima in the period between 10 April and 20 May (at alternating temperatures of 10/20 °C), with about 60% of the seeds germinating. After the first half of June there is only limited amount of germination (almost no germination at all in its native land), because high temperature makes the majority of seeds to enter secondary dormancy. It has to be noted, however, that some Hungarian publications (e.g. UJVÁROSI) report on continuous germination throughout the summer period. Personal observations also suggest that the closure of germination with the onset of the warmer period is not quite obvious as in American populations which may indicate the adaptation of the species to Hungarian conditions.

All of the studies support the fact that light stimulates the germination of ragweed seeds, but here, too, the effect is a complex one: seeds kept in continuous darkness germinate at lower temperatures only, because at alternating temperatures of 5/16 °C or above these values, conditional seed dormancy (or light demand) sets in. If seeds existing in conditional dormancy are given light (even a short impulse can be sufficient) they regain their germination ability. Thus, if seeds resting in the soil are not disturbed, primary dormancy will form in spring which will turn into secondary dormancy by early summer. Such an interrelation between light and heat requirements was ignored by many of the laboratory investigations, although it well explains why maximal germination occurs at lower temperatures in open fields than what is expected from literature data.

As to soil water potential, values around -0,06-0,00 mPa are the most favorable, and there is no germination below -0,08 mPa. The effect of salinity concentration has not been studied directly, but it is known that the common ragweed survives in saline and coastal areas (although its seeds do not germinate in sea water. The removal of the scales from the achenes improves germination success.

Under natural circumstances, it is the depth at which the seed rests in the soil that can modify (or allow to be expressed) the effects of temperature, light, humidity, CO₂ and O₂ tension. Seeds located deeper down receive less light, and soil temperature rises slower to the suitable level, therefore worse germination rates are expected. Laboratory studies have proved several times that germination is the best when seeds are found directly at the soil surface, and as depth increases, germination rate gradually worsens. However, in field circumstances the surface is more exposed to extreme changes in external environmental factors, water supply is worse too, thus seedlings can more easily die. It is probably because of these reasons that in Hungary the optimal depth was found to be 3 cm. Germination success at

the surface was 0% in many cases, whereas at depths greater than 7 cm even if germination is successful, the seedling cannot reach the surface (these figures, of course, can be different, depending on soil type and weather conditions in the given year).

The adaptive significance of this complex germination behavior is probably related with the pioneer and disturbance-preferring strategy of the ragweed, because this is what makes it possible for a vast amount of seeds to germinate when the soil receives light due to being disturbed or due to the opening up of vegetation cover, and this is what lets a suitable amount of seeds remain in the soil for opportunities arising later on. In addition, secondary dormancy prevents germination under less favorable, summer conditions (drought, greater competitive pressure, shorter vegetative period).

According to phenological studies having performed in Hungary, in case of seeds sown early, on 7th April, an average of 119 days pass before flowering, and a total of 183 days before seed production. These plants grew to a height of 170–180 cm. Plants that germinated in June–July had flowers in only 80 days, and needed 155 days to produce seeds. Thus, independently from the time of germination, the period between flowering and seed production is fairly constant, being generally only slightly more than 60 days. In case of plants that germinated in late August, only 34 days were necessary for them to produce flowers, but the seedheads could not ripen under such conditions, and the height of the plants remained only 8–12 cm. Growth is intensive until flowering sets in, but then it slows down.

As Canadian investigations, covering a span of 8 years, have revealed, the start of common ragweed flowering fell into a period only 12 days long. The same studies have revealed that plants flowered earlier towards the north, and their vegetative growth was less intense.

A. artemisiifolia can reproduce only sexually. If any vegetatively propagating, rhizomatous ragweed is found in Hungary, most probably it is the perennial ragweed (*A. psilostachya*) which is still rare in Hungary.

The common ragweed is a wind-pollinated plant; insects sometimes found in its male flowers only collect pollen. Under glasshouse conditions it has been demonstrated that seeds are produced by both autogamous and allogamous pollination, but the significance of this feature under field conditions is still unknown. This species shows sexual variability: although it is generally monoecious, there are specimens at a rate of about 5% which bear exclusively female flowers. In these plants either there are no terminally located male flowers at all, or they are replaced with female heads. It has been showed that in closed stands the dominant influential factor in creating the sexual character is the height of the surrounding vegetation, and that there is correlation between male character representation in the population and plant height. When mostly or exclusively female flowers are born, it is typically on plants that are short and are in a shaded position. An earlier study by HEGI reported that in dense ragweed stands it is male character that dominates, but this conclusion may be attributed to the higher, more conspicuous specimens (nevertheless, the relative pollen production of dense stands is higher). In the case of solitary specimens, however, there is no correlation between height and sexual character. Generally, such specimens have relatively strong female character in all circumstances. In plants that germinated late in the season it has been observed that as early as in their four-leaf stage they produced a few apical female flowers, but there were no male flowers at all.

The opening of male flowers precede that of female ones by about 7–10 days, and flowering starts earlier on main stems than on secondary branches. The release of pollen starts some time in the period between 13rd July and 4th August. The opening of individual male flowers in the flowerhead follows one another. The most intense pollen production of any male flower raceme lasts for about 7–10 days, the plant thus releasing pollen for a period of more than a month.

The amount of seeds depends greatly on the time of germination: Hungarian studies have revealed that plants that had germinated in early April produced 3–4000 seeds, whereas those germinating in late August produced only 14–16. In the United States, too, the number of seeds per plant is around an average of 3.000 (the highest value being 62.000), whereas from Ukraine a so-called "gynaecus" form yielding 150.000 seeds is reported.

The seed is usually dispersed together with the surrounding head. There is no special seed dispersal mechanism for this plant. The seeds are scattered around the parent plant by the wind in a

range of just a few meters. They can be dispersed also by birds feeding on them, and the propagule can attach itself to the coat of furry animals with its tiny teeth. Seeds can travel with water too: intensive expansions were observed in Australia after larger floods. The most significant dispersal is done by humans, through the transportation of infested sowing-seed, earth and mud, carried away by vehicles.

HABITAT PREFERENCE

The ragweed is a plant typical in disturbed, open habitats. Stimulated by disturbance, it appears anywhere apart from extreme conditions or with very low insolation. Where bare soil surfaces are created in larger extents, it spreads immediately, thus it is the most typical plant of first-year abandoned fields, and is a permanent accompanier of constructions and earthworks. Its constant presence can be expected in locations where disturbance is repeated regularly, i.e. in arable fields, roadsides, and, generally, in places where human activities cause disturbance. Accordingly, it is almost totally absent from undisturbed, near-natural habitats and secondary habitats that have been in the process of regeneration for a longer time. Several ragweed associations have been described from disturbed habitats, primarily from arable fields.

Generally, the ragweed has wide tolerance of various environmental factors. It is only light that is required in greater amounts in the period of growth, but after flower production has started, shading is tolerated well. Its heat demand is relatively high, a fact that may have influenced its spreading speed in various regions throughout Hungary, yet its distribution is limited by climatic reasons only in the highest regions of our hill ranges. From the aspect of reproductive success, an alternating range of 26/32 °C proved to be the most optimal temperature (reproductive success decreasing significantly at higher temperatures), meaning that Hungarian conditions are absolutely favorable for this plant. As to soil characteristics, the ragweed is not too demanding. Generally it proves to be successful on loose-structure soils that can warm up well (brown forest soils, alluvial soils, loose, sandy loam, black earth or chernozem, eroded ruderal soils). Having strong roots that penetrate the soil to considerable depths, it grows well even on extremely dry soils such as drift-sand, but also tolerates soils that become moist occasionally. In the process of growing it successfully survives dry spells: based on Hungarian investigations, the critical water saturation deficit of the ragweed is very high (75–73%), meaning that in case of dry weather it can regenerate well after losing much water. Similarly, no matter that water supply is bad, the photosynthetic activity of the ragweed stays at a high level. As regards soil pH, it has wide tolerance, although it is reported in literature that it does best on neutral or slightly acidic soils (pH 6,6–7,0). It tolerates saline conditions badly, but where the salinity of the soil is low, it is found in great expanses. The ragweed prefers medium or high nitrogen supply. Its reproduction is greatly influenced by nutrient availability. How the ragweed behaves in areas with heterogeneous nutrient distribution, is an open question, though. In some investigations it was found that by its differentiated root growth it can very effectively utilize soil patches that are richer in nitrogen, but other experiments seem to have proved just the opposite i.e. that the root system of the ragweed is the most effective in utilizing soils with homogenous nutrient distribution.

Its photosynthetic activity stays high amidst a broad range of environmental variables. If CO₂-concentration of the outer atmosphere is raised and appropriate nutrient supply is ensured, its assimilation strongly increases. Several experiments have been carried out to find out how intense its growth and pollen production will be if CO₂ quantities of the atmosphere continue to grow. It has been found that if CO₂-concentration becomes twice as high as it is today (which is realistic by 2050 with a view to the growth rate of an annual 2ppm measured today), the dry matter production of the ragweed could grow by 30–50%, its pollen production by nearly 250% (due to higher number of florets and the larger size of inflorescences), and also flowering would start somewhat earlier.

Being a short-day plant, the ragweed is retarded in its growth if daytime exceeds 14 hours in its photoperiod. At a continental scale this is one feature that limits its distribution towards latitudes more to the North. The optimal duration of illumination is around 10–14 hours.

BIOTIC INTERACTIONS

The negative allelopathic effect of the ragweed on the germination of several cultivated plants and on the reproduction of soil green algae has been proved under laboratory conditions. The strongest effect was achieved when using leaf extract, but extracts from inflorescence and fruit also seemed to cause significant inhibition. The effect is most probably caused by phenoloid and terpenoid compounds. The importance of allelopathy under field conditions is not known; observations are quite different (stimulative effects have also been noted).

As to the competitive ability of the common ragweed, data are contradictory. In its original habitats, the ragweed is a dominant species of disturbed areas – primarily abandoned arable fields – from where it recedes after a few initial years of dominance. According to BAZZAZ, the ragweed is the archetype of r-strategist plants. Some investigations have found it to be the strongest competitor among the dominant species of the first couple of years: its growth was not influenced at all by other species growing around it, and the ragweed itself had strong negative effects not only on annual plants but also on perennials such as *Plantago lanceolata* or *Agropyron repens*. In other studies it has been found that in the presence of annual plants germinating in the autumn, growing in the winter and thus starting in the spring with an advantage such as *Conyza canadensis* and *Stenactis annua*, the height, biomass and reproductive success of the ragweed were considerably reduced (whereas its density did not change), and the effect of predation also increased. All this finally lead to its confinement and reduction. When the mechanisms of competition in abandoned arable fields were investigated, it was found that the effect of underground competition is much more restrictive on the ragweed than competition above the ground.

In closed plant associations, shading is found to be clearly inhibiting both the germination and the vegetative development of the ragweed.

The number of consumer species (herbivores) associated with the ragweed in North-America is estimated to be more than 300. Many of these are poliphagous or oligophagous, but there are many monophagous species, too. The most important arthropod agents that have been studied from the aspect of possible biological control are the following. *Euaresta bella* (Diptera: Tephritidae) is a seed eater, but it destroys only small proportion of the seeds. Gall-forming species on stems, leaves and flower include *Asphondylia ambrosiae*, *Rhopalomya ambrosiae*, *Contarinia parthenicola* gall midges (Diptera: Cecidomyiidae) on stem; the moth *Epiblema strenuana* (Lepidoptera: Tortricidae) on leaves; the mite *Eriophyes boycei* (Acarina: Eriophyidae), and the moth *Coleophora annulatella* (Lepidoptera: Coleophoridae) on leaves. A stem parasite is the gall midge *Neolasioptera ambrosiae* (Diptera: Cecidomyiidae). The weevil *Cylindrocopturus quercus* (Coleoptera: Curculionidae) is a stem-parasite in its larval stage and is a leaf-eater as an adult, whereas another beetle *Acropteroxys gracilis* (Coleoptera: Languriiidae) feeds on the stem as well. Larvae of the longhorn beetle *Dectes texanus* (Coleoptera: Cerambycidae) is a stem-eater (this species is a pest of soy-bean, too). Leaf-eaters are the leaf-bugs *Ophraella communis*, *Zygogramma bicolorata*, *Z. suturalis* (Coleoptera: Chrysomelidae), and the caterpillar life stage of the noctuid moth *Tarachidia candefacta* (Lepidoptera: Noctuidae).

Several arthropod species have been collected on ragweed in its secondary distribution area, including Hungary. In feeding experiments in Yugoslavia, 28 of 100 native insects were found to feed on ragweed, although not all of them succeeded in developing to adult stage. In a study performed in Hungary a total of 174 phytophagous species were collected on ragweed and identified during a period of two years (only 73 occurring more than once). Of the 73 species 25 were cicadas, 26 hemipterans, 7 orthopterans, 13 beetles, and 2 aphids. The majority of these species (similarly to species collected in other regions of Europe) were poliphagous or oligophagous with no proof of whether or not the ragweed is a suitable feeding plant for them, or, if it is, whether they can cause any harm to the plant. The bulk of insects collected on ragweed in the secondary distribution area of the plant are agricultural pests, therefore are unsuitable for being used in biological ragweed control. Grazing animals do eat ragweed, but do not tend to particularly like it. Its cellulose and hemicellulose content is too low (25 and 1–3%, respectively), whereas its raw protein content is pretty high (25–29%). The annual ragweed reacts quite sensitively to damage caused by herbivorous animals: upon loosing 1/3 or 2/3 of its foliage, seed production is reduced by 75% and 97%, respectively.

Research done on plant pathogen organisms living on ragweed in its original distribution area has revealed several harmful fungi and bacteria. The most promising from the aspect of biological control are two North-American rust fungi *Puccinia conoclinii* and *P. xanthii*. Their host spectra are narrow, with theoretical threat in Europe posed to another group of invasive species belonging to the genus *Xanthium* (the *forma specialis* of these fungi pathogenic to *Xanthium* species is already present in South-Europe).

Several native pathogenic fungi have been collected in Hungary which are capable of seriously damaging the ragweed. As reported in studies performed abroad, the white mildew *Albugo tragopogi* reduced pollen and seed production by 98%, as well as retarded the increase of plant height by 79%. *Plasmopara halstedii* (a pathogen of sunflower) causes ragweed to die at the terminal period of the vegetative season. *Verticillium dahliae* causes tracheo-mycotic wilt, whereas *Rhizoctonia solani* attacks the roots. *Macrophomina phaseolina* was collected from dying specimens. The mildew *Entyloma polysporum* is another species known from Hungary, and *Septoria epambrosiae* was first described from Hungary. Some of the species listed above are pests that have quite wide host spectra, and some others are only little known, therefore their utilization in biological control is possibly out of the question. An exceptional event in 1999 was the quite considerable damage caused on almost the entire Hungarian ragweed population by *Phyllachora ambrosiae*, a fungus already known in America. Caused by the fungus which is normally not pathogenic but became virulent due to the wet weather that year, pollen production of the ragweed was terminated about one month earlier than normally. The following year this fungus species could not be found again in the country. Among parasitic plants, *Cuscuta campestris* has been observed on ragweed.

The common ragweed is characterized with arbuscular-vesicular type of mycorrhiza. In an experimental investigation focusing on the effect of *Glomus etunicatum*, it was found that this symbiotic fungus raises the phosphorus-uptake of the ragweed quite considerably, having positive effect on its growth and root density. In sandy habitats arbuscular-vesicular mycorrhizal association has been shown in Hungary too.

ECONOMIC IMPORTANCE

European *Ambrosia* species are not utilized by economy, with the only exception being *A. maritima*, the extract of which, due to its anti-mollusk effect, is used for killing aquatic mollusks that are vectors of human parasites in tropical waters. In its native range, the common ragweed has traditional medicinal uses: its sap is applied for reducing local bleedings and to cure digestive disorders. It has been suggested that the high oil content, bearing good drying characteristics, be used in the chemical industry. The fruit of the ragweed could be a supplementary feed for game birds in wintertime.

Ragweed has become the most significant, dangerous weed of agricultural lands. According to data obtained in the Hungarian Nation-wide Weed Surveys in winter wheat and maize, the significance of the common ragweed has gradually increased: in 1950 it was ranked as only 21st, and by 1997 it has become first in the ranking. As revealed by the 1997 data, its coverage in agricultural lands is 4,7%. Demonstratively, this means something as if agriculture would be producing ragweed in monoculture on nearly 300 000 hectares. Based on the monitoring surveys that have been performed by the Agrochemical Department of the Ministry of Agriculture and Rural Development, the expansion of ragweed has been radical in the last ten years (which is related with the transformation processes going on in agriculture). With annual weed control done as normally, ragweed-infested areas in 1990 totaled up to 418 736 hectares, and in 2001 this value reached 2 935 794 hectares. Out of the 6.2 million hectares of arable lands found in the country, ragweed is present on about 5 million hectares. The degree of infestation is different among various regions of the country, but there is expansion everywhere.

The common ragweed is present in all of the important plant cultures. It causes the greatest problem in vegetables, and it is the most critical in sunflower fields. It has less importance in grain crops, rape, and in densely sown crops. It is difficult to estimate the damage caused by this weed, but the sum is most likely to reach a hundred million EURO.

The pollen of the common ragweed is the most significant aero-allergen in Hungary today. In its native range, the ragweed is thought to be one of the main causers of hay-fever, together with *Artemisia*

trifida. (Also allergenic, *A. psilostachya* is usually not a great problem, due to its much lower numbers.) A single plant specimen releases 1 million pollen grains a day, totaling up to 10^{12} particles during its lifetime. A one-hectare expanse of ragweed produces 66 kg pollen in a single season. Transported by the wind, pollen grains can travel to more than 300 km from their origin. Allergy usually develops after a period of 2–4 years after exposition to ragweed pollen, but it also can happen that symptoms express themselves only after a maximum of 15 years following the first exposition. The plant or its pollen can cause skin irritation (contact dermatitis), too. Its ethereal oils increase photosensitivity, i.e. the skin becomes sensitive to solar radiation, and thus can cause phytic photo-dermatitis. Ragweed pollen is a strong sensitizing agent, meaning that it increases the likelihood of evoking sensitivity to other potential allergens in people who are otherwise sensitive to ragweed. Currently, ragweed pollen is the most aggressive among all other plants found in Hungary, and the concentration of its pollen at flowering time is manifold that of all grasses combined (ranked next in pollen production). About 15–20% of the Hungarian human population suffer from pollen allergy, and the majority of allergic people are sensitive to ragweed pollen.

NATURE CONSERVATION SIGNIFICANCE

The common ragweed can appear in all sorts of non-extreme, near-natural grassy habitats (mostly on light soil), but its populations are short-lived, and are found only in the disturbed patches of the habitat. Its permanent presence in near-natural habitats suggests that there is prolonged disturbance (from this aspect it can be an indicator plant in nature conservation sites). A potential threat is that the long-lived seeds can gradually accumulate in the soil and repeated disturbance can thus result larger and larger ragweed populations. Habitats that are most prone to ragweed boom are mostly sandy areas with treading, grazing, horse-riding, etc. It is a question, though, if disturbance meant by the natural movement of drift sand is enough in itself for the permanence of ragweed in the area.

Being a dominant pioneer species of secondary, disturbed habitats, theoretically the ragweed can inhibit the regeneration of such areas. In its native range there is no such effect attributed to the ragweed: succession in abandoned arable fields proceeds at a uniformly steady speed, independently from the amount of ragweed being present. Normally, it is one of the dominant species in the first year, but by the third or fourth season its quantity is strongly reduced. Studies performed in Ukraine revealed somewhat different picture, however: in the initial four years of the regeneration of the area there was considerable difference in the composition and development of the vegetation between ragweed-disinfested and control plots, and the invasive ragweed withdrew much slower. This can be explained with the fact that in Europe there are no specialized consumers of the ragweed, meaning that the ragweed is in a much favorable competitive situation here than in its native land. Nevertheless, this fact does not seem to be influencing long-term habitat regeneration processes. Hungarian experiences, too, are reassuring in this respect. In any case, it must be considered that even if the regeneration of the area is successful in secondary habitats, considerable amounts of ragweed seeds can remain in the soil.

In near-natural areas, it is mostly the more frequented areas and visitor zones where the ragweed can cause problems. Areas designated for visitor access are subject to increased disturbance, and in buffer zones often there are many newly abandoned fields. It is important to consider what kind of impression the visitors may gain about nature conservation in an abandoned, ragweed-infested landscape that looks pretty neglected.

In a particular field of nature conservation, which has been quite overlooked in Hungary, the ragweed appears as an important modifier of associations. In segetal associations it threatens rare, vanishing plant associations that have partly disappeared due to intensive agricultural techniques. Research data in this field in Hungary is quite limited, but in the north-western plain region it has been shown that certain rare segetal associations have become poorer in their species composition due to the aggressive behavior of ragweed, even in extensive arable fields.

The perennial ragweed (*A. psilostachya*) preferring similar habitats has much more restricted significance even in its native homeland, therefore it is unlikely that nature conservation problems could be

caused by this species in the foreseeable future (although information about this species is too limited to allow any firm conclusions). The giant ragweed (*A. trifida*), however, has a greater potential risk, because in America it persists longer in disturbed areas and thus inhibits the natural regeneration of the site.

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ROUGH COCKLEBUR

(*Xanthium strumarium* subsp. *italicum* (MORETTI) D. LÖVE)

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TAXONOMY

It's applied as valid, nearest to its real taxonomical status, but officially not accepted scientific name: *Xanthium strumarium* L. subsp. *italicum* (MORETTI) D. LÖVE. The rough cocklebur (*Xanthium italicum* MORETTI 1822) is not acknowledged as an autonomous species neither by the British-based Flora Europaea, nor by the American ITIS (Integrated Taxonomic Information System), though in the Hungarian literature it is featured by this taxonomical rank. We remark already here that from the morphological part for the sake of better understanding, traceability and to the effect of simplification we also discuss the complexes of *X. strumarium* (vide infra) wrote out at the end of the taxonomical chapter as they would be autonomous species. Going by the nomenclature of Flora Europaea, the oftener associate names (synonyms) of the rough cocklebur are the followings: *Xanthium italicum* MORETTI, *X. echinatum* MURRAY, *X. californicum* GREENE, *X. intermedium* CAUTREC., *X. occidentale* BERTOL., *X. strumarium* L. subsp. *canavillesii* (SCHOUW ex DIDR.) D. LÖVE et DANS. The list of its synonyms gets even longer taking into consideration the hybrids of the rough cocklebur too: The hybrids of *X. strumarium* subsp. *strumarium* and subsp. *italicum* have the following synonym names: *X. riparium* ITZIGS. et HERTSCH, *X. macrocarpum* DC., *X. saccharatum* WALLR., *X. orientale* L., *X. albinum* (WIDDER) H. SCHOLZ subsp. *riparium* (ČELAK.) WIDDER et WAGENITZ, *X. brasiliicum* VELL., *X. albinum* (WIDDER) H. SCHOLZ. Obviously the inferior taxa of the synonym names are invalid, accordingly for example many of the names quoted by Soó's Synopsis too: *X. orientale* L. f. var. *italicum* f. *morettii* TUZSON, *X. saccharatum* WALLR. subsp. *italicum* HAY., *X. echinatum* NOCCA et BALBIS 1821 non MURRAY 1784. (Since the correspondences of the associate names are much more complex than mentioned above, reading of the taxonomical part is definitely suggested.) Its names are partly relative to *X. strumarium* group: English names: Italian cocklebur, Italian cocklebur, hunter burr, ditchbur, sheepbur, common cocklebur, rough cocklebur, common clotbur.

Rough cocklebur belongs to the Asterales order, the Asteraceae (Compositae), daisy or sunflower family and the Asteroideae subfamily, and within it to the Heliantheae tribe, Ambrosiinae subtribe. The number of species of the *Xanthium* genus is disputed between different literature, giving its rate in between 2 and 30. The official sources generally differentiate two species within the *Xanthium* genus, the spiny cocklebur, *X. spinosum* and the rough cocklebur, *X. strumarium*. Previous one belongs to the *Acanthoxanthium* and latter one to the *Xanthium* (syn. *Euxanthium*) subgenus. *Xanthium spinosum*, spiny cocklebur can easily be identified by the 1-3 armed, yellow stipule spines that springing at the leaves base, by the white or grey hairy abaxial surfaced, above oil-green colored, intact or 3-5 lobed, rather lanceolate leaves and by the tapering beaked, crooked shaggy fruits that are smaller than they are at the other *Xanthium* taxa. The invasion of *X. spinosum* of American origin – causing serious agricultural problems – was culminated in Hungary in the midst of the 19th century. Nowadays, it has spread only in arable fields and ruderal habitats that are heavily disturbed, thus it can cause problems on the over-grazed pasture-lands with damaged surface, where chiefly it affects adversely the quality of wool. It does not endanger the natural or semi-natural habitats, namely it is not of transformer quality. An

exhaustive documentation of its invasion is given by VINCE BORBÁS (1893) that study is far ahead of its time in this topic. Into the *Acanthoxanthium* subgenus – if it is considered to be an autonomous species – the Argentinean native *X. ambrosioides* can be rated too.

X. strumarium (sensu lato) L. can be regarded as a strongly polymorphic species, within it for example LÖVE and DANSEREAU (1959) separated eight more or less distinct morphological complexes: *strumarium*, *cavanillesii*, *echinatum*, *pensylvanicum* (sic!), *italicum*, *orientale*, *chinense* (= *occidentale*), *oviforme*. The descriptions of complexes were chiefly build upon the morphological distinctivenesses of the fruit (fruit-complex), and less of the leaves, but they did not get autonomous formal taxonomical status. Officially the same situation stands for the time being too, although earlier WIDDER (1923) separated, by similar criteria, already seven species within the *Orthorrhyncha* subsection of the *Euxanthium* section of the genus: *X. strumarium* (sensu stricto), *X. indicum* KÖNIG, *X. japonicum* WIDD., *X. sibiricum* PATR., *X. brasilicum* VELL., *X. abyssinicum* WALLR., *X. inaequilaterum* DC., and twelve species within the *Campylorrhyncha* subsection: *X. occidentale* BERT., *X. pungens* WALLR., *X. inflexum* MACK. et BUSH, *X. decalvatum* WIDD., *X. orientale* L., *X. cavanillesii* SCHOUW., *X. saccharatum* WALLR., *X. italicum* MOR., *X. riparium* ITZIGS. et HERTS., *X. echinatum* MURR., *X. californicum* GREENE, *X. oviforme* WALLR. It should be noted that MILLSAUGH and SHERFF (1919) separated 19 species only within the latter subsection. LÖVE and DANSEREAU, in their earlier mentioned study, have tried to settle the taxonomical matter of the morphological complexes essentially by their origin, according to this Old World autochthonous is *X. strumarium* subsp. *strumarium*, while New World autochthonous – indicating of that they are all originated from the ‘*cavanillesii*’ complex – is *X. strumarium* subsp. *cavanillesii* (SCHOUW.), and they wanted to summarize them under the D. LÖVE et DANS. name. The Flora Europaea regards *X. strumarium* L. subsp. *italicum* (MORETTI) D. LÖVE name as a synonym of the latter, consequently this is the official taxonomical name of the New World origin ones, leastwise according to the Flora Europaea. To sum up, the alignment of *X. strumarium* L. taxa occurring in Europe is the following in the interpretation of the official nomenclature: 1) *X. strumarium* L. subsp. *strumarium*, namely the synonyms of the Old World origin: *X. strumarium* L. (sensu stricto), *X. sibiricum* PATRIN ex WIDDER., 2) New World origin, the synonyms of *X. strumarium* L. subsp. *italicum* (MORETTI) D. LÖVE: *X. californicum* GREENE, *X. echinatum* MURRAY, *X. intermedium* CUATREC., *X. italicum* MORETTI, *X. occidentale* BERTOL., *X. strumarium* L. subsp. *cavanillesii* (SCHOUW ex DIDR.) D. LÖVE et DANS., 3) The hybrids of the Old World and New World origin, synonyms of *X. strumarium* subsp. *strumarium* × subsp. *italicum*: *X. albinum* (WIDDER) H. SCHOLZ, *X. albinum* (WIDDER) H. SCHOLZ subsp. *riparium* (ČELAK.) WIDDER et WAGENITZ, *X. brasilicum* VELL., *X. macrocarpum* DC., *X. orientale* L., *X. riparium* ITZIGS. et HERTSCH, *X. saccharatum* WALLR.

What could be the reason of the high degree of heterogeneity of *X. strumarium* group? The reason of it is shown by some regional case study. Of the complexes described by LÖVE and DANSEREAU, the ‘*chinense*’ – in case MILLSAUGH and SHERFF’s (1919) observation is reasonable, that was verified by many others since (for example WIDDER (1972), McMILLEN (1971, 1972, 1973a)), according to it this complex is a synonym of *X. pungens* and *X. occidentale* – is native in the Eastern part of the United States and in the Caribbean area. It spread out from here into India and Australia. In the system of LÖVE and DANSEREAU these taxa can be featured also as *X. strumarium* subsp. *cavanillesii* (SCHOUW.) LÖVE et DANS. var. *glabratum* (DC.) CRONQ. (The ITIS system only accepts *X. strumarium* var. *glabratum* (DC.) CRONQ. name.) Many authors suggest to give this taxon *X. chinense* MILL. name on priority basis (McMILLEN 1975). According to LÖVE and DANSEREAU the ‘*pensylvanicum*’ complex is a highly polymorphic group, resembling to ‘*italicum*’, that is defined as *X. californicum* by McMILLEN (1973) in a narrower interpretation, with this intrinsically he follows WIDDER’s (1923) standpoint. According to McMILLEN the species provisionally described with this name (*X. californicum* GREENE) shows gradation towards the ‘*chinense*’ and the ‘*cavanillesii*’ complexes. Namely – as McMILLEN (1973a, 1975) points it out – the morphological distinctiveness of the substances that conquered Australia are essentially indistinguishable from *X. californicum* ones described in California, and is the species itself he considers to be an introgressive form evolved between ‘*chinense*’ and ‘*cavanillesii*’. Even according to McMILLEN (1973a) and WIDDER (1923) the South American native, possibly started up in the area of Argentina

'*cavanillesii*' complex can be defined to be an autonomous species, that is a synonym of *X. australe* MILLSP. et SHERFF described by KILLSPAUGH and SHERFF (1919). This complex is already represented in North Africa and of the European areas in Spain and in Ukraine, its contingent further spreading is expected. According to LÖVE and DANSEREAU the '*italicum*' complex develops introgressive hybrid complex with '*pennsylvanicum*'. Some author range into the '*italicum*' complex – partly inconsistently – such earlier described species, like *X. italicum* MOR., *X. pennsylvanicum* WALLR. and *X. saccharatum* WALLR. For that matter the '*italicum*' complex showed up in Europe presumably early in the 1800's on the coasts of the Apennine peninsula, it follows that the taxa with bigger fruit (*X. orientale*, *X. macrocarpum*) of hybridogenous origin – or only counted to be so –, either were not evolved in Europe, or if they were, then they are of subsequent formation. In case of the Australian acclimatization of the '*italicum*' complex, McMILLEN (1975) presumes a previous introgressive hybridization of the complex with the '*chinense*' complex. Similar phenomena and multiple hybridization are presumptive to happen between '*strumarium*' and '*italicum*', as well as '*strumarium*' and '*cavanillesii*' complexes, between the forms occurring in Europe too. Because of the observed high polymorphism and the introgression LÖVE and DANSEREAU (1959) suggested *X. strumarium* subsp. *cavanillesii* var. *cavanillesii* taxonomical name equally for the '*pennsylvanicum*', the '*italicum*' and the '*cavanillesii*' complexes. By virtue of the comprehensive study of cockleburs occurring in North America CRONQUIST was also led to the conclusion that within the *X. strumarium* group at the most two taxa can be separated: *X. strumarium* L. var. *glabratum* (DC.) CRONQUIST and *X. strumarium* L. var. *canadense* (MILL.) T. et G. On the thorns of the fruit are no pronounced hairs, on the latter one's there are. The taxa of LÖVE and DANSEREAU, and of CRONQUIST lap over a lot: the difference derives from that '*chinense*' complex belongs to the taxon of CRONQUIST, var. *glabratum*.

Three complexes of *Xanthium strumarium* group occur in Italy, '*italicum*', '*strumarium*' and '*orientale*', namely successively one American, one Eurasian autochthonous and one presumably of hybrid origin. Within the complexes – contrary to the significant genetic differentiation of the complexes – the genetic variability of the examined locuses is quite low. This genetic structure affirms the dominant autogamy. The crossing-over rate valued on some sampling places is rated to be between 8 and 17%. Of the three complexes each is polyploid ($2n$), the different alleles of some chromosomes cannot recombine because of the prevalence of self-pollination. In case the alleles are different, one kind of steady-state heterozygosity evolves, the rate of that was successively 25, 25 and 16% in the cases of the '*italicum*', the '*strumarium*' and the '*orientale*' complexes. The examinations implies that the polyploidisation preceded the formation of the complexes, namely the three studied complexes had one common ancestor, in what in the course of geographical adaptation various alternative alleles remained on some locuses, and the self-pollination have stabilized these. Not by the way the fixated heterozygosity of the duplicated locuses sustained such kind of genetic diversity that ensured the appropriate adaptability of complexes to the different habitats, besides this it moderated the maleficent effects of inbreeding. Synthetizing the so far results, it can be stated that the large scale heterogeneity of the *X. strumarium* group arises from the polyploidy ($2n=36$, $x=9$), the formation of the introgressive hybrid forms, moreover from the dominant self-pollination, that stabilizes in some extent the restrictedly stabilized hybrids of different allele prevalence, namely the frequent self-pollination associates with rarely forthcoming alien pollination. The geographical separation arising from the different climatic demands of some taxa also conduces to the subsistence of discontinuity between the forms. As none of the isolation mechanism is much strong – especially not in between the forms deriving from America and the Old World autochthonous ones – diversified hybrid complexes can form, those can subsist for shorter or longer time periods, namely they can show up in taxonomical documentations. It is quite probable that all complexes of the *X. strumarium* group can be traced back to one common diploid ancestor, the native country of which similarly to the *Xanthium* genus is in America, probably Central America. The extant genetic differences in between the populations of the given complexes intensify further more the large scale morphological diversity, moreover because of the fixated heterozygosity even similar environmental effects can form diverse morphological series, namely even on the level of the complexes' populations the environment-dependent phenotypic plasticity is high. At the same time the complexes of some areas can be separated from each other by the statistical analysis of data of their morphological series (trait analysis).

Because of their hard usability most of the scientific articles, field guides and even remarkable flora works disregard the usage of the official names. Thus usage of the somewhat updated version of the complex's names defined by LÖVE and DANSEREAU (1959) became a fairly established custom, supplemented with the interpretation of forms of probably a hybridogen origin, but at least appearing to be invariant in reason as species. The taxa of complex level of the *strumarium* group noticed from Hungary: *X. strumarium* L. (sensu stricto), *X. italicum* MOR., *X. ×saccharatum* WALLR. Probably the data of *X. brasilicum* reported from the surrounding of Vésztő by BORBÁS (1881) is mistaken. By the way the „species” noticed from Hungary can be put under two „better” species: 1) *X. strumarium* (morphotypus *strumarium* + *brasilicum*), 2) *X. italicum* (morphotypus *italicum* + *saccharatum*), intrinsically (de facto) in the last fifty years the Hungarian literature – excluding some work specifically of taxonomical purpose – manages the members of the *X. strumarium* group in this sense. Taxa noticed from Europe (giving the most often occurring interpretation, or the ones those seems to be the most established): *X. strumarium* L. (sensu stricto) (incl. *X. sibiricum*, *X. japonicum*, *X. indicum*, excl. all other); *X. italicum* MOR. (incl. *X. echinatum*, *X. pensylvanicum*, excl. *X. cavanillesii*, *X. californicum*, *X. intermedium*, *X. occidentale*, *X. ×saccharatum*); *X. cavanillesii* SCHOUW. (incl. *X. chinense*, *X. californicum*, *X. intermedium*, *X. occidentale*, *X. australe*, excl. *X. italicum*, *X. saccharatum*); *X. ×saccharatum* WALLR. (incl. *X. (×)oviforme*, *X. (×)campestre*, excl. *X. pensylvanicum*, *X. italicum*); *X. ×albinum* (WIDDER) SCHOLZ (incl. *X. ×riparium* – riparian cocklebur, *X. ×ripicola*, *X. ×brasilicum*, *X. ×antiquorum*, excl. *X. cavanillesii*); *X. ×orientale* L. (incl. *X. ×macrocarpum*, *X. ×canadense*, *X. speciosum*, excl. *X. californicum*, *X. pensylvanicum*). *X. albinum*, *X. italicum*, *X. orientale* and *X. saccharatum* can be summarized into the “big fruited cockleburs” species group (*X. orientale* agg.).

In practice *X. italicum* can be mistaken for any taxon belonging to *X. strumarium* (sensu lato) group. Usually it can be presumed that even *X. ×saccharatum* is written off as *X. italicum*, namely most of the studies of reviewer kind do not separate the two, for example they draw the two horns of the fruit in broad arch bending towards each other, that is rather a distinctiveness of *X. ×saccharatum*. Identification – principally – can only be made by mature fruit that is possibly of higher number, and on the individual it can be regarded as normal sized one, at the same time we can not exclude the possibility of the modifications caused by the habitat (see also „*X. arenarium* LASCH”), the variability between species and fruit-development abnormalities that is told to be common in the genus (cf. sparse thorns of *X. italicum* „var. *nigri* FIORI, *X. nigri* CES., *X. strumarium* var. *hausmanni* WIDDER.”). *X. italicum* of vegetative state of development can be mistaken with the also invasive *Iva xanthiifolia* NUTT. (iva) species, and its seedlings are similar to the ones of the jimsonweed (*Datura stramonium* L.), of course without their smell reminiscent of toad.

In Hungary out of the three above mentioned species, it is quite possible that *X. albinum* also occurs here, namely to North West from Hungary, alongside the rivers of Germany, Poland and the then Czechoslovakia, their strong propagation was already registered at the beginning of the 1960's, and its approaching hauling was presumed that time. The species itself is still quite common there at the present time, intrinsically it is so kind of invasive – but only since the years of 1830' – like *X. italicum* is in our country. There are phytosociological data of its occurrence (from 1961.) from Croatia (alongside the Sava) too. Until now the occurrence of this species or any nearly related taxon (see also above) were not reported from Hungary. Its possible reason can be the un-recognition, taxonomical insecurities, and the absence of the knowledge of traits suitable to differentiate the species. Already following this study was ready, but before it was given to press it became clear that the *Xanthium* specimens collected by LAJOS BALOGH in 9 October 2002 next to Ikervár (Vas county) – that was since confirmed by ISTVÁN BAGI – can be categorized with big certainty into *X. albinum* (WIDDER) H. SCHOLZ subsp. *riparium* (ČELAK.) WIDDER et WAGENITZ taxon. It is quite possible that *X. orientale* (= *californicum*) – Californian burr occurs in Hungary too, that was identified already at the beginning of the 1960's alongside the rivers of the areas belonging to Ukraine of Transcarpathia. The Ukrainian occurrences of *Xanthium* are quite interesting: the flora of the Soviet Union enumerates six species (1959): *X. spinosum*, *X. strumarium*, *X. californicum*, *X. sibiricum*, *X. occidentale*, *X. riparium*. The flora of Ukraine besides the previous first three

flares with *X. occidentale* (1962), and in 1964 it was completed with seven additional taxa: *X. italicum*, *X. brasiliicum* (!), *X. pensylvanicum*, *X. cavanillesii*, *X. speciosum* KEARNEY, *X. riparium*, and *X. strumarium* var. *hausmanni* WIDDER.

“*Xanthium strumarium* [...] may require a flexible taxonomy”. McMILLAN (1974b)

Is it necessary to differentiate the complexes of *X. strumarium* group occurring in Hungary? The distinction of the native ‘*strumarium*’ is desirable by all. This is already done in the SIMON (2000) field guide. The identification of the adventive complexes can cause difficulties because of the reasons detailed above. At the same time *Xanthiums* of one, not much extensive geographical region – in the opinion of LÖVE and DANSEREAU – can still be sorted quite well. For this in the area we need to choose those kind of distinctivenesses for the even that time topically existing genetic type on the grounds of what the separation is quite secure. In our opinion the *Xanthiums* known from the Carpathian Basin and the further possible occurring ones – build upon adequate quantity and quality – can be assigned to one-one already described complexes even by the distinctiveness of the fruit: these are *strumarium*, *italicum*, *saccharatum*, as well as *albinum* (differentiating *riparium*), and additionally *orientale*.

In the taxonomy of the *X. strumarium* group the breakthrough can be expected from the usage of molecular methods. The examinations so far on the area of the United States have sorted the examined individuals by geographical latitude, separating a Northern and a Southern genetic types, among those there are transitory types too. A valid cross checks with the traditional complexes – if it is possible at all – still needs to be done.

MORPHOLOGY

X. italicum is a large (30–150 cm high) annual plant that develops many lateral shoots if standing free. In dense homomorphic stands it runs up, has only few small lateral shoots, whilst under unfavorable circumstances (on drier habitat, on soil of low nutrient content or on a fast desiccating one) it remains small, some ten centimeters high. In all three cases it is capable of maturing fruits that contributes to its permanent subsistence on some areas. Contrary to the intrinsically scentless *X. strumarium* and *X. albinum*, it has strong, characteristic odor. It is a herbaceous annual plant that does not propagate itself in vegetative way. Its root is strong that fathoms around 20–30 cm deep into the soil. Its stem is upstanding, erect, with upon impressed hairs. It is coarse because of the granules on it. Its stem and petiole is yellowish green, with sparsely longitudinal reddish brown streaks (with flecks). In a typical case it has no anthocyan patches or stripes. The leaves are simple, alternate, spiral, petioles are 3–10 cm long, their blade is ovoid or three-squared, or maybe reniform, poorly three-five lobed (especially the upper ones), 3–15 cm long and their width is less than their length. The leaves are rough to the feel, finely punctuated, dully serrate. The base of the leaf blade is cordate or cuneate. The leaves of *X. albinum* are usually cuneate. Their abaxial surface is green and the leaves have no stipule-spines. Even within some complexes of *X. strumarium* group a large phenotypic plasticity is typical, main elements of what is primarily determined by the environmental factors, less by the geographical vicinity.

The plants are monoecious, the inflorescences are unisexual, two shaped, the flowers are small and all of them are tubular ones. The self-pollination is common. In its natural populations the rate of the alien pollination is presumptive to be only between 0 and 12 (17–21)%.

The male flowers stand in apical flowerhead, the head of the staminate flowers are multiple flowered, spherical, approximately 5 mm wide, their stamens are cohering. The short spikes of the heads of staminate flowers are angularly bent, upstanding. The pollen production is quite low, it is one of the reasons of the common self-pollination, and because of this the cocklebur is considered to be a less dangerous allergen. The pollens in their appearance are similar to the ones of ragweed: spherical shape, 24.5–26.0 µm of diameter, tricolporates, or rarely tetracolporates. The colpi (grooves) are 2.5–3.5 µm long, the pores are 2.0 µm of diameter. The exine of the pollen wall is tectate, approximately 1.5 µm thick. The surface sculpturation is microechinate (with tiny spinules), the length of spinules is less than 0.6 µm, and they are about 2 µm far from each other. The pollens of *X. spinosum* are smaller (19.0–25.0 µm), the spinules are longer (<1 µm) and stand more sparsely (3 µm).

The female flowers are near the base of the leaves. The heads of the pistillated flowers are two flowered. The pistillated flower has no corolla and is of wind-pollinating. The two-locular pistillated head is surrounded by alternated head-squamules covered by crooked thorns, only the flower's stigmata emerge through the gap in between the two apical horns. The envelop of the fruit-complex differentiates from the inflorescence axis, intrinsically it is an alternated flower-head, the thorns on it are of head-squamules, namely of bract origin. In the course of fruit-complex ripening the flower-head and the thorns on it harden, closing in the developing achenes. The double achened fruits developed in this way are bright green at the beginning and yellowish brown, reddish, never have anthocyanins, thorns are crooked and shaggy haired at their base. The fruit weight of the so called European type of *X. italicum* is 310–320 mg, the length of the fruit is 22–26 mm and the width 6–8 mm, the length of the apical horns is 5 mm and of the body thorns is 4 mm. The distance between the two apical horns is 4 mm. The apical horns emerge, are hard, almost parallel to each other, their basal parts are hairy and on them excretum granules and petiolate glands can be found. On their top they have robust, scraggy hook. The two beaks of the apical horns are more or less splayed, erect and yellowish green. The dispersion of the body thorns is relatively loose, less compact. The 120–140 body thorns are in spiral arrangement. The fruit body is bare, hairless, excretum crystals can be found on it. The fruit weight of the Canadian type is less, the length size of the fruit is slightly bigger than it is at European type. (The fruits of *Xanthium strumarium* are smaller, around 15 mm long, greenish brown, their horns are 2–4 mm long and are not shaggy at their base, however the ones of *X. saccharatum* are bigger 24–28 mm long, 6–8 mm wide, lips are synclinal in bow and are of reddish color.) At each of *Xanthium strumarium* complexes occur varieties with sparsely thorned fruit. The two locules of one fruit-complex close in themselves one-one, relatively large achene, a smaller upper one and a bigger lower one. The oil content of the embryo that is located in seeds approximates the 40%.

The seedlings are about 3 cm in high, their shoot width is 2 mm. The parts under the cotyledon of the seedling are long and thick, commonly of reddish coloration. The cotyledons are big, fleshy, and lancoelated, flat at apex, at the bottom narrowing into petiole jointed with the base, and photosynthesize. On the cotyledon next to the main vein, the two, not branching longitudinal lateral veins are well visible too. The first true leaves are opposite, they have short petioles, narrowing, ovoid shaped, apexes are flat or tapering, the base of the lamina is rounded and the leaf margin is unequally finely serrate or undulatory. On the leaves, chiefly on the edges tiny hairs can be found. The subsequent leaves are alternate, more heavily serrate and are more hairy on the abaxial surface.

Rough cocklebur just like the other species of the genus is polyploid, number of chromosomes is $2n = 36$, basic number of chromosomes is $x = 9$.

ORIGIN, DISTRIBUTION

The *X. strumarium* group is prevalent on the whole World, from the Northern latitude of 60° (Scandinavia) till the Southern latitude of 33°, but it is most common in the temperate zones. It weeds severely in Australia, India, South-Africa and in the lands of the American continent. The original, native country of the complexes of this group is controversial are now, MUNZ and KECK presume the American origin of each complexes of the group, whilst LÖVE and DANSEREAU – accordingly to the write-offs of the taxonomical chapter – divide the today existing complexes into American originated ones and Old World autochthonous ones. From a phylogenetic point of view, taking into consideration the present frequency distribution of the taxa it is quite obvious that the *Xanthium* genus itself evolved in America (in all probability in Central America) and very likely the same is true for the *X. strumarium* group too. The question is whether or not the complex 'strumarium' of *X. strumarium* evolved in America and then spread out into Eurasia too (namely cosmopolitan with American origin), or it isolated from the other complexes of the group in Eurasia and only later spread out into North America (namely cosmopolitan with Eurasian origin), or it evolved in America and it got into Eurasia only following the discovery of America (namely alien in Europe), or perchance it just got into America from Europe by human transmission (namely alien in America)? According to our present knowledge the most probable place of origin of the 'strumarium' complex is the area of the Mediterranean Sea.

However the native country of the '*italicum*' complex is beyond all questions North America. Present time it is a common weed of South and Central Europe. In Australia it propagated alongside the Hunter River (the "hunter (cockle)bur" name derives from this). It appeared alongside the bigger rivers of Ukraine, in West Europe it is sparse (Alsace), further north from Hungary it is scarce (Slovakia) or missing (Czech Republic, Poland). In Europe it has Mediterranean – Continental chorological feature that occurs mostly on the southern-like parts of *X. strumarium* (sensu lato) species group's permeation area. In the study of BORBÁS published in 1893 the occurrence of *X. italicum* is mentioned so: „on seashores: it occupied even the weedy areas of Fiume and Buccari”. The phrasing indicates that the species is not a long-ago settled on these places. The following thought of him supports above observations that by alluding to ASCHERSON presumes the American origin of *X. italicum* (and *X. macrocarpum*). The most probable period of its appearance in Europe is the early years of the 19th century, but there are no obvious data about its occurrence previous to its documentation in 1822 by MORETTI. It detected at the Sub-Danube in 1908. Its first occurrence was noticed from the area of the historical Hungary, from Óbecse. On the Tisza-segment between the rivers Maros and the Körös this species started to spread along the waterfronts in the 1920's, moreover it detected in some of the dryer ruderal associations too. In 1922 ISTVÁN GYÖRFFY founded it in the flood-plain of Tisza River, on the Boszorkány Island (near Szeged) and at the Maros tributary. This year is considered to be its first data regarding the present area of Hungary. GYÖRFFY was who has found *X. italicum* near Apátfalva in 1923. During the 2nd World War, and the time after he tells about its intense dispersion on the inshore areas of the Tisza River and chiefly tributary Körös. In the contemporary phytosociological records it shows up already in large rate. Around the end of the 1950's and particularly in the 1960's a very heavy propagation of *X. italicum* was observed not only alongside the Tisza and all of its tributary streams, but alongside the Drava and the Danube too. The species spread over from the foreshores onto the flood-plains, then onto the arable fields, primarily onto row crops cultures and other agricultural areas. The most infected counties in Hungary are: Hajdú-Bihar, Békés, Jász-Nagykun-Szolnok, Csongrád. Around 30% of the infected areas altogether are in these four counties. In the Transdanubia Region a larger infection can be found in Tolna County. In Hungary *X. italicum* causes damages on larger and larger areas of the arable fields, as by now, it only slightly sensitive to the herbicides used for row crops. In Hungary it piled up from the floodplain territories of the rivers of alluvial soil. By the increased usage of chemical fertilizers, together with the decrease in the usage of atrazin-type herbicides, it spreads exceptionally fast lately.

The first inland mention of the hybrids formed by *X. italicum* together with *X. strumarium* is dated from 1924 (GYÖRFFY), who identified the hybrid as *X. ×wideri* SENNEN that was so far only know from Italy and Spain. In the course of latter spreading of *X. italicum* this hybrid was found several times too.

Presumably *X. ×saccharatum* originated from hybridizing ancestors of different allele frequency, that as a steady-state hybridogen complex shows a spreading pattern roughly similar to an autonomous self pollinating species: it appeared in Venice (1902–1907), Rotterdam (1912), Duisburg (1922), at several areas of the Balkan since 1891 and it is known from Austria since 1948. In Hungary it has been spreading alongside the larger rivers from the 1960's, its write-off took place in 1971. Presumably it is more widespread than we would guess from the available floristic data, moreover probably several data of *X. italicum* refer in fact to *X. ×saccharatum*, or possibly to the hybrids of these two.

The presumably hidden in Hungary *X. albinum*'s first write-off derives from the surrounding of Elba River from 1849, probably it settled down in the 1830's. According to some presumption it is originated from *X. ×saccharatum*, but this is quite doubtful. It is more likely that its development is originated in the hybridization of some element of the '*strumarium*' and the '*cavanillesii*' complexes. *X. albinum* had spread fast alongside the rivers of the German-Polish Plain. Meantime it separated into two „subspecies”: Besides the subsp. *albinum* showed up the subsp. *riparium* too, that spread more eastern, alongside the Odera river. Both of the subspecies in the course of their spreading towards south have reached the area of the Carpathian and the Alps. Their further spreading besides the geographical barriers was slow down or stopped by the meantime appearing *X. italicum* (and *X. ×saccharatum*). (As it was already mentioned in the taxonomical chapter the occurrence of *X. albinum* subsp. *riparium* in Hungary was confirmed meanwhile from the collection of LAJOS BALOGH in Ikervár in 2002.)

X. californicum – here used as a synonym of *X. orientale* – described from the Transcarpathia presumably spread out alongside the Don and the Dneper rivers from the Mediterranean harbors, where it is common even at the present time. If it gets into Hungary in this way then its appearance or its finding is more probable alongside the Upper-Tisza. But there is an other possibility of its accession, because of the warming up of the climate the permeation area of the 'orientale' complex that is common further south from us at the present time and is of big fruit, mostly similar to *X. saccharatum* can dislocate more towards north, so it can cross the border from south too. The former area of the complex was Atlanto – Mediterranean (North Spain, France, South West Germany, Alsace), but it becomes of continental character more and more. It may show up in Hungary too.

LIFE CYCLE

Xanthium italicum is a spring germinating post-summer annual. Its germination starts only in spring, about from May, following the warmth of soil, on same, or on 1–2 °C lower temperature than the maize, during germination the fruit-envelope often rises above the soil surface too. In field seemingly it germinates with higher vitality, than under laboratory conditions, as it happens more often there that out of the double achene-fruit both of the achene develops. The reason of this phenomenon can be that on fields the degradation and/or the wash-out of germination inhibitors is of larger scale, but it can even be influenced by more heavy thermal effect that can be on fields sometimes. The rough cocklebur, under floodplain conditions, germinates en masse and at the same time, there is no lagged behind germinating specimens. It sprouts not only from the upper 4–8 cm stratum of soil, but from much deeper (10–20 cm) too, the germination from deeper than 15 cm or on the arable field from the surface happens only scarcely, on fresh floodplain it germinates well from the surface too. The bigger the fruit it, the better the achene inside germinates. When the achenes reach a well-specified size, they germinate with a ratio of about 100%. Even according to literature data more than 80% of the fruits are capable of germination. Indeed the germination ratio of seeds is worse than this, because there can be found two achenes, or rather seeds in the enveloped fruit-complexes, out of those the upper, namely the one that is closer to the beaked end of the fruit-complex (already smaller in virtue of its size) is of reduced germination capacity. Positive correlation can be detected also between the average fruit-weight and the average seedling-weight. The upper achene has a spare role in the double achene-fruit. The spare upper achenes make possible the shooting of new seedlings, in case for any reasons, for example because of a flood the first spouted seedlings would perish. Other literature sources imply, that in the first year the lower then in the next one the upper achene germinates (we can believe this to happen rather on habitats outside of flood-plains). The different water-soluble germination inhibitors (mostly ABA – Abscisic acid) ensure the dormancy of the seeds those dissolve in presence of oxygen. (According to some presumptions the toxic compound of seeds the carboxiatractylosid-glycosid is also of germination inhibitor nature, and its function would be to inhibit the germination of the other achene in the fruit-envelop.) Many different factors play role in the solution of dormancy of seeds, in case of the two seeds neither of them have the same effect. The primer dormancy peters out already on 22°C in case of the lower seed, while only on 33°C in case of the upper one. Long lasting warm generates induced dormancy. In the retention of the germination inhibitor materials the fruit-envelop plays a part, at the same time – not proved perfectly – it is ascribed to have ponderousness in the inhibition of the oxygen's diffusion, and by this in the delay of the biochemical processes (increased respiration, ATP-, and ethylene production) those take a part in the relaxation of dormancy. The diffusion of oxygen takes place more easily in case of the lower achene, for this those germinate at first. It emphasizes the role of oxygen, that the longer water overlay induces secondary dormancy. The light has different effect on the germination of the upper and the lower seeds: of the primer dormant seeds the lower ones germinate unconditionally, but the upper ones only if light effect is present, namely they are positive photoblastic. Following the loss of primer dormancy the difference between the seeds breaks off. More rarely both of the achenes germinate almost at the same time, the proportion of this kind of fruits is extremely inconstant, according to our observations this phenomenon is more common on field, than under con-

ditioned circumstances, but its proportion is not higher than 10–15%. The seedlings developing from the double germinated achenes are broadly of same size, and usually smaller. In denser stands they are excluded due to the self-thinning processes. Presumably this selection mechanism ensures the evolutionary advantages of the single germinations. The period for how long the seeds can retain the capacity of germination depends in large from the environmental factors, thus the literature data scatters in between wide borders (1–16 year).

All characteristics of development of *X. strumarium* (sensu lato) known practically till the smallest details, till the level of cell differentiation of the organs, from this point of view it is a real model and reference plant. The cotyledons are large and thick. They can provide an adequate quantity of nutrition to the seedling in the initial period of development by their photosynthesis. The life-span of cotyledons is around 3 weeks that means a quite significant proportion of the plant's complete lifetime. By the ablation of shoot part above the cotyledons the ageing process of the cotyledons slows down. At the base of the developing leaves initial lateral shoots show up. It brings larger lateral shoots only when it is solitary (this time the plants are large, mature and brings plenty of fruit), in dense stands the plant runs up, its lateral shoots are small-sized or they are missing, and accordingly they bring less fruit. Under conditioned circumstances the number of fruits shows strong positive correlation with the weight of the parent plant's vegetative parts, furthermore there is a statistically proved negative correlation between the number and the size of the fruits. In dense monodominant stands self-thinning can be observed. The process provides a kind of intraspecific competition, those individuals endure that are in advantage in their development, at the same time – as the fruit size is a less inheritable trait within one-one complex – the individuals of larger fruits can not work up an independent evolutionary line commences towards larger fruit size. The cockleburs are of C_3 photosynthetic pathway, the functioning of their stomata is regulated rather by the light conditions than by the carbon dioxide concentration of the intracellular space. Positive correlation can be detected between the total surface of the photosynthetic membranes and the latitude.

It blossoms from the middle of July till September. It is a short-day grown plant. Hundreds of articles get down with the conditions and possibilities of manipulation of the blossoming induction. The number of staminate inflorescences per plant can exceed even the one thousand (it can be even 1500), there are 100–150 staminate flowers in every inflorescence. The staminate flowers show up earlier than the pistillate ones, the inchoation of pollen dispersion also precedes by few days the turning to fertile of pistillate flowers. The pollens get onto the stigmata of pistillate flower, those are immediately beneath the staminate flowers, by the impact of wind or rain, accordingly self-pollination takes place, alien pollination eventuates only in exceptionally strong wind, in case of traversed growth of two plant individuals' branches, which is rather a haphazard phenomenon within the *Xanthium* genus. Beside the self-pollination the apogamy would lead to a very small genetic diversity of some populations too, but the opinions of the different literatures are divided regarding the occurrence of the apogamy. The fruits developing from the flower-heads and the two pistillate flowers closed into it grow large gradually through August, their color is green at the beginning, then its brighter and brown at the end; its maturation finishes by September-October. Their number can exceed the five thousands too on plants developing in free-standing, their quantity depends in large from the length of the vegetative growth season, namely from the period elapsed between the germination and the supervision of the short-day grown season that induces the blossoming, from the stand density and the environmental conditions. The quantity of the available nutrients has a significant effect on the number and proportion of the staminate and pistillate flowers per plant. For instance according to the results of an investigation: on a plant developing on poor soil for 455 staminate inflorescence got 1519 pistillate inflorescence, same data on rich soil are 750, respectively 2966, on soil of medium nutrient level 787, respectively 2365. Bluntly the number of the staminate inflorescence approximates the maximum already in the case of medium nutrient level (perchance it can exceed it too); the number of pistillate inflorescences monotonously increases by the amelioration of the nutrition supplement. This reveals itself in the number of mature fruits too, in some cases their number were successively 1601, 2389 and 3134, it is worthy of note that the average of the weight of fruits comes up with the ones on plants developing on well supplemented soil already in case of medium nutrition supplement, in some cases their numbers were successively 0,251, 0,273, 0,274 g.

As the germination capacity, but particularly the size of seedlings, by this its early competitive capacity depends in large from the fruit weight, the approximation of the genetically encoded potential greatest possible fruit size seems to be an essential strategy in favor of avoid to be selected out.

The fruits drop off the dried branches gradually during autumn and winter, some of them can remain on stalk even till next spring, ensuring better chance for spreading by epizoochory, perchance by anemochory. Most of the fruit flutter to the ground during winter, flood drives some of them, if there are floodplain circumstances. Other part of the fruit hang onto different plant parts found on the ground with their crooked thorns, are not adrift, remain there and next year they germinate there pushing an advantage on the adequate aptitudes of the production site. Consequently the fruit can propagate by epizoochory, antropochory and hydrochory, less often by anemochory. In the case of spreading by epizoochory way it is propagated mostly by bigger animals (boar, neat, and sheep). The propagation by antropochory would be significant at the building of roads and railways at an early stage of its propagation. The propagation by hydrochory has big importance chiefly on the flood-plain habitats. In spite of that according the literature the fruits of *X. strumarium* group can float on the water surface for even 30 days, in our observations the set afloat fruits (500 pieces) of *X. italicum* remained on the surface for only about six days, then nearly at the same time, one week later all of them submerged. Under natural circumstances the overflowing river can carry away too for the same time floating fruits afar off even so. On drier habitats the seeds retain their capacity of germination for a few years, but under moist flood-plain conditions there is no long lasting propagulum supply in the soil. Probably the humid circumstances decompose fast the fruits and the achenes inside. The plant has to rebuild its propagule supply regularly, on habitats of humid soil probably yearly. The cockleburs do not propagate in vegetative way.

In short, the successfulness of *X. italicum* (and usually of *X. strumarium* group) in the occupation of newer habitats in a great part dues to the following qualities: efficient fruit propagation strategy, wide ecological amplitude, large quantity of propagules with high germination capacity and able to germinate on multifarious habitats, high capacity of reproduction, fast seedling-development and well developed root system.

HABITAT PREFERENCE

Autoecology

Xanthium italicum is relatively warm demanding; it is connected with the appropriate climate of the zone of thermophilous woods and woody steppes. The warm of the Carpathian Basin's climate can contributes to its spreading as a tillage weed. It can tolerate the under 0 °C temperature only in fruit form. It is a light demanding plant, does not tolerate the shading. The members of the *X. strumarium* group are short-day plants those do not flower if the length of daylight exceeds the 14 hours. However it is a practical fact that some of the complexes, sometimes some individuals differ in this aspect, because some of them flowers even in case of 16 hours of lighting ('*strumarium*'). Usually the induction of flowering does not happen if the dark period is shorter than 9 hours. It is probable that even within some of the complexes there are different geographical biotypes regarding the short-day nature, those in Europe on the north are near to the neutrality by the photoperiod. According to Australian examinations the length of the critical dark period of the observed complexes are the following: '*occidentale = chinense*' – 10,5 hours, '*italicum*' – 10 hours, '*cavanillesii*' – 9,5 hours, '*pensylvanicum*' – 9,25–9,5 hours. On the continent the permeation areas of the complexes characteristically follow one another in the above-mentioned order from North towards South. The intermediate critical value of the sympatric areas denotes hybridization. In case of *X. italicum*, the area of which in Europe is on the southern part of *X. strumarium* group's permeation area, the short-day photoperiod is quite presumptive too. (According to data regarding Turkey and Israel the critical dark period demand of the '*italicum*' complex is 9,0–9,25 hours there.) Through summer the length of daylight exceed the 14 hours on the higher latitudes. Thus far that day comes when the length of lighting gets shorter than 14 hours, the flowering of the rough cocklebur is inhibited. On the latitude of Hungary the flowering accordingly is shifted toward the end of summer (more exact date can not be given as in unclouded weather the light of the full moon can provisionally

intermit the induction of flowering). The cotyledons do not play a part in the induction of flowering. The induction of flowering is not followed by significant alteration neither in the parameters related to the water balance, nor the ones related to the photosynthesis. Theoretically, by the intermission of the dark period (illuminating with light of red component) the flowering of the short day plants, by this their fruit production can be interfered. Namely in case of the short-day plants a phytochrome system „measures” the time spent in dark, only after a certain long time in the dark that is encoded in the plant runs out get released some kind of compounds of hormonal effect that eventually actuates the process of flowering. If the dark period discontinues, the time-keeper starts afresh the measuring of time. Nonetheless the start up of flowering can be induced by a one-three short-days event.

It occurs on wet, eutrophic and base-rich, humus molding-, alluvial- and aeolian soils, it is less sensitive about the mechanical consistence of the soil, it can be found on sand-base soil and on hard clay ones too. It prefers the eutrophic habitats, for example the flood-plains infested with new alluvia from year to year, or the (in general) manured arable fields. By its extended root system it has effective nutrition intake capacity. Its capacity to redistribute the essential nutriments into the fruits contributed unequivocally to its success as weed. By the end of fruit maturation 90–95% of nitrogen that was divided in the vegetative parts of the plant at the beginning of blossoming get lumped into the seeds. The distribution into the fruits from the aboveground parts of the plant is more than 50% in case of K, Mg, Mn, Cu, and Zn, in case of P it is between 40–50%, while at the Ca and Fe it is of a lower rate. In dense stands the larger plants siphon off the available nitrogen from the smaller ones in higher ratio than their weight is. The attenuate availability of nitrogen reduces the number of staminate and pistillate inflorescences per plant. The cocklebur is able to take up the nitrogen in form of nitrate and ammonium too. It is a plant of neutral soils. It is not salt evasive, although over here it occurs more rarely on much salty or on alkali soils. The measure of its growth reduces under salt stress, but then the higher CO₂-level increase its salt tolerance. The germinating seeds are able to siphon off the water from the salt moisture of high osmotic activity too.

Its appearance usually indicates more humid soil. It is particularly water-demanding at the time of germination. If the water content in the soil is lower than the 75% of the water capacity, it does not germinate or germinates only scantily. By its elder age it becomes distinctly drought tolerant (these conditions can come about on arable fields especially in dry years), at the same time it tolerates short and partial inundation too, but it tolerates less a longer-lasting awash: in shallow water it takes a stand against the water overlay for 6–9 weeks, whilst it can produce collateral roots from the awash parts of its stem.

Rough cocklebur has considerable phenotypic plasticity, in this regard that it can regulate its development in accordance with the environmental circumstances. It can be demonstrated that the allocation of biomass in between the different organs, the growth scale of seedlings, the extent of ramification, the physiological processes (respiration balance, water utilization efficiency), and the final dimension of the plant individuals depends a lot on the quantity of disposable resources. However the phenotypic features separately often does not show statistically significant coherence with the reproductive successfulness, albeit per se there is a positive correlation between the availability of resources and the reproductive success. Similarly regarding their growth features the populations of the ruderal and the semi-natural habitats do not differentiate in a statistically verifiable way.

Phytosociology

The species is common on disturbed or injured areas with opening vegetation. Its main habitats are the flood-plains and arable fields. In a closer vegetation, for example on pasture-lands often it can only be found in seedling form, its fruits are washed off by water (rain, flow, inland waters) from the neighboring agricultural areas. It is particularly common on maize fields, but it can be of high account in the sunflower too. It can not develop in between the adequate dense cereals. Often it shows up on meters and by the roadsides. *X. italicum* is a plant of ruderal weed-associations of flood-plains and marshlands. Its germination comes before the germination of almost all the other plants, in a dense monodominant state it can shade easily its competitors. On the slobby shore and watercourse margin of the Tisza and the Maros it associates with *Atriplex hastata*, where it forms a quite high stability community character-

ized by numerous constant species. *X. italicum* can supersede (recently it does supersede too) *X. strumarium* in most of flood-plain communities and alongside our bigger rivers it is mostly of undisturbed by other factors beyond the flow caused by the water level fluctuation. Also the mud plants of river basins are of frequent occurrence. In spite of that the river basin ruderal associations are also common in Hungary, this habitat was strongly confined because of the stabilization of water level by barrages on the areas of the western states of European Union, that's why it appears on the Annex I. list of the NATURA 2000. On the river basin habitats of surrounding countries *X. italicum* is of similar phytosociological character. In Italy (and generally in the Mediterranean) it is a species of the coastal sand dunes too. The European and the outside Europe habitats of the other complexes are delineated in detail by LÖVE and DANSEREAU (1959).

BIOTIC INTERACTIONS

Allelopathy

The cocklebur species – similarly to numerous examined Asteraceae species – have allelopathic effects. The allelopathic effect depends a lot on the age of plant, the weather (especially from the precipitation), the characteristics of soil, and last but not least from the plant that endures this effect. Under controlled circumstances for example it inhibits more the growth of root than the hypocotyl stalk of alfalfa, in case of the sugar-beet it chiefly inhibits the sprouting and of the garden cress the growth of the stalk. The essence of cockleburs is surpassingly strong inhibitor of sprouting and initial development of seedling of otherwise close relative *Parthenium hysterophorus* (false ragweed) that is a noxious weed of the subtropical – tropical areas. It can explicate allelopathic effect even in an indirect way, by inhibiting the nitrification bacteria (*Azotobacter*, *Nitrobacter*), just as against the pulses working upon the *Rhizobium* nitrogen-fixing bacteria too. Wide range of compounds of allelopathic effect can be detected from the *Xanthium* species, for example different kinds of coumarin acids, coumarins and cinnamomic acids.

Competition

In monodominant stands the cockleburs show typical self-thinning processes. According to the observations the death of stunted individuals is not caused primarily by the struggle for light, but the level of the available nitrogen being in relative pessimism. The larger individuals utilize higher proportion of the nitrogen available than the ratio of their weight is, besides this their nitrogen balance and by this their nitrogen expropriation capability is better, because they shed their leaves less than the smaller ones. Besides they feature longer average nitrogen restraint time, better nitrogen productivity and higher efficiency of nitrogen utilization. Even the nitrogen content of the falling down leaves of smaller individuals in big rate ends up in the larger ones. Those individuals that grow higher shade the smaller ones, those at the end perish. The above strategy is working against other species too, thus the cocklebur species regarding their strategy (social behavior) are ruderal competitors.

The other competition related question, why did or rather why does *X. italicum* crowd out *X. strumarium*? The fruit of *X. italicum* is larger than of *X. strumarium*, if they sprout about the same time, than *X. italicum* get in growth advantage. This time the individuals of smaller size according to the rule of self-thinning, perish. As the self-pollination is dominant, hybrids do not spring up, or only in trace, thus only *X. italicum* brings fruits. As a result of the above processes, the two taxa can coexist only for a very short period. This „swap” in Hungary is not unexampled, the same happened in Corsica too, on those parts of the island where *X. italicum* showed up, *X. strumarium* practically disappeared.

About the competition in between the cockleburs and the farm crops, about the circumstances those have effect on it, and about the role of the artificial interventions those modify the competition plenty of library literature is available. Usually in the higher crops, like for example in the maize, as a respond to the competitive effect of maize, independently from which complex the cockleburs belong to, increased growth of the stalk, decrease in number of offshoots and developing fruits occur. In shorter crops (sugar-beet, soya, pea) without maintenance the cockleburs display significantly different behavior than on ruderal habitats.

Parasites

In dense monodominant stands often *Cuscuta campestris* infection can be observed. The seeds of the western field dodder germinated in the first part of June and its shoots curled on the cocklebur individuals, those were four-leaved that time. Infected patches of about 2–3 m in diameter arose in cocklebur stands. In some habitats the dodder is able to inhibit the development and yield production of the cocklebur. Similarly to sunflower *Orobancha ramosa* can parasites on cockleburs too.

Pathogenes

The *Xanthium* genus is host plant of CMV (cucumber mosaic cucumovirus) and MYMV (mung bean yellow mosaic virus) wide host-range mosaic virus.

Of the fungi damaging the North American cocklebur stands 14 was already known at the beginning of the 80's, among of those *Puccinia xanthii*, a microcyclical rust fungi without intermediate host has the highest host specificity, that follows the geographical spreading of the cocklebur species. It occurs on the whole area of the United States, on the southern parts of Canada, on many parts of Europe, but it was also found in India. Besides the cockleburs, it damages the ragweed too. Its infection becomes multitudinous in August and September, it infects the aboveground parts of the plant except the flowers. It generates elliptical, humping lesions on the leaves, and protuberant, riving patches on the petioles and on the stem. The infected plants run down their periods of life cycle faster than the healthy ones, they are characterized by reduced respiration rate, dry weight, fruit production and lower germination ratio. The spores of the fungus over-winter on the withered plants. The first appearances of the rust fungi in Hungary was noticed in 2002 and then in the summer of 2003 from many different parts of Hajdú-Bihar County, the executed morphological examinations and pathogeneity tests verified unequivocally the taxonomical place of the fungus. Cocklebur damaging parasite fungus can get on them from the sunflowers too, like the *Alternaria helianthi* fungus, that causes leaf spots, winters on the dead plants, then at the beginning of the vegetation period its conidia get firstly on the lower leaves by wind or by slamming by means of water and then the newly formed conidia infect the upper ones too, a heavier infection can cause the devastation of the plant. The mildew of sunflower (*Plasmopara halstedii*) infects the rough cocklebur too. On the cocklebur such kind of *Plasmopara* pato-type evolved that is able to infect the so far resistant sunflower genotypes too. The cocklebur, as an alternative host plant gives way for the evolution of the *Plasmopara*, and by this way it renders more difficult the work of the sunflower-enobling. In South Baranya, in Hungary in 2003 *Phomopsis*-infection (Fungi imperfecti: Coelomycetes) was detected. The infected plants withered, loose their foliage, and then perished totally. The first symptoms appear on the leaves margin in form of dark brown necrosis, that progresses alongside the main veins, on the leaf blade towards the petiole, the disease gets into the stem too through the petiole, then reddish brown patches form, those surround the leaf base (*Phomopsis* – canker). The inflorescences become brown and then perish. The lesion of the plant vessels can cause the termination of the nutrient and water circulation and at the end the plant shrivels. It needs further examinations to find out whether the *Phomopsis* damaging the cocklebur and the sunflower is same species or not. Further cockleburs damaging fungi are the followings: *Septoria xanthii*, *Albugo tragopogonis*, *Botrytis cinerea*, *Cercospora xanthicola*, *Colletotrichum xanthii*, *Diaporthe arctii*, *Erysiphe cichoracearum*, *Mycosphaerella xanthicola*, *Phymatotrichum omnivorum*, *Plasmopara halstedii*, *Puccinia canaliculata*, *Rhabdospora xanthii*.

Herbivores

Several phytophagous insects damage on different organs of the cocklebur species. Only in California already at the beginning of the 80's consumers of species of *X. strumarium* group had some 60 known species representing five insect orders and 29 families. Only a smaller part (eight-nine) of their imago or larvae can be considered as nutrition specialists. It can be presumed that on the original area of the *X. strumarium* group – in the central parts of the United States – the number of species of these phytophagous groups is higher, more differentiated from nutrition point of view in contrary to California where some of the insects changed to cocklebur from ragweed following that the propagation of cocklebur reached this area too. Among pests the longhorn beetles have a particular place, and within them

species of *Mecas* and the *Nupserha* genera specialized on the cocklebur native to Pakistan and India (*Mecas saturnina*, *Nupserha vexator*, *N. antennata*), and *Apagomerella versicolor* native to Argentina. The larvae of these species develop in the shoots and masticate themselves till the root collar, where at the end only one of their imagoes develops. The parasitoids of the longhorn beetles are also known, till present time we know three on the *Apagomerella*. The caterpillars of the Pakistani *Oeobia verbas-calis* (Lepidoptera: Pyralidae) belonging to the pyralid moth family masticate the shoots of cockleburs. The American autochthonous *Epiblema strenuana* (Lepidoptera: Tortricidae) stem-galling moth lays its eggs on the leaf of cocklebur species, the larvae consumes for the first time in the leaf. Later the larvae migrate into the top of the shoot and consume the apical meristem till it reaches a size of about 1 cm. The developing caterpillar stimulates the increased growth of the plant, around it an about 1 cm broad and 2 cm long gall develops, on one plant there can even be 20-30 too. The galls encumber the circulation of substances of plant by the degradation of the vascular bundles that leads to the devastation of cocklebur. The moth damages only the species of the Ambrosiinae subtribe (*Xanthium*, *Ambrosia*, and *Parthenium*) within the Asteraceae, and aside from these the *Chenopodium* species too. Pre-dispersal predator of cocklebur seeds is the *Phaneta imbridana* (Lepidoptera, Tortricidae), furthermore the *Eua-resta aequalis* (Diptera, Tephritidae), which lay their eggs into the developing pistils. The *Oedopa capito* (Diptera, Otitidae) that is native to the temperate subtropical areas of North America damages the roots of the cocklebur species, but it is less host-specific; furthermore it can be presumed that its primary host plants were from the *Helianthus* genus.

The following eelworms are known from the cocklebur species: *Aphenchoides ritzema-bosi*, furthermore the *Meloidogyne* species.

Symbiosis

Adventitious roots of cockleburs floating in the water are often overrun by green algae (*Dedogonium*: Oedogoniales) species which can contribute to the aeration of plant by their oxygen production. Under experimental circumstances the species of *X. strumarium* group can be colonized easily with AM (arbuscular mycorrhizas) fungi, it implies that in the nature they also form mycorrhizal associations. In the inoculation experiments a mixture of *Glomus* species was used: *Glomus etunicatum*, *G. leptotrichum*, *G. mosseae*, namely out of them at least one colonised the *Xanthium* too. The *G. xanthium* arbuscular micorrhiza species was noticed from the maritime, primarily from the Mediterranean areas (from *X. spinosum*), the spores of which attach close to the roots, often can be found within the roots too, its color varies between light yellow and cream colour, it is of spherical or near spherical shape: (23–)50(–70) μm of diameter, the ovoids are 20–55 \times 45–100 μm of size. The spore wall is rigid, constituted of three well distinct strata. The fungus works up developed hypha grid both in the roots and in the soil. The analysis of ITS and the LSU, just as the nuclear rDNA sequences categorized the *G. xanthium* into the 'Glomus Group A' molecular clade. *G. xanthium* does not appear to be host specific, with it for example the maize can be colonized too, its occurrence on fields was not noticed up to now (December 2004). The experiments regarding the mycorrhization, even the ones performed by us, implies that the *Xanthium* species – even though we consider them to be weed-like – can develop mycorrhiza quite easily with multifarious less specific *Glomus* fungi. Under conditioned circumstances there are no significant differences in the state of development between the mycorrhized and the not mycorrhized plants, under natural, competitive circumstances probably the advantages of the mycorrhization predominate more.

ECONOMIC IMPORTANCE

Nowadays the agricultural importance of *X. italicum* increased, it gradually crowds out *X. strumarium* at several places. In Hungary it causes the biggest damages – merely due to the is large area – in the maize, but its a noxious weed of the sunflower, sugar-beet, potato and of other row crop cultures cultivated on more heavy soils too. In the specific succession of the after war maize's weed flora, induced by chemicals the cocklebur represents the third big wave. This period developed in the 1980-90's with the increased sweep of the annual dicotyledonous (T_4) weeds those are less sensitive to the carbam-

ide type herbicides. These species piled up chiefly on the sunflower, soya and potato fields treated with carbamide type herbicides; as a consequence of it they are present in high quantity in the maize without atrazine weed-killers. In Hungary by the end of the 80's the rough cocklebur infection of the maize reached the 17–18% (165–175 thousands hectares). *X. italicum* and its relatives are important weed of the soya and cotton acreages of the warmer temperate zones. The protection against the weeding *Xanthium* species takes quite a huge money, the formation of resistant biotypes requires the application of more and more new herbicides and agrotechnical methods from the traditional (here: not bio, not GM) agricultural technologies. The proportion of *Xanthium* species increases gradually in the nationwide weed records. The researchers intrinsically estimate the *X. strumarium* group, within this the ratio of the 'italicum' complex is increasing: In course of the 1st record (1947–1953) it took up the 130th place, then successively in the 2nd (1969–1971) 113th place, the 3rd (1987–1988) 24th place, the 4th (1996–1997) 16th place. Between the 3rd and the 4th records the overlay ratio changed to 0.55% from 0.27%, thus intrinsically it duplicated. The data regarding the complexes of the *X. strumarium* group separately presumably are not much trustworthy, because of the identification and data appraisal problems, and the non-standard literature, furthermore the data can differ in some years of the monitoring period. Thus the ranks published by HORVÁTH *et al.* (1998) should be treated with caution. Here it is completed with the data (here given in brackets) of the Central Service for Plant and Soil Protection regarding one year of each surveying period. The ranks of *X. italicum*/*X. strumarium*/*X. spinosum*, respectively was in the 1st survey: -/126(107)/-(262), in the 2nd: 370(219)/98(116)/298(343), in the 3rd: 43(54)/24(29)/102(112), and in the 4th: 31(32)/16(20)/-(73). In the smaller parcels the *Xanthium* infection is usually higher. The fruits of the cocklebur can cause serious damages on the sheep raiser countryside by mingling into the wool it decreases the value of it.

The fruits and the seedlings of *X. italicum* are strongly toxic. By the further development of plant the quantity of the toxic compounds decreases precipitously. For grazers the seedlings still having their cotyledons are especially dangerous, as the fruits closed into the stringing envelop are not accessible for animals and the palatability of the elder plants decreases because of their bitter taste and coarse texture. However, the consumed fruits sometimes can damage physically the intestines. The symptoms of poisoning develop within 2–24 hours (lack of appetite, unconsciousness, vomiting, fast and weak pulse, weakened muscle movement, trepidancy expanding onto leg and back muscles, muscle paralysis) then the animals perish within three days. In parallel with the above mentioned symptoms the blood sugar level decreases, hypoglycemia develops because of the disconnection in the oxidative phosphorylation processes. (Under experimental circumstances the phenylbutazon decreases the toxicity of glycosides, because it can induce the synthesis of one detoxifying enzyme free from cytochrome P450.) The increased permeability of the blood vessels damages severely the gall bladder and the peritoneum, out of them liver necrosis occurs. Further symptoms of poisoning are the followings at different animal species. Pigs, poultries, sheep, horses, goats and presumably several wide animal are sensitive, but especially cattle, at the latter ones the symptoms of poisoning are combined with blindness and hypersensitivity to the external stimulus, just as death usually within 12 hours. The poisoning leads to death, in case the animal consumes seedlings equivalent of its 0,75% – 1% of bodyweight (0,3% of seeds would have same effect). There is a good chance of the consumption of this quantity, as the dormancy of seeds of *Xanthium* species ceases about the same time, thus there can be a high quantity of seedlings available simultaneously. To avoid the poisoning it is advised to feed fat and oily materials (lard, milk, and linseed-oil) with animals. The t poisoning is primarily caused by a sulphate-laden glycoside, the carboxy-atractyloside that accumulates in the seeds and the cotyledons, it does not loose its toxicity neither following the drying of plants. In case of flood-plain grazing farming at the designation of the pasture land the above mentioned danger can not be left out of consideration, the animals can not be taken to the areas dominated by the sprouting or young cocklebur, or their grazing needs to be limited onto these areas, thus especially in late spring and early summer these places needs to be forborne. It follows from the above that by grazing the rough cocklebur can not be controlled. The extracts of the cocklebur's crop and leaf usually poisoning less the insects, however the repellent (discouraging) effect can be significant in the case of some observed beetle species (*Leptinotarsa decemlineata* – Colorado potato beetle).

The *Xanthium* produce materials of allelopathic effect in significant quantity and of variegated compounds. Although the researches are of a very initial stage still, the usage of the developing en masse *Xanthium* biomass as a herbicide cannot be foreclosed. Mostly the protection against the *Parthenium hysterophorus* L. seems to be far-gone; the allergen, dermoirritant, invasive outside Central America plant that was qualified to be noxious weeds on relatively dry habitats, hence the cocklebur's materials of allelopathic effect do not get washed out in a short while neither under field circumstances.

The *Xanthium* species belong to the wind-pollinated Asteraceae, their pollens are of allergen quality. The scale of pollen production's quantity is middle, thus the cockleburs are not the most dangerous allergens, but at the same time the skin tests made for pollens prove its potential sensitivising quality. Although taxonomically it is close to the ragweed (*Ambrosia*), it shows only few cross-reaction with it, hence it needs to be treated separately from allergiological point of view. In the cause of pollen allergy a glycoprotein (Xan VIa) carbohydrate compound of 17 thousands dalton molecular weight takes part. The touch of the plant's leaf and stem can cause allergic reactions the agents of the common contact weed dermatitis are definitely the sesquiterpen lactons.

In the 80's the alcohol based essence of *Xanthium* species got into consideration as a possible medicine of phytotherapy against breast cancer. In the Indian folk therapeutics the leaves are used against herpes, they consider the powdery-mildew infected ones to be more effective than the healthy ones. The alcohol based essence of *X. strumarium*'s leaf appears to be of antitripanosomal activity (tested on *Trypanosoma evansi* sleeping sickness parasite) in a dose of 100–300 mg/kg, in vivo it elongates substantially the surviving period of the tested infected mice, used in higher concentration its toxic effect predominates. It is also effective against the jungle fever. Its antimicrobial effect – ascribed to the sesquiterpene-xanthanol – can be detected against the following organisms: *Proteus vulgaris*, *Staphylococcus aureus*, *Bacillus subtilis*, *Candida albicans*, *C. pseudotropicalis*. The scientific name of the genus derives from the Greek xanthos – means yellow – word, as the decoction of its fruits was used as yellow hair dye.

NATURE CONSERVATION SIGNIFICANCE

Though the cocklebur, that crowds some habitats, narrows the numerical conservation values of the concerned community, but it needs to be noticed that the alien cockleburs (except the spiny cocklebur) are much similar to the autochthonous 'strumarium' complex. As detailed comparative analyses are not available, we can only presume that the change of *X. strumarium* to *X. italicum* did not amount to the significant alteration of the physiognomy. By the similar behaviour of the two complexes it can be presumed too that under flood-plain conditions in Hungary the alien cockleburs do not endanger other natural substances, like *X. strumarium*. Although the species of *X. strumarium* are ruderal competitors, have no transformer feature.

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SUNFLOWER SPECIES

(*Helianthus* spp.)

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TAXONOMY

The two most familiar and economically most important representatives of the genus of sunflowers (*Helianthus*) are the common sunflower (*Helianthus annuus*) used for vegetable oil production and as a honey source, and the Jerusalem artichoke (*Helianthus tuberosus*) growing tubers rich in carbohydrates. A number of species and hybrids are grown as ornamentals. There are data about the escaping and even naturalization in the adventive range of several representatives of the genus, grown for various purposes. Problematic species for nature conservation are not the rare garden escapees (e.g. *Helianthus pauciflorus*, *Helianthus* × *laetiflorus*), but the spontaneous expansion of taxa belonging to the Jerusalem artichoke species group (*Helianthus tuberosus* agg.), whose identities have not been clearly settled even until now. This species group has become a significant invasive element in Europe in the second half of the 20th century, especially in floodplains. The genus *Helianthus* is native to America. It comprises 66 species. It belongs to the Heliantheae tribe in Asteroideae subfamily of the Asteraceae family. Species within the genus can be divided into three main groups: a) shrubby South-American species (17), b) rhizomatous and tuberous perennial North-American species (including the Jerusalem artichoke and several species that are grown as ornamental too), c) tap-root grassland perennials, and annual plants, mostly in the western parts of North America (the most familiar annual is *H. annuus*).

Based on phenetic, cladistic and biosystematic analyses, the 49 North-American species of the genus are categorized by SCHILLING & HEISER (1981) into four sections and seven series. These are as follows (only species occurring in Central Europe as cultivated, escaped or naturalized plants are mentioned):

Section I: **Helianthus** (syn.: *Annui* TORREY *et al.* 1842, sect. *Annui* HEISER *et al.* 1969). It contains 11 annual, diploid species, mostly native to the south-western part of North America, generally to Texas and Florida.

1. ***H. annuus*** L. 1753 (syn.: *H. indicus* L. 1767); common names: common sunflower, annual s., mirasol; chromosome number: $2n = 34$ (diploid); native to Mexico, southern parts of USA; intraspecific taxa: only the following is accepted by ITIS (2004) from the described subspecies: subsp. ***annuus***, with two varieties: a) var. *annuus* (syn.: *H. cultus* WENZL. 1911, *H. ruderalis* WENZL. 1911); common names: wild sunflower, weed s., ruderal s.; in Central Europe it occurs as run wild in segetal weed vegetation; b) var. *macrocarpus* (DC.) COCKERELL 1914 (syn.: *H. macrocarpus* DC. 1826, *H. annuus* var. *oleifer* THELL. 1919); known as a cultivated variety only, grown in Europe as a crop plant and as ornamental.

2. ***H. argophyllus*** TORREY *et* GRAY 1842 (syn.: *H. annuus* var. *argophyllus* ALEF. 1916); common name: silverleaf sunflower; chromosome number: $2n = 34$ (diploid); native to South-Texas; it is an ornamental in Central Europe, occasionally it can escape.

3. *H. debilis* NUTTAL 1841; common name: weak sunflower; chromosome number: $2n = 34$ (diploid); intraspecific taxa: from its five subspecies, data of wild occurrence in Hungary is available on the following only: subsp. *cucumerifolius* (TORR. et A. GRAY) HEISER 1956 (syn.: *H. cucumerifolius* TORR. et GRAY 1842, *H. debilis* var. *cucumerifolius* (TORR. et GRAY) A. GRAY 1884); common name: cucumberleaf sunflower; native to Southeast USA: from Southeast Texas to Maine; it is grown in Central Europe as an ornamental and for honey production.

4. *H. petiolaris* NUTTAL 1821; common names: plains-sunflower, petioled s., prairie s., lesser s.; chromosome number: $2n = 34$ (diploid); native to central and southern parts of the USA, southern part of Canada; in Central Europe it is a ruderal weed, in the area of the former Soviet Union it is a quarantine weed; intraspecific taxa: a) subsp. *petiolaris*, b) subsp. *fallax* HEISER 1958.

Section II: **Agrestes** SCHILLING et HEISER 1981. Only the annual diploid *H. agrestis* POLLARD 1900 belongs here, which is native to southeast USA (Georgia, Florida), with no data on its wild occurrence in Hungary.

Section III: **Ciliares** SCHILLING et HEISER 1981 (syn.: sect. **Ciliares** HEISER et al. 1969). It contains six perennial species, with tap-roots or long creeping roots. They are diploid, tetraploid or hexaploid. Series 1: **Ciliares**; series 2: **Pumili**. They are native to Western USA and Mexico. There are no Hungarian adventive data on species belonging to these taxa.

Section IV: **Divaricati** SCHILLING et HEISER 1981 (syn.: sect. **Divaricati** HEISER et al. 1969). It contains thirty-one perennial species with rhizomes, tubers or crown buds (except for the annual *H. porteri* (A. GRAY) HEISER 1979). They are diploid, tetraploid or hexaploid. They are native to the eastern and central areas of North America. The main centre of distribution is the Appalachians; secondary locations are Ozark and Florida.

Series 1: **Corona-solis** (TORREY et A. GRAY) SCHILLING et HEISER 1981 (corresponds to **Divaricati** HEISER et al. 1969 and **Gigantei** HEISER et al. 1969 series).

5. *H. decapetalus* L. 1753 (syn.: *H. trachelifolius* MILLER 1768, *H. tenuifolius* ELLIOTT 1824); common names: thinleaf or thin-leaved sunflower, ten-petal¹ s., forest s.; chromosome number: $2n = 34, 68$ (diploid, tetraploid);² native to Northeast USA, Southeast Canada; it is an ornamental in Central Europe, sometimes it can escape; intraspecific taxa: there are several horticultural varieties.

6. *H. giganteus* L. 1753 (syn.: *H. subtuberosus* BRITTON 1901); common names: giant sunflower, swamp-s., tall s.; chromosome number: $2n = 34$ (diploid); native to Northeast USA, Southeast Canada; it is an ornamental in Central Europe, sometimes it can escape.

7. *H. mollis* LAM. non WILLD. 1789 (syn.: *H. pubescens* VAHL. 1791, *H. canescens* MICHX. 1803); common names: ashy sunflower, hairy s.; chromosome number: $2n = 34$ (diploid); native to central-western and north-eastern coastal states of the USA; it is an ornamental in Central Europe, sometimes it can escape.

1 The currently used Hungarian common name of this species ("multifloral" or "manyflower" sunflower) probably originates from earlier times when the relationship between *H. decapetalus* and *H. ×multiflorus* (the latter actually having several flowers in an inflorescence) was not clarified. Its number of florets in one inflorescence does not really differ from that of other species belonging to the section *Divaricati*. Moreover, the invasive species widespread in Hungary is probably not this one. Even in the case of the latter, it is not the number of florets per inflorescence what is numerous, but the number of inflorescences. Consequently, the author suggests that the currently used Hungarian common name for *H. decapetalus* is rejected and replaced with the common name used in other languages (*ten-petal sunflower*).

2 The type with doubled chromosome number scarcely differs morphologically, and was obviously created by autopolyploidy (SMITH 1960).

8. *H. salicifolius* A. DIETR. in OTTO et DIETR. 1834 (syn.: *H. orgyalis* DC. 1836); common names: willowleaf or willow-leaved sunflower; chromosome number: $2n = 34$ (diploid); native to central parts of the USA: Eastern Kansas, Western Missouri, Northeast Oklahoma, Northeast Texas; it is an ornamental in Central Europe, sometimes it can escape.
9. *H. strumosus* L. 1753 (syn.: *H. macrophyllus* WILLD. 1816, *H. mollis* WILLD. non LAM., *H. decapetalus* DARL.); common names: paleleaf woodland sunflower, pale-leaved wood s., rough-leaved s., swollen s.; chromosome number: $2n = 68, 102$ (tetraploid, hexaploid); native to eastern side of the USA; it is an ornamental in Central Europe, sometimes it can escape; intraspecific taxa: a) var. *mollis* (WILLD. non LAM.) TORR. et GRAY 1842; b) var. *macrophyllus* (WILLD.) BRITT. 1894; c) var. *willdenowianus* THELL. 1913 (syn.: *H. macrophyllus* var. *sativus* GRAEBNER); common name is not known in English, but it has German names: Helianthi, Salsifis; known only as a cultivated plant; experiments of its cultivation for its tubers and as forage were done in Europe in the early 20th century; d) var. *tomentulosus* HOUSE 1924.
10. *H. tuberosus* L. 1753 (syn.: *H. tomentosus* MICHX. 1803; *H. tuberosus* var. *subcanescens* GRAY 1884, *H. subcanescens* (A. GRAY) E. E. WATSON 1929)³; Amerind names: hxiben, hxiquebi; English common names: Jerusalem artichoke, Jerusalem sunflower, girasole, topinambur, tuberous s.; chromosome number: $2n = 102$ (hexaploid); native to eastern and central parts of the USA, southeastern part of Canada; it is an old cultivated plant in America and later also in Europe which can run wild; intraspecific taxa: a) var. *typicus* COCKERELL 1919; b) var. *nebrascensis* CKLL. 1919; c) var. *alexandri* CKLL. 1919; d) var. *purpurellus* CKLL. 1919; e) var. *fusififormis* CKLL. 1919; f) var. *albus* CKLL. 1919; g) var. *purpureus* CKLL. 1919; h) var. *multituberculatus* CKLL. 1919.

Series 2: **Microcephali** (TORREY et A. GRAY) SCHILLING et HEISER 1981. No adventive taxa belonging.

Series 3: **Atrorubentes** (TORREY et A. GRAY) SCHILLING et HEISER 1981.

11. *H. atrorubens* L. 1753 (syn.: *H. sparsifolius* ELL. 1824); common names: dark-red sunflower, dark-eye s., Appalachian s., hairy wood s., purple-disk s.; chromosome number: $2n = 34$ (diploid); native to central-eastern parts of the USA; it is an ornamental in Central Europe, sometimes it can escape.
12. *H. pauciflorus* NUTTAL 1818; common name: stiff sunflower; chromosome number: $2n = 102$ (hexaploid).
- 12/a. subsp. *pauciflorus* (syn.: *H. pauciflorus* NUTT. var. *pauciflorus*, *H. laetiflorus* var. *rigidus* (CASS.) FERN. 1946, *H. rigidus* (CASS.) DESF. 1829, *H. scaberrimus* ELLIOT 1824 non BENTH., *Harpalium rigidum* CASS. 1826); common name: stiff sunflower; its native range is distributed from north of Eastern Texas through the central-western states to Manitoba, Canada; it is an ornamental in Central Europe, sometimes it can escape.
- 12/b. subsp. *subrhomboideus* (RYDB.) O. SPRING et E. SCHILLING 1990 (syn.: *H. pauciflorus* NUTT. var. *subrhomboideus* (RYDB.) CRONQ. 1991, *H. laetiflorus* var. *subrhomboideus* (RYDB.) FERN. 1946, *H. rigidus* (CASS.) DESF. subsp. *subrhomboideus* (RYDB.) HEISER 1969, *H. subrhomboideus* RYDB. 1900); common names: nearly 4-sided sunflower, rhombic-leaved s., few-leaved s.; its native range is distributed from north of West Texas through the central-western states to Alberta and Ontario, Canada; it is an ornamental in Central Europe, sometimes it can escape.

Series 4: **Angustifolii** (TORREY et A. GRAY) SCHILLING et HEISER 1981.

13. *H. angustifolius* L. 1753; common names: narrow-leaved sunflower, swamp s., swamp sneezeweed; chromosome number: $2n = 34$ (diploid); native to south-east USA: from Eastern Texas to Connecticut; it is an ornamental in Central Europe, sometimes it can escape.

³ Some authors treat it as a separate variety besides var. *tuberosus*. We hereby list varieties described in COCKERELL (1919).

Hybrids treated as species:

Intrasectional ones (Divaricati × Divaricati):

14. *H. ×doronicooides* LAM. 1789 (pro sp.) (= *H. giganteus* × *H. mollis*), (syn.: *H. pilosus* TAUSCH 1828, *H. ×doronicooides* JACKSON 1957); common name: oblong-leaved sunflower; chromosome number: $2n = 34$ (diploid); native to northeastern USA: from Michigan and Ohio to Missouri and Arkansas; according to some opinions, this may be the species that was experimentally grown in Europe in the early 20th century with the name *helianthi* or *salsifis*.

15. *H. ×laetiflorus* PERS. 1807 (pro sp.) (= *H. pauciflorus* subsp. *subrhomboideus* × *H. tuberosus*), (syn.: *H. serotinus* TAUSCH 1828, *H. ×laetiflorus* CLEVINGER et HESIER 1963); common names: cheerful sunflower, mountain s., showy s.; chromosome number: $2n = 102$ (hexaploid); native to northeastern quarter of the USA; it is a common ornamental in Central Europe, sometimes it can escape.

Intersectional one (*Helianthus* × Divaricati):

16. *H. ×multiflorus* L. 1753 (pro sp.) (= *H. annuus* × *H. decapetalus*), (syn.: *H. decapetalus* var. *multiflorus* hort., *H. ×multiflorus* HEISER et SMITH 1960); common names: manyflower sunflower, double s., thin-leaved s.; chromosome number: $2n = 51$ (triploid, ± infertile); it is an artificially created ornamental, with much more florets per inflorescence than in *H. decapetalus*, florets sometimes ± full.

MORPHOLOGY

Members of the genus *Helianthus* native to North America are mostly tall, herbaceous annuals (therophytes), or often perennials over-wintering in the soil near its surface (hemicyptophytes) or totally in the soil (geophytes).⁴ The stem is thick, hollow and slightly ligneous below. Leaves are simple; at least the lowermost ones are opposite. Ray florets are large and yellow. Phyllaries are nearly equal length or slightly overlapping, usually green. The flower head is flat or low-conical, chaffy, the involucre bracts embracing the achenes. Disk florets are hermaphrodite and fertile. Style branches are compressed, hispid on both sides (at least distally), and the styles are poorly developed. Achenes are thick, slightly flattened, glabrous or sometimes pubescent. Hybrids are quite frequent. The identification key for the upper mentioned sunflower species is provided below:

Identification of sunflower species occurring in Central Europe as cultivated, escaped or naturalized populations:

1. a. Annual plants. The receptacle is flat or nearly so. Disc corollas are generally purple colored or sometimes yellow 2
- b. Perennial plants. The receptacle is generally convex or low-conic. Disc corollas are purple, brown or yellow 5
2. a. Composite heads are big or very big, the receptacle being wider than 3 cm. Involucre bracts are broader than 4 mm. The plants are usually taller than 1.5 m 3
- b. Composite heads are medium sized; the receptacle is not wider than 2 cm. Involucre bracts are smaller. The plants are usually smaller than 1.5 m 4
3. a. Leaves, involucre and stem are stiff-haired

Helianthus annuus L. Common sunflower

b. Leaves, involucre and stem are covered with dense, silvery-white, wool-like hairs

H. argophyllus TORR. et GRAY Silverleaf sunflower

⁴ According to VERBURG *et al.* (1996), CRAWLEY (1997) and KONČEKOVÁ (1998), *H. tuberosus* is a pseudo-annual plant: i.e. the entire plant dies off after the vegetative season, only the tubers surviving in the soil as propagules, producing new, genetically identical plant individuals in the next growth season. They are clonal plants, without continuous temporal interclonal connections.

4. a. Leaves are generally entire, twice as long as wide or longer, glaucous
H. petiolaris NUTT. Prairie-sunflower
- b. Leaves are generally serrate, shorter than twice their width, not glaucous
H. debilis NUTT. Weak sunflower
5. a. Leaves are very narrow, narrower than 1/10 their length, rarely broader than 1 cm (except sometimes the lowest ones), the disk is generally red-purple 6
- b. Leaves are broader than 1/10 their length, lanceolate, ovate-lanceolate or ovate, at least few of them being broader than 1 cm 7
6. a. Stem glabrous, sometimes glaucous, rhizome elongated
H. salicifolius A. DIETR. Willow-leaved sunflower
- b. Stem ± hairy, rhizome scarcely developed
H. angustifolius L. Narrow-leaved sunflower
7. a. Involucral bracts are appressed, rounded or acute, but not narrowing acuminate, generally strikingly unequal in length 8
- b. Involucral bracts are loosely standing, narrowing to a sharply pointed tip, hardly differing in length at all 10
8. a. Disk florets are red or purplish-brown. Involucral bracts are overlapping, strikingly unequal in length 9
- b. Disk florets are yellow. Involucral bracts almost unnoticeably differ in their length. It is a plant with thickened rhizome
H. ×laetiflorus PERS. Cheerful sunflower
9. a. Leaves on the upper stem are very small, bract-like, the lower ones abruptly narrowing to a winged stalk. The rhizome is scarcely developed
H. atrorubens L. Dark-red sunflower
- b. Stem is evenly leaved; the upper leaves are just slightly smaller; lanceolate or rhomboid, gradually narrowing to a short stalk. It is a plant with slightly thickened rhizome
H. pauciflorus NUTT. Stiff sunflower
10. a. Leaves are lanceolate, 2–3 cm wide. Lateral veins are weak. All leaves apart from the lowest ones are alternately arranged
H. giganteus L. Giant sunflower
- b. Leaves are oval, ovate-lanceolate or ovate (usually broadest under their middle), with two strong lateral veins running along a curved line at the base or the lower third of the leaf, making the leaf appearing as “three-veined”. The lowest and middle leaves or all of them are opposite 11
11. a. Leaves are sessile. The plant is greyish-white, the stem and the involucral bracts are densely covered in whitish down
H. mollis LAM. Ashy sunflower
Note: Another sunflower with sessile leaves is *H. ×doronicoides* LAM. (*giganteus* × *mollis*), the oblong-leaved sunflower, but here the bracts are not downy.
- b. Leaves have stalks. The plant is green or glaucous; the bracts are not downy 12
12. a. Involucral bracts are blackish or dark green. The upper leaves are alternately arranged (it is only on undeveloped specimens that all the leaves are opposite). The stem is covered in tough hair (cultivated forms) or is sparsely hairy, nearly glabrous (wild forms). In autumn the rhizomes bear elongated, thin (wild forms) or roundish (cultivated forms) tubers
H. tuberosus L. s. l. Jerusalem artichoke
- b. Involucral bracts are green, yellowish on their lower part, with protruding veins. Generally, the stem leaves are all opposite. The stem is hairless or nearly hairless. The rhizome is only slightly thickened 13
13. a. Leaves are relatively narrow, usually at least three times as long as wide, the middle and upper ones are seldom broader than 4 cm. The leaf blade is thick, the upper side coarsely hairy, with strikingly lucid papillae at the base of the large trichomes; the underside is glaucous, whitish blue-green. Leaf margin is slightly serrate or entire. Involucral bracts are only slightly loose, only slightly or not at all exceeding the disk
H. strumosus L. Paleleaf woodland sunflower

- b. Leaves are broader, sometimes they can be three times longer than their width, often broader than 4 cm. Leaf blades are thin, hairless or only slightly rough, and leaf margin is definitely serrated, often roughly serrate. Involucral bracts are very loosely arranged, evidently exceeding the disk 14
14. a. The stem is nearly or completely hairless, with slight down present only on its upper section. The composite head has 8–12 radially arranged, 10–25mm long ray flowers; the diameter of the disk is about 7 mm. Achenes are produced *H. decapetalus* L. Ten-petal sunflower
- b. The stem is slightly covered in rough hair. The head has more ray flowers which are longer than 25 mm, the head filled to its half or entirely by them; the diameter of the disk is greater than 7 mm. The plant is almost or completely infertile, thus no achenes are produced
H. ×multiflorus L. Manyflower sunflower

In line with the primary objective of our book, only species important for the clarification of ecological weed taxa in Hungary are dealt below in detail. These species are tall, rhizomatous (and sometimes tuberous) perennials. Their leaves are large, taper-pointed, most often ovate-lanceolate or lanceolate.

5. *H. decapetalus* L. – Ten-petal sunflower

Rhizomes have dense ramification, they are thin, sometimes thickened at their tips, but no tubers are produced. The stem is 0.5–1.5(–2) m tall, hairless down from the inflorescences which are covered in short hair. Leaves are thin, pale on their underside, moderately scabrous or subglabrous, broadly lanceolate to ovate, 8–20 cm long and 3–8 cm broad, taper-pointed, with (usually sharply) serrate margin, their base ± abruptly narrowing to a 1.5–6 cm long stalk; the upper leaves are usually alternate; the disk is yellow, its diameter is 1–2 cm; involucral bracts are very loosely arranged, thin and green, conspicuously ciliate, occasionally hispidulous on the back, narrowing-pointed, at least some of them usually conspicuously exceeding the disk; the number of the 1.5–3.5 cm long ray florets is 8–15. Achenes are 3.5–5.0 mm long. — Plants with diploid and tetraploid chromosome numbers ($2n = 34, 68$) are reproductively isolated, and should be valid species, but they cannot be clearly distinguished by morphological characteristics. Generally, tetraploid plants are more robust, have broader leaves and somewhat larger disks. They can hybridize with several other species, for example with the diploid *H. annuus* or the tetraploid *H. strumosus*.

9. *H. strumosus* L. – Paleleaf woodland sunflower

Rhizomes are normally well developed, thin or thicker, may sometimes be tuberous. The stem is 1–2 m tall, hairless or has sparse, long hairs downwards from the inflorescences, often glaucous. The leaves are opposite or the uppermost alternate, relatively thick and firm, their upper side is stiff-haired and rough, the underside sometimes green with medium-short hairs but more often glaucous and almost hairless, mostly broadly lanceolate or ovate, 8–20 cm long and 2.5–10 cm broad (sometimes narrower), tapering to a long point, their margin is shallowly toothed or nearly entire, their base commonly narrowing to a 0.5–3 cm long stalk. The disk is yellow, its diameter is 1.2–2.5 cm; involucral bracts are almost equally long, lanceolate, somewhat loosely arranged, especially the long-acuminate tips, which commonly equal or slightly exceed the disk; the number of ray florets is 8–15, their length 1.5–4 cm. Chaffs are 3-toothed or nearly entire, and pubescent on tips and heels, the achenes are 4.5–5.5 mm long. — This is the most variable “species” among perennial sunflowers. It is due to its extreme polymorphism that American researchers (HEISER *et al.* 1969) regard it as the “wastebasket species” of the genus, the pool of several perennial forms found in the eastern part of North America which cannot be classified with any other species. One reason for its great variability is its aptness to hybridize with a number of other perennial species. Such species hybrids can be formed with *H. annuus*, the tetraploid form with *H. decapetalus*, and the hexaploid form with *H. tuberosus* or *H. pauciflorus*. These hybrids and their derivatives are then classified into the above defined *H. strumosus*.

10. *H. tuberosus* L. – Jerusalem artichoke

Rhizomes are slender, but are swollen or bear tubers at their terminal parts. The stem is thick, 1–3 m tall, ± covered with rough hairs. Leaves are numerous, positioned oppositely on the upper half or upper 2/3 of well developed specimens, rough on their upper side and bearing short hairs on their underside, broadly lanceolate or broadly ovate, being 10–25 cm long and 4–12 cm broad on better developed individuals, with serrate margin and with their base abruptly contracted or somewhat tapering to the 2–8 cm long winged stalk. It often has lot of composite heads standing in a corymbiform inflorescence, the disk is yellow with 1.5–2.5 cm in diameter; its involucre bracts are usually dark, especially near their base, narrowly lanceolate, tapering to a long point, the ones positioned above the middle are loosely arranged, erect or sometimes reflexed at maturity and often covered with rough hairs. The number of 2–4 cm long ray florets is 10–20. The chaffs have 3 teeth, and are pubescent at their tips. The achenes are hairless, 5–7 mm long, 2–3 mm wide and 1.5–2 mm thick. The var. *subcanescens* A. GRAY is a smaller (–1 m) plant with greyish down, chiefly with oppositely arranged leaves. — This species is extremely variable too, even if somewhat less than *H. strumosus*. However, it can be relatively easily distinguished from all other species except for *H. strumosus*. Generally, *H. tuberosus* is characterized with denser hair, rather alternate leaf arrangement, more strongly serrated leaf margin, broader and more decurrent leaves, a greater pubescence on the underside of the leaves, darker bracts, and longer ray florets than those of *H. strumosus*. The most important distinguishing feature of *H. tuberosus* is the presence of tubers, even if they are quite variable in color, size and shape. In addition to this species, the only one with definitely swollen rhizome tips and thus being somewhat tuberous is *H. strumosus*. Besides *H. annuus*⁵, *H. tuberosus* can easily hybridize with several other members of the Divaricati section, including for example the hexaploid *H. strumosus* and *H. pauciflorus*. Its hybrid with the latter is *H. ×laetiflorus*.

12. *H. pauciflorus* Nutt. – Stiff sunflower

Rhizomes are strong, often somewhat swollen terminally, but do not develop tubers. The stem can have coarse hair, can be rough or nearly hairless, more or less hairless in its upper section, the heads have long peduncle. Almost all of the leaves are alternately arranged (not more than 15 pairs under the inflorescence), being rough or covered in short hair on both sides, normally (2–)2.5–8 times longer than their width, having three veins most of the times, serrate or entire, tapering to a short stalk or stalk base, the middle leaves being sometimes much smaller at flowering time than the lowest ones. The disk is red-purple, with a diameter of 1.5–2.5(–3) cm; the involucre bracts are clearly overlapping, broad, firm and appressed, mostly ovate or broadly lanceolate, with a sharp or blunt tip, conspicuously ciliolate, otherwise generally hairless. The number of 1.5–3(–3.5) cm long ray florets is 10–21. Achenes are 5–6 mm long and are nearly hairless. — *H. pauciflorus* can be crossed with *H. annuus*, *H. strumosus* and also *H. tuberosus*. Its hybrid with the latter is *H. ×laetiflorus* which can be easily confused with *H. pauciflorus* and its subspecies.

12/a. subsp. *pauciflorus*

It is a robust, 1–2 m tall plant. It has 9–15 pairs of leaves below the inflorescence, their shape being oblong-lanceolate to lanceolate-ovate, the tip tapering to a long point, leaf length reaching 8–27 cm.

12/b. subsp. *subrhomboideus* (RYDB.) O. SPRING et E. SCHILLING – Rhombic-leaved sunflower

It is a smaller, 0.3–1.2 m tall plant. It has 5–10 pairs of leaves below the inflorescence, their shape being rhombic-ovate to lance-linear, the tip being pointed or blunt, leaf length reaching 5–12 cm.

15. *H. ×laetiflorus* PERS. (*H. pauciflorus* × *H. tuberosus*) – Cheerful sunflower

Its appearance is much like *H. pauciflorus* subsp. *pauciflorus*, but: rhizomes are more swollen at their terminal parts, although still without tubers; the disk is yellow; leaves are often larger and have longer stalk (up to 5 cm); involucre bracts are on an average a little narrower, generally being (2–)2.5–4 mm wide, less overlapping, more pointed, and sometimes with sparse, short hair on their back side. It differs from *H.*

5 The English common name for the hybrid between Jerusalem artichoke and the common sunflower is sunchoke.

pauciflorus mostly by its yellow disk florets and its sharp bracts; and from *H. tuberosus* by its shorter bracts and rougher leaves. — It is probably the hybrid of *H. pauciflorus* subsp. *subrhomboideus* and *H. tuberosus*. Earlier it was considered to have natural origin, now it is thought to have been created artificially.

In addition to the identification key and morphological descriptions appearing above which were compiled on the basis of various literature resources (mostly American ones), a table (see below) produced based on the author's own investigations provides an overview of the features important for the differentiation between Hungarian populations of wild and cultivated forms of Jerusalem artichoke,⁶ cheerful sunflower and stiff sunflower. (The latter two are the most commonly grown ornamental representatives of the genus in Hungary.)

TABLE 1 *A comparative table of perennial sunflowers escaping most often in Hungary*

Feature	wild Jerusalem artichoke (<i>H. tuberosus</i> sensu lato, incl. wild forms, <i>H. decapetalus</i> auct. eur. centr. non L.)	cultivated Jerusalem artichoke (<i>H. tuberosus</i> sensu stricto, incl. cultivated forms)	cheerful sunflower (<i>H. ×laetiflorus</i> = <i>H. pauciflorus</i> × <i>H. tuberosus</i>)	stiff sunflower (<i>H. pauciflorus</i>)
Total height	1.5–3.5 m	1.5–3.0 m	0.5–2.0 m	0.5–2.0 m
Stem surface	almost hairless, or bearing sparse, appressed, small hairs mostly higher up	stiff-haired	hairy	slightly hairy
Below-ground parts: rhizome length	15–20 cm	8–10 cm	5–10 cm	20–25 cm
Below-ground parts: modifications of rhizomes and their shape	rhizomes with terminal swellings, and often narrow (approx. 2–3 cm wide) fusiform, ± elongated tubers	rhizome lateral shoots with large, mostly rounded or thick, fusiform tubers	rhizomes with medium-thick terminal swellings	rhizomes with just slightly swollen terminal parts
Leaf arrangement	alternate; opposite further down	alternate; opposite or tripartitely whorled further down	opposite, only the uppermost ones are alternate	opposite, only the uppermost ones are alternate
Leaf surface	rough on upper side, and appressed, finely lanate-puberulent on underside (mostly on veins)	rough on upper side, and whitish shaggy puberulent or downy on underside	rough on both sides	rough on both sides
Shape of leaves on medial section of stem	ovate-lanceolate – ovate – triangular	ovate – triangular – cordate	broadly lanceolate – rhombic-ovate (greatest width below the middle of stem)	narrowly lanceolate – rhombic
Leaf nervation	ramifying from leaf base	ramifying from leaf base	ramifying from above leaf base	ramifying from leaf base
Leaf blade size	8–18 × 15–30 cm	7–16 × 15–25 cm	6–9 × 20–30 cm	3–5 × 13–20 cm
Leaf margin	rough serrate	serrate	serrate	slightly serrate or ± entire

⁶ For the sake of mentioning easier these names in the followings we use these short formulas: wild Jerusalem artichoke, and cultivated Jerusalem artichoke.

Length of peduncle	8–12 cm	5–15 cm	10–30 cm	12–25 cm
Number of heads	(5–) 40–100 (-150)	3–7	10–25	2–6
Head diameter	7–12 cm	4–8 cm	6–12 cm	6–8 cm
Overall color of disk florets	brownish-yellow	brownish-yellow	yellow	purplish-brown or ruddy
Number of ray florets	10–20	10–15	20–30	15–25
Involucral bracts arrangement	the outer ones loose and erect	the outer ones loose and erect	even the outer ones ± appressed	even the outer ones appressed
Involucral bracts shape	linear-lanceolate – lanceolate	linear-lanceolate – lanceolate	narrowly ovate – elongated-ovate	elliptic – elongated-ovate
Involucral bract length	± the same length	± the same length	slightly differing length	clearly differing length
Involucral bract color	blackish	blackish or dark green	mostly light green	mostly dark green
Flowering period	August–October	October–November (or not reaching the flowering stage)	September–November	August–September
Grown	rarely as ornamental	for food, rarely as ornamental	ornamental	ornamental
Degree of naturalization	naturalized, invasive	casual (occasionally escaping)	casual (occasionally escaping), naturalized	casual (occasionally escaping), naturalized
Most typical habitats	floodplain weed communities, rarely wet old-fields near water and ruderal areas	regions it was formerly grown in, old-fields, forage fields for game	thrown away from gardens, rather in xerophilous or sometimes mesophilous weed communities	thrown away from gardens, rather in xerophilous weed communities, sand grasslands
Chromosome number	2n = 102*	2n = 102	2n = 102	2n = 102

* Chromosome number of Hungarian populations studied so far.

There are different views in literature about adventive sunflowers (*Helianthus*) regarding the question which species have naturalized in Europe or have spread as weeds, partly (and first of all) in waterside plant communities⁷ and partly in drier habitat types.⁸ A reason these problems is the fact that the majority of herbarium specimens, identification manuals and flora monographs lack descriptions of distinguishing features of below-ground parts. Some authors claim, however, that these features are not decisive because for example morphological variations of the tubers can lead to the appearance of biotypes or ecotypes created by habitats characterized with different environmental conditions. Nevertheless, referring to the above descriptions and comparisons of various species, it can be stated that *H. tuberosus* and its close relatives (*H. decapetalus*, *H. strumosus*) are species that are difficult to differentiate between, and often appear to grade into each other.⁹

H. tuberosus is a highly variable species in its North American native distribution area. In Europe where it has been cultivated for long, several varieties are grown. These differ from each other in their flowering time, tuber shape and color, leaf shape and hairiness. Jerusalem artichoke that was first imported had purple-red tubers, but very soon forms with white tuber jacket also appeared. The shape of tubers is rounded, potato-shaped or fusiform; some races are apt to producing ramified tubers.

7 Most of the times *H. tuberosus* and *H. decapetalus*, rarely *H. strumosus* and *H. giganteus* are mentioned.

8 Most often *H. xlaetiflorus* and *H. pauciflorus* are reported.

At this point, we must mention the *Helianthus* species called “salsifis” or “helianthi” which was experimentally grown as a vegetable, for honey production and, most of all, as forage from the first decade of the 20th century, especially during World War I, in many places throughout Europe (France, Germany, Austria), including Hungary. The cultivation of this prospective industrial crop which first appeared to be promising but then failed to become successful was later discontinued. Reports about this plant date back to the middle of the 20th century. Because herbarium specimens are not available, the exact taxonomic identity of this plant is still unclear. Its most recent description known for us is published by I’só (1955).¹⁰ Most of its contemporary identifications describe it as *H. strumosus* L. var. *willdenowianus* Thell. (according to the majority of authors = *H. macrophyllus* Willd. var. *sativa* Graebner), but it was also believed to be *H. decapetalus* L. and *H. doronicoides* Lam. (= *H. giganteus* × *H. mollis*) too. However, according to WAGENITZ (1968) it is likely that the plant mentioned in 1907 in Paris with the names “salsifis” or “helianthi”, and grown in 1920 in Berlin as “Helianthi” is the wild form of *H. tuberosus*. WAGENITZ believed that older descriptions of “Helianthi” allow for this explanation.

After World War II a numerous reports were published throughout Central Europe about the mass spread of a species belonging to the *H. tuberosus* agg., especially along watercourses. This plant, which has naturalized since then in Hungary as well as in other European countries, is regarded by the majority of West-European authors and by some of Central-Europeans as one belonging to *H. tuberosus*, whereas other Eastern-European researchers consider it to belong to *H. decapetalus*. The most important basis for the opinion that invasive populations belong to *H. tuberosus* is in the Central-European flora monograph (Flora von Mitteleuropa) which wrote that the herbarium specimens sent to America by WAGENITZ (1968) for identification were classified by HEISER – the greatest expert overseas – as the wild form of *H. tuberosus*. However, this European plant shows such significant morphological differences from both the cultivated Jerusalem artichoke and the true North-American *H. decapetalus*, that caution is needed for accepting this as an unquestionable identification.

Typical chromosome number for the genus is $x = 17$. There are diploid ($2n = 34$) species, typically the shrubby South-American species and the North-American representatives of annual or tap-root perennial grassland plants. The most species-rich, polymorphic group is that of rhizomatous and tuberous North-American perennials, including diploid ($2n = 34$), tetraploid ($2n = 68$) and hexaploid ($2n = 102$) species. Certain species have races with different ploidy level, possibly caused by autopolyploidy (e.g. in the case of *H. decapetalus*). The increased aptness for hybridization has a role in creating the great diversity of species. Hybridization of annual species is easy with other annuals, less easy with perennials, and again very easy between perennial species of high degree of polyploidy, thus also creating natural hybrid groups. In the case of the latter, hybrids with reduced fertility can be resulted which can spread by vegetative reproduction. The aptness of species to hybridize is increased even in their American native distribution range by the fact that the barriers separating species and distribution areas of geographic races have disappeared almost completely due to human traffic and transportation.

9 The Hungarian monograph on Jerusalem artichoke (I’só 1955) wrote: “Actually, all races or landraces of Jerusalem artichoke are vegetative progeny of heterozygote parents and cover different race components. Thus, if any bred race or selected landrace is simply propagated in a generative way, an endless variation of different forms will result due to genetic splitting. As early as in the 19th and 20th centuries P.-A. L. VILMORIN (1809) and SHOEMAKER (1927) reported on the striking diversity of seedlings. As SHOEMAKER put it: »They show extreme variation in all of their attributes. It is a fact, not only a phrase that there are no identical ones among them. Even an observer not used to perceiving minute shades of variation will agree after looking at the population for a few minutes.« For an expert, the kaleidoscopic diversity of variously combined morphological attributes which is seen when looking at a stand of such seedlings is a truly dazzling sight. The most striking differences are in leaf shape and size, stem height and ramification, flowering time and flower head size. But stem thickness, height, hairiness, color, leaf texture, margin serration, color, the number of inflorescences, the color of the pistils, tuber position, shape, size and number, etc. also show extreme variation. There is hardly any attribute in which one cannot find such variability.”

10 Salsifis differs from Jerusalem artichoke mostly in its tuber shape and leaf shape. Its tubers are finger-breadth, growing on thin, elongated-fusiform far-running rhizomes. Its leaf shape is somewhat narrower than that of Jerusalem artichoke, and the dark green leaf surface is strongly recessed along the veins, making differentiation between them easy even for the first sight. It develops faster and flowers 3-4 weeks earlier than Jerusalem artichoke. Its inflorescence is similar to that of Jerusalem artichoke. Its stolons are denser and more tubers are produced. However, because of the small weight of the tubers, it yields much less crop than Jerusalem artichoke.

The analysis of chromosome-numbers in three West-Hungarian invasive wild Jerusalem artichoke populations yielded that $2n = 102$. Considering the already known chromosome numbers of the phenetically similar species, it appears that they do not belong to *H. decapetalus* ($2n = 34, 68$). (Besides *H. decapetalus* and *H. strumosus* only one sunflower species is known to have two races with different ploidy levels.¹¹) If it is assumed that we are not dealing with an unknown hexaploid race of *H. decapetalus*, than it can be either *H. tuberosus* ($2n = 102$), *H. strumosus* ($2n = 68, 102$),¹² or their common hybrid (see below).¹³

On the other hand, it is interesting to note that news published about the cultivation experiments of “salsifis” or “helianthi” in the first half of the 20th century were replaced in the second half of the century by reports on an intensively spreading “unknown” species. According to WAGENITZ (1968), it is possible that there is connection between them, and it is actually the plant once grown as “salsifis” or “helianthi” that is the naturalized newcomer to Europe. The author agrees with this assumption, but whereas *H. tuberosus* is suggested by WAGENITZ (1968), we believe that the perennial sunflower spreading invasively in recent decades could also well be an artificial¹⁴ or natural hybrid¹⁵ between Jerusalem artichoke (*H. tuberosus*) and the plant once cultivated with the name salsifis (possibly *H. strumosus*).

ORIGIN, DISTRIBUTION¹⁶

Native range

The above detailed species of the genus *Helianthus* are native to North America, almost exclusively east of its centerline, their present-time ranges overlapping significantly (except for *H. pauciflorus* subsp. *subrhomboides* whose range is west to the other species¹⁷). However, their original (historic) distribution areas are difficult to define, due to strong human influence. This particularly regards the most commonly cultivated *H. annuus* and *H. tuberosus* species, which were grown by Amerinds well before the time of Columbus. The former species is thought to have originated from Mexico from where it could have reached present-time areas of the USA. Jerusalem artichoke is said to be native to the region of the Great Lakes or the valleys of Ohio and Mississippi. As proved by archaeological finds, *Helianthus* species, including *H. tuberosus*, were grown in the Mississippi valley as early as around 3000 B.C. The first written information about *H. tuberosus* originates from French traveler Samuel de CHAMPLAIN who noted this plant in 1605, grown in an Amerind garden near Nauset Harbor (Cape Cod, Massachusetts).

Adventive range

The first tubers of *H. tuberosus* were imported to Europe (France) by LESCARBOT, travel companion to CHAMPLAIN, possibly in 1607. It became widespread in Paris by 1617 both as human food and forage for animals with the name “topinambaux”.¹⁸ In the meantime it was taken to other countries too, including the Netherlands (1613), Italy (1614), England (1617), Germany (1627), etc. Its first botanical descrip-

11 *H. ciliaris* DC. (blueweed), $2n = 68, 102$.

12 The Flora Europaea (HANSEN 1976) mentions *H. strumosus* among the species which occur as escapes from cultivation, and may be in process of becoming naturalized, but it is not known which sources are used and what areas are considered.

13 Possible hybrids between the species mentioned: *H. strumosus* × *H. decapetalus*, *H. strumosus* × *H. tuberosus* (after HEISER *et al.* 1969 and ROGERS *et al.* 1982).

14 Experiments for creating a cross between Jerusalem artichoke and salsifis were performed mostly in Germany, in the first half of the 20th century. Their hybrids were believed to be promising, one characterized with particularly massive leafy stem yield, proliferated stolon production and good tuber shape (ŒSÓ 1955).

15 Hybrid species can often have greater vigor (vitality) than its parent species (cf. the Central-European career of *Fallopia ×bohemica*, the hybrid between *F. japonica* and *F. sachalinensis*).

16 Further parts of this chapter deal only with species that are notable from the aspect of the scope of the book.

17 Distribution areas of individual species are specified in the section on taxonomy.

18 The name “topinambaux” or “topinambour” was given to this plant after a Brazilian Amerind tribe (tupinambas) some representatives of which even reached Paris in the early 1600s, due to the misbelieve that the plant was imported from Brazil. Other contemporaries believed it to have Canadian origin. In Italy it was given the name “girasole” (girare = to turn, sole = sun). In its English common name (“Jerusalem artichoke”), the first part of the phrase is senseless, because it is a transcription of the wrong pronunciation of girasole; the second part is from CHAMPLAIN who first described the taste of tubers as resembling that of artichoke.

tion and illustration is by F. COLUMNA (1616) who got to know this plant in Archbishop Farnese's garden and identified it as "Flos solis Farnesianus, sive Aster Peruanus tuberosus". The first data of Jerusalem artichoke escaping in Europe is from the middle of the 19th century, and its massive expansion and naturalization in (near-)natural habitats along watercourses has been dealt with in literature since the middle of the 20th century. Today *H. tuberosus* is distributed in North America: east of the Rocky Mountains, to 32–52° northern latitude, the majority of this range being adventive. Its (mostly wild) forms are found today introduced to California, Canada, Central-, Eastern- and (in some place) South-Europe,¹⁹ the British Isles, certain temperate zone areas of Asia (e.g. Central Asia, Ussuri-region, Sakhalin, Japan), in tropical areas of South America, further in the Azores, Southeast Africa and New Zealand. Wild Jerusalem artichoke is regarded as an ecological weed in Central and Eastern Europe. In the Carpathian Basin it occurs in almost all of neighboring countries of Hungary. Sometimes data sources make a distinction for var. *subcanescens* (Ukraine). It is typical for the expansion dynamics of this species that whereas it used to be infrequent along the Subcarpathian section of Tisza River and its tributaries in the 1970s, today they are widespread. Based on the above interpretation, data about the escaping and naturalization of *H. decapetalus* are regarded as information about wild forms of *H. tuberosus*.

The European flora monograph reports about the naturalization of *H. ×laetiflorus*, having been grown as an ornamental in a number of countries.²⁰ Later, this plant appears in the floristic literature of other European countries too²¹, together with *H. pauciflorus* although the latter is thought to escape only occasionally.²² In addition to the aforementioned species, the European flora monograph alludes to the possibility that the true *H. decapetalus* L. and *H. strumosus* could also have escaped and naturalized. The latter species was reported to have done so in the Czech Republic and Transcarpathian part of Ukraine, as well as in Japan. *H. giganteus* is known to have escaped in Switzerland and Germany.

Distribution in Hungary

Since the beginnings, writings about the cultivation of *H. tuberosus* have all dealt with its ability to escape. One of such piece of earlier information on its occurrence in the Carpathian Basin says that in Temes county "it is grown or it has escaped" (BORBÁS 1886). Other early examples on its presence are from Vas county: Kőszeg (WAISBECKER 1891) and Sorkitótfalu (JÓZSEF MÁRTON, in herb. BP, 1891). According to PRISZTER (1997), the first data on the escaping of the plant known in the recent half century as *H. decapetalus* (having naturalized for quite a while) dates back to 1910. Since then it has spread along watercourses throughout Hungary, especially in the hilly regions of the country. Its often homogenous stands are lining the banks of watercourses for kilometers at certain places.

The first news about *H. pauciflorus* escaping in Hungary is from Celldömölk, Vas county (GÁYER 1913). It has occurrence data from Budapest and surroundings, shorelines of Lake Balaton, Baranya, Győr-Moson-Sopron and Vas counties. The subsp. *subrhomboideus* was found in Zala county near Zalacsány and Hévíz, (DANCZA 1999). The first record of escaped *H. ×laetiflorus* is from 1959 (PRISZTER 1997); its occurrences include Budapest and surroundings, western and southwestern regions of Hungary. The possibility of *H. strumosus* being present in Hungary was raised by the author (BALOGH 1996).

LIFE CYCLE

The various biotypes of Jerusalem artichoke – cultivated, riverbank and segetal weed – vary greatly in their tuber shape, seed production and regeneration ability. The growth and development of cultivated Jerusalem artichoke originating from seeds or tubers show considerable difference. The germination time of achenes sown is normally shorter than the time needed for the tubers planted at the

19 Albania, Austria, Belgium, Czech Republic, Netherlands, Croatia, Poland, Hungary, Germany, Italy, parts of Romania inside the Carpathian Basin, Spain (Catalonia), Switzerland, Serbia, Slovakia, Slovenia and southern parts of former Soviet Union.

20 Denmark, France, Germany, Netherlands, Hungary and central parts of the former Soviet Union's European region (HANSEN 1976).

21 E.g. Austria, Czech Republic, Poland and Ukraine.

22 E.g. Austria, Czech Republic, Italy, Switzerland and Ukraine.

same time, to shoot out. However, plants developing from tubers are faster in their initial growth than those growing from seed. Plants grown from tubers will produce tubers sooner than those developing as seedlings. The majority of seedlings grow taller than plants developing from tubers. The germination ability of achenes produced by seed-grown plants is significantly greater than that of achenes produced by tuber-grown specimens. For successful germination the achenes need a period of dormancy. In the case of *H. tuberosus* this dormancy can be disrupted with a cold-treatment of 1.7 °C lasting for seven days. Because Central-European wild Jerusalem artichoke populations tend to spread with vegetative propagules i.e. their below-ground tubers, hereby we prefer to focus on the development of plants growing from tubers rather than seeds. The development of leafy stems growing from the tubers in April is initially slow, then accelerates – depending on environmental conditions – in the summer months, and lasts until the first stronger frost. The nutrient supply stored in tubers from the previous year runs out by late June, causing the tubers to die off. Shortly afterwards, new tubers start to develop, initiated by the appearance of rhizomes (or stolons). In the case of wild Jerusalem artichoke this happens sooner than in cultivated varieties. The stolons sometimes grow longer than 1 m and run 10–20 cm below the soil surface. Their development is continuous throughout the vegetative season, but their numbers gradually decrease due to the tubers developing on their terminal sections. Tuber production, i.e. the swelling of rhizomes is slower in the summer and faster in the autumn. Some authors claim that tubers continue to grow even after the leaves and stem have died off following the first stronger autumn frosts, sometimes into January. (If this is true, it may be related with water absorption.) However, sooner or later they will reach a stagnant stage, during which they never sprout even if conditions are otherwise suitable. This dormancy – said by many authors to be a natural delayed ripening process – can be disrupted if gibberellic acid or 0 °C cold treatment is applied. Individual tubers are produced on the terminal parts of rhizomes, by the swelling of the last 5–10 internodes. A single plant can produce as many as 75 tubers, but tuber production can quite as well fail to happen. Tuber size and shape is variable. They can become round, pear-shaped, ovate, fusiform or irregular. Their color, too, can be of many shades: a) white (off-white, yellowish white), b) pink (red, purple, bluish), c) smoke-color (bronze). (In our experiment with wild Jerusalem artichoke stands in Vas county, the tubers produced within a single population were significantly different: dark claret or light yellow). Plant individuals developing from tubers that belong to the three major tuber color categories are different in their growth rate, crop producing ability and composition. Cultivated varieties generally produce larger tubers closer to the stem, whereas wild forms yield smaller tubers, more distally from the stem. (In our above mentioned experiment, the weight of below-ground plant body mass – of which 90% was made up by tubers – grew to seven times as much in the second year of the plants.) From the aspect of tuber and flower production, cultivated *H. tuberosus* is a short-day plant. In the majority of Jerusalem artichoke varieties grown in Hungary, flowering starts in late September, early October, and often lasts well into the first autumn frosts, thus no ripe achenes are produced. However, a selected French variety (cv. Blanc commun D. 19.) flowers from early or mid-July to late August, producing achenes. This early-flowering cultivar is strongly ramified, with 20–80 composite inflorescences (an average of 40–50) produced all over the ramifications of the stem, whereas late-flowering types are usually less ramified, with 1–10 inflorescences produced on the terminal parts of the stem. The early form shows a generative character as opposed to the general (vegetative) Jerusalem artichoke type. Wild Jerusalem artichoke, known to be an invasive species, starts flowering similarly early, in mid-August, blooming into mid-October. In its more ramified individuals maybe 80–100 composite heads.²³ Besides this generative type, the less ramified vegetative type bearing smaller amount of flowers is also present in the invasive populations.

The rim of the composite head is bordered by large-petal, sterile, alluring ray florets. Disc florets open from the margin of the head concentrically inwards. Jerusalem artichoke is an insect-pollinated (entomogamous) and geitonogamous plant. In this case the latter means that pollen must originate

23 On 9 October 1997 the author counted 202 (!) composite heads on a 320 cm tall specimen at Nagyrákos, by the side of creek Zala, Vas county.

from a different population in order for seed production to be successful. Self-pollination was found to be successful at a rate of only 0.29%. If temperature at flowering time is too low, the success rate of fertilization and seed development will be reduced. Fertilization rate is found to be very low in Hungary, successful only in the earliest terminal composite heads of the main stem, and more effective in drier habitats than in wet places. The majority of achenes produced are empty. In our investigations performed in populations in Vas county, no ripe achenes were found on *H. pauciflorus*, *H. ×laetiflorus* and in a cultivated variety of Jerusalem artichoke, only empty ones sometimes. However, among the two – morphologically more or less distinguishable – types²⁴ of wild Jerusalem artichoke, originating from different populations, relatively proliferant (50–60 achenes/100 inflorescences) yield was recorded in one (“a” / generative type), whereas very moderate (1/100) seed production occurred in the other (“b” / vegetative type). The density of fruits in the evaluable, generative type (“a”) was 4.5–6.0 g per 1000 achenes. Germination tests showed that while achenes of the vegetative (“b”) type did not germinate; those belonging to the generative type (“a”) were able to do so. Germination success was much higher in second year than in first year. Some of the plants grew from the seedlings flowered and produced achenes in the second year. The above results (BALOGH 1999, 2000), together with data collected in the Czech Republic (KONVALINKOVÁ 2003), show that wild Jerusalem artichoke can reproduce – in addition to the typically vegetative way relying on rhizomes and tubers – generatively in Central Europe, too, even if this is relatively infrequent. This can be important for the preservation of the genetic diversity of populations, and can improve the chances for the creation of hybrid populations. Natural selection can also play a role in the spreading of types that flower earlier and thus produce fruit more effectively.

The leafy stem can start losing the yellowing, drying leaves in summer, but, depending on the ecotype, the stem can keep its green leaves until the first autumn frosts. Both the parts above ground and the rhizomes in the soil then die off, only the tubers over-wintering. If they become exposed on the soil surface, they are prone to dehydration, and thus become more sensitive to cold and dry winter conditions. Carbohydrates stored in the tubers and swollen, terminal parts of rhizomes ensure that the clone survives until the next season, and provide standby energy resource for rapid growth in spring. It has been shown that individuals invest more of their resources into tuber production if their inflorescences removed than individuals with intact flower heads. This plasticity is clearly adaptive, especially in areas where herbivores and weather conditions often prevent generative reproduction. Some clones reallocate their resources for generative reproduction to producing large tubers, whereas other clones producing lot of small tubers. Populations existing in strong competition with other plants invest into producing strongly competitive ramets from large tubers, whereas populations experiencing higher random mortality invest into producing higher numbers of small tubers.

Ways of spreading. The achenes of wild Jerusalem artichoke have no pappus; therefore it is mostly moving waters and birds that can act as vectors in their spreading. The latter, however, has only secondary importance. The most important propagators are rivers and brooks, which can transport the tubers to great distances. Small mammals feeding on the tubers have a similar role, capable of founding new plant populations either in the floodplains or further away. The regeneration ability of Jerusalem artichoke is very good; the plant easily re-grows from below-ground parts. Regeneration is more effective from tubers than from stolons, especially when these parts are located deeper in the soil. New plants can develop even from dissected tuber pieces. As a general rule, the biological factors ensuring the success of already established wild Jerusalem artichoke populations are as follows: a) a high expenditure of energy on initial growth of stem, branches and leaves, b) great energy allocation into rhizome and tuber production, c) phalanx-like growth, facilitating capture of both above- and below-ground resources, d) good nutrient mobility within the plant, e) good regeneration ability, f) constancy of nutrient allocation to clonal structures, g) allelopathic effect, h) resistance to the majority of diseases and pests, i) tolerance of poor soils. In their native range, these factors are supplemented by a moderate level of seed production, and in their adventive distribution areas, by the lower number of natural enemies.

24 For their description see: BALOGH (1998).

HABITAT PREFERENCE

Autecology

Native range. *H. tuberosus* occurs mostly in moist areas with clay soil, open or shady habitats, riversides and fallows; in the eastern parts of North America it is a common roadside plant, as a remnant of cultivation long ago by native people. Being a frost-tolerating species that over-winters with its below-ground parts, it has adapted well to a number of different climatic regions including the majority of North America and Europe. From the investigation of cultivated varieties it was found that the vegetation season must last for more than four months for tuber production to be successful. Having said that, Jerusalem artichoke grows better in the northern parts of the USA than in the south, moreover it is also successful in Alaska and in Europe's northern countries. It grows best in areas with abundant rain. Jerusalem artichoke is less tolerant of arid conditions than the other hexaploid sunflower species, yet there are data that it was growing relatively successfully in a year with dry summer in Kansas. All of its biotypes share the characteristic that they grow best in nutrient-rich, sandy, light, well-draining soils of river valleys or in alluvial terrains. Within arid prairies, locations with the above features serve as primary habitats for wild populations. One example for a high altitude occurrence: Colorado, 1200–1500 m.

H. decapetalus grows in shady, moist forests, usually on nutrient-rich soils, sometimes surviving in clearings or in clear-cut areas, and along watercourses. *H. strumosus* is frequently found in dry forests, but also in completely open habitats, on watersides, roadsides and prairies. *H. pauciflorus* subsp. *pauciflorus* prefers dry or moderately moist prairies and roadsides, whereas subsp. *subrhomboideus* grows best on dry, open areas. *H. xlaetiflorus* occurs in prairies, open forests, along roads, and in other disturbed, mostly dry habitats, predominantly as an escapee.

Adventive range. Because of the taxonomic interpretation problems, ecological indicator data by BORHIDI (1995) for the invasive wild Jerusalem artichoke are listed under *H. decapetalus*, whereas those regarding cultivated Jerusalem artichoke are specified at *H. tuberosus*. ELLENBERG (1991), however, deals with a "single" *H. tuberosus*. Among these, we hereby deal with the autecology of wild Jerusalem artichoke only, sometimes with a view to our own investigation results too, noting that usually there are no significant differences among them. With abundance that could threaten natural habitats, wild Jerusalem artichoke occurs almost exclusively in moist or wet conditions, along rivers, brooks in hilly or mountain areas, but also besides lakes. It forms continuous stands mostly directly on watersides, e.g. on embankment edges of moving waters, especially on sandy or silty belt-shoals of river-bends, and on more or less humic, clay-, loam- or sediment-based soils forming on fine-particle alluvium of inundation areas. It is a heliofrequent species, occurring predominantly in full exposition with no upper vegetation cover or in partial shade. In the latter case it does not grow well. It is a thermofrequent species, not having reached higher altitudes. Hungarian populations are found below 300 m a.s.l., and in Poland they occur up to 420 m. Its flowering time is determined not only by photoperiodic conditions (day length), but also by summer temperatures. From earlier data it is known that in years of better grapevine yields, its flowering starts earlier and fruit production is more successful. The tubers having good frost tolerance ($-30\text{ }^{\circ}\text{C}$), they can survive the severest winters experienced in Hungary. Based on its tolerance of extreme climatic effects, it is considered not to be a sub-oceanic, rather a sub-continental species. It has relatively high water demand. It is tolerant of a few weeks of flooding, but if ground water level remains permanently close to soil surface (-20 cm), this is detrimental to its development, especially to tuber forming. For some time it tolerates water shortage – showing symptoms of drying –, but if water supply returns to normal, it regains its strength and continues to grow normally. As to soil pH, it prefers slightly basic soils. The fact that wild Jerusalem artichoke occurs mostly on nutrient rich soils of waterside habitats does not mean its high nitrogen demand. It is related that habitats disturbed repeatedly by floods provide ideal conditions for the reproduction of this species: vegetative expansion is easy in the light soil of continuously re-created bare surfaces, with little or no competition. Based on our own observations, it is mostly the vegeta-

tive type of plants that tend to occur in the lower, wetter habitats along flowing waters with light soils, whereas further away from the water, on higher, less wet, heavier soils it is mostly the generative type that grows well. It must be briefly mentioned that the cultivated types of *H. tuberosus* (Jerusalem artichoke and varieties sensu stricto) are mostly found escaping near its former cultivation sites or in ruderal habitats. These are mostly drier habitats than the ones suitable for wild Jerusalem artichoke migrating in floodplains.

Phytosociology

Native range. In available literature sources, no data have been found about the exact syntaxonomic character of *H. tuberosus* in its native range. *H. pauciflorus* is a member of the tall bunch-grass community occurring mostly in prairies of sandy soils, characterized with the following grass species: *Andropogon gerardi*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Tripsacum dactyloides*, *Panicum virgatum* and *Spartina spartinae*.

Adventive range. The escaping, naturalization and invasion of *H. tuberosus* s. l. (incl. wild forms, *H. decapetalus* auct. eur. centr. non L.) affect mostly natural vegetation types (agriophytic occurrences). It appears in various herbaceous communities of waterside or floodplain habitats: in their margins or actually substituting them; such are for example reed beds, sedges, tall herb communities along brooks and bogs. In woody communities it colonizes in their fringes or glades, e.g. in willow-bushes and softwood galleries, but also in poplar plantations and sometimes in bogwoods. Thus, wild Jerusalem artichoke is a representative of the characteristic autumn aspect of invasive species spreading intensively in alluvial weed communities. It occurs individually or in groups of various sizes, but most often it is almost entirely subdominant or monodominant, forming a particular facies.

However, *H. tuberosus* s. l. acts as a weed not only in near natural vegetation types, but also in strongly anthropogenic environments including ruderal habitats and abandoned lands, sometimes in segetal habitats, too. Among such epiphytic occurrences WAGENITZ (1968) and VIŠŇÁK (1996) mention it from burdock (*Arctium lappae*), MÜLLER (1983) and LOHMEYER & SUKOPP (1992) from roadside weed (*Artemisia vulgaris*), and OBERDORFER *et al.* (1994) from *Artemisienea* communities or as being typical for these. As an example of its occurrence in farmland weed communities, PÁL & TERPÓ (1990) found it in a soybean field in Szabolcs-Szatmár-Bereg county, accompanied by *Abutilon theophrasti*, *Amaranthus retroflexus*, *Sonchus asper* and *Galinsoga parviflora*. Recently, BALOGH observed its flowering population in a floodplain corn field along the Órség section of river Rába, Vas county. Phytosociologically, the escapee occurrences of the cultivated varieties of Jerusalem artichoke (*H. tuberosus* s. str.) are similar to the epiphytic occurrences of wild type, usually being small-scale appearances only, near its former growing areas.

The stiff sunflower (*H. pauciflorus*) is mentioned by MUCINA (1993) as a neophyte predominantly occurring in alluvial weed communities (*Senecionion fluviatilis*). Its Hungarian wild occurrences are known mostly from the surroundings of gardens, in dry ruderal weed communities, sandy grasslands (*Artemisi-etea*). One of its largest, seemingly most virulent naturalized populations seen by the author expands in a mesophilous reed bed near the city of Győr, Győr-Moson-Sopron county. The phytosociological character of the cheerful sunflower (*Helianthus ×laetiflorus*) is similar to that of the former species.

BIOTIC INTERACTIONS

Allelopathy

One of the factors leading to the competitive success of wild Jerusalem artichoke is its allelopathic effect. Such allelopathic chemical compounds found in *H. tuberosus* are sesquiterpenoid lactones belonging to terpenoids, and phenolic acids belonging to phenoloids. In the early 20th century, it was even recommended in Canada that this plant can be used as herbicide, although the weed killing effect was then attributed to the deeply shading effect of its foliage. The fairy-ring pattern in the grass around stiff sunflower (*H. pauciflorus*) growing in prairies is possibly also result of allelopathic regulation.

Competition

Once it has established *H. tuberosus* out-competes almost all other plants with its rapid, phalanx-like growth form. This is especially so in cultivated Jerusalem artichoke stands, but the wild populations growing in near-natural vegetation also create extremely species-poor stands. (Among the two types of Jerusalem artichoke observed as occurring in Vas county, the generative (“a”) type usually grows individually or in low density patches, whereas the vegetative (“b”) type normally occurs in the form of larger, continuous, closed populations.) The biological factors listed in the life history section provide wild Jerusalem artichoke with considerable competitive advantage (maybe its highly effective vegetative reproduction is the most important factor). A good example is that it can out-compete *Urtica dioica*. *Urtica* is one of the most successful native plants that are able to dominate moist, nutrient-rich, disturbed habitats in Central Europe. This highly successful strategy is achieved by its clonal growth, and by the reallocation of the carbohydrate and nitrogen content of its ramets dying back. Rhizomes of *H. tuberosus*, however, run deeper in the ground than *Urtica*’s one, and by re-mobilizing nutrients stored in the tubers in spring, it grows faster, creates dense coverage, and its ultimate height (3–3.5 m) is also greater than that of *Urtica* (max. 2 m). Actually, Jerusalem artichoke “undermines” the *Urtica* population or the community dominated by nettle. Rhizomes of establishing wild Jerusalem artichoke creep under the *Urtica* stand, forming tubers on the terminal parts of the rhizomes. The next year, growth and expansion under the *Urtica* will be continued multilaterally from the tubers, developing 3–8 individuals from a single individual. The dense and tall foliage parts of *Helianthus* overgrow and considerably shade the *Urtica* stand. As this process is repeated year after year, wild Jerusalem artichoke completely undermines and shades out the *Urtica* population. Among native herbaceous plants there are only very few species – mostly rhizomatous perennials similarly to *Urtica* – that can permanently resist this aggressive strategy (LOHMEYER & SUKOPP 1992). As shown by the results of our studies performed in Vas county, it is *Phalaris arundinacea*, *Aegopodium podagraria*, *Urtica dioica* and *Calystegia sepium* that can best tolerate root competition, shading and allelopathic effects in more or less homogenous wild Jerusalem artichoke stands. In the case of closed wild Jerusalem artichoke populations, mostly it is only *Calystegia sepium* as a climber that is capable of generative reproduction, as opposed to the other three species which have much lower vitality under the same conditions and usually cannot complete their entire life cycle because they do not reach flowering stage. As it has been mentioned in the phytosociological description, wild Jerusalem artichoke often co-occurs with other invasive tall herbs and climbers. Among these, its most remarkable competitor is another invasive species: *Fallopia ×bohemica*, capable of even suppressing or outgrowing wild Jerusalem artichoke.

If the density of shoots in a wild Jerusalem artichoke stand exceeds a certain degree, the individuals start competing with each other. During the self-thinning sets dominant individuals shade over the smaller ones, thus the population’s density is decreased. In populations along Slovakian rivers, the highest shoot density was recorded in May–June, to be followed by a reduction in their numbers; by autumn the density lessened to about one half its previous level (FEHÉR & KONČEKOVÁ 2005a).

Herbivores

Native range. As shown by Canadian experimental garden studies, *H. tuberosus* is damaged by the larvae of the beetle *Strauzia longipennis*, causing the leaves to wilt, become chlorotically discolored and die off. The following insects have also been found on Jerusalem artichoke: *Diabrotica longicornis*, *Adalia bipunctata*, *Empoasca fabae*, *Sitophilus granarius* and *Apis mellifera*. Also revealed by Canadian studies, sunflower beetle (*Zygogramma exclamationis*) does not like Jerusalem artichoke. The weevil damaging sugarbeet (*Cosmobaris americana*) and the leafhopper *Publilia concava* can be hosted by Jerusalem artichoke. Aboveground parts of the plant can serve as food for herbivorous mammals, whereas the tubers provide carbohydrate supply for game animals.

Adventive range. As found by I’só (1955) in Hungary, there are hardly any pest animals damaging cultivated Jerusalem artichoke. Polyphagous insects such *Hypanthria cunea*, *Melolontha* sp., *Agriotes* sp. larvae, and other occasional pests may sometimes cause minor damage, but no specialised pests are

known to be threatening Jerusalem artichoke, either from literature or from field observations. Among animals acting as pests for cultivated Jerusalem artichoke, the most serious damage is caused by *Microtus arvalis* which rodent often feeds on tubers when the plants are still standing. Minor damage is sometimes caused by rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) which can dig up the planted tubers or chew at young shoots or seedlings. In a well established Jerusalem artichoke field, however, these damages are almost insignificant, as reported by I'só (1955). According to Central-European literature sources, in addition to these species, other small mammals feeding on wild Jerusalem artichoke tubers include *Arvicola terrestris*, *Rattus norvegicus*, *Ondathra zibethica* and *Mus musculus*. Tubers can serve as food for larger herbivorous (e.g. *Capreolus capreolus*, *Cervus elaphus*) and omnivorous animals (e.g. *Sus scrofa*), too; the author has observed signs of such digging in wild Jerusalem artichoke stands.

Pathogens

As far as it has been revealed, the so-called wild species of sunflowers are less sensitive to pathogens than the cultivated annual sunflower. *H. tuberosus*, too, has relatively few diseases. For example, the viral diseases so significant in potato hardly occur at all in Jerusalem artichoke, and nematodes are completely absent. Among pathogens, fungi have greater importance. The following pathogens are known to have occurred in *Helianthus* species.

Fungi: Phycmycetes: *Plasmopara halstedii* is a polyphagous mildew causing leaf diseases in *Helianthus* species. *Pl. helianthi* f. sp. *perennis* causing sunflower mildew among others, attacks perennial *Helianthus* species (*H. tuberosus*, *H. pauciflorus*, *H. maximiliani* etc.). *Pl. helianthi* f. sp. *patens* is another specialist of perennial *Helianthus*, e.g. *H. strumosus*. *Rhizopus stolonifer* (syn.: *Rh. nigricans*) is a black mould type of polyphagous fungus causing soft rot in stored tubers. In Minnesota it was found to be among the commonest fungal pests on cold-stored tubers.

Ascomycetes: the most significant disease of Jerusalem artichoke is the sclerotic stem- and tuber rot, which occurs mostly in wet summers. It is caused by the polyphagous fungus *Sclerotinia sclerotiorum* which occurs, in addition to *H. tuberosus*, on *H. annuus* and many other cultivated and wild plant species. Besides the over-wintering sclerotium corpora, infected tubers are also vectors of this fungal disease. In cultivated Jerusalem artichoke, damage is usually greater in stored tubers than in the field. Varieties with purple tubers are more resistant to this disease than those with yellow tubers. *Erysiphe cichoracearum* causing sunflower mildew and *Sphaerotheca fuliginea* causing leaf disease are polyphagous fungi attracted to Jerusalem artichoke, too, the plants becoming entirely white in cases of strong infection. *E. cichoracearum* was found to be one of the most significant Jerusalem artichoke pests in Georgia between 1980 and 1982. *Oidium helianthi* auct., an accessory, conidial form of one unclarified *Erysiphe* species, is common on *H. tuberosus* and other *Helianthus* species. In addition to the cultivated annual sunflower, Jerusalem artichoke can also be infected by *Leptosphaeria lindquistii*, causing the black spot symptoms of stems and leaves.

Basidiomycetes: *Puccinia helianthi* is a parasite specialized on annual and perennial *Helianthus* species, causing the leaf disease called sunflower rust. It is said to have been one of the two most serious Jerusalem artichoke pathogens in Georgia between 1980 and 1982. Hungarian authors, however, claim that instead of this species, *P. helianthorum* (syn.: *Puccinia helianthi* f. sp. *tuberosi*) is the one that develops on Jerusalem artichoke. *P. helianthorum*, although it does occur in Central Europe, has not caused agricultural damage, and has not been recorded in Hungary (until 1985).

Deuteromycetes: *Coniothyrium helianthi* and *Diplodina helianthi*, as well as *Septoria helianthi* causing leaf spot occur on members of the *Helianthus* genus. *Sclerotium rolfsii* is a thermophilous, polyphagous parasitic fungus causing stem base disease, root collar rot and seedling-age disorders in Jerusalem artichoke. In Georgia it caused damage during the growing season. *Penicillium* species and *Botrytis cinerea* were among the most frequent pathogens in Minnesota, on cold-stored tubers. The latter is a polyphagous fungus, causing disease sometimes on the green leafy stem of Jerusalem artichoke, but more often on the stored tubers. It infects mostly through wounds. The affected parts turn brown, and a grey or greyish green mould coating develops on them. The fungi *Alternaria helianthi* and *A. helianthinificiens*

causing brown spot disease on leaves, stems and petals occur on members of the genus *Helianthus*. *A. alternata* and *A. tenuissima* were found on Jerusalem artichoke leaves in Canada. *Fusarium* species belong to the most frequent pathogens of Jerusalem artichoke tubers stored in cold depots or in the field.

Viruses: Viral diseases can also affect *H. tuberosus* (especially on seedlings), causing the foliage to develop spotty salting and distortion (curling up of leaf margins). Viral diseases are only seldom found on vegetatively propagated plants.

Bacteria: Apical chlorosis and leaf spot were described from Minnesota in 1984, caused by the bacterium *Pseudomonas syringae* pv. *tagetis*. The sprouts of Jerusalem artichoke penetrating the soil surface often cannot survive a stronger infection. However, if the pathogen attacks a fully grown plant, growth will be reduced only insignificantly. In the mentioned year in Georgia, damage was caused by *Pseudomonas* species in Jerusalem artichoke tubers stored in cold depots and in the field.

Flowering plants: Jerusalem artichoke is usually known as a plant resistant to *Orobanche* sp. that attack *H. annuus*.

Symbiosis

No mycorrhizal association has been found in *H. tuberosus*. No data are available for other members of *Helianthus* genus.

ECONOMIC IMPORTANCE

Benefits

Amerind people used to collect seeds from several *Helianthus* species native to North America, including *H. annuus* subsp. *lenticularis*, and *H. argophyllus* another wild sunflower species somewhat more closely related with today's cultivated sunflower. Species with tubers were also used as a food source, such as *H. tuberosus* and *H. maximiliani*. As archaeological evidence shows, the domestication of the annual (common) sunflower started somewhere around the first millennium B.C. Respected as an easily available food source, Jerusalem artichoke is a similarly old cultivated plant, which had been cultivated for long before America was discovered. Among *Helianthus* species, the second most significant species after the economically most important *H. annuus*, is *H. tuberosus*, this preference being justified by the fact that an acceptable nutritive value is accompanied by high biomass yield and carbohydrate content. Originally, it was predominantly a human food and animal forage, and its popularity kept fluctuating during times. Today Jerusalem artichoke is cultivated in North America, France, Italy, Germany (upper Rhine-valley), the European part of former USSR, North China, and also – with less success – in certain tropical countries, too (India, Indonesia, Malaysia, Congo, Zaire, Nigeria). The highest production rate is in France where, in some provinces, it is cultivated on larger total area than what is devoted to potato.

In Hungary, it is first mentioned by János LIPPAY with the name “ground apple” (1664). In those times it was used as a food for humans, because potato was still unknown in Hungary. When potato became widespread, Jerusalem artichoke was effaced. In 18th–19th century, several authors reported on it, and recommended this undemanding, high-yield tuber crop to be re-used as forage. Between the two world wars, it was grown on approx. 250 hectares, mostly in Tolna county, and by 1953 this rate had increased to approx. 1600 hectares. Since then, its growing area has been decreasing. In earlier times it was also a delicacy for children, and sometimes it was used as a medicinal plant. According to FARKAS (1895), “the uncooked tubers are very useful for scrofulous people, and are quite well known among folks as a medicine for this disease.” A study on ethnobotany performed in Árapatak, Transylvania in the early 1970s reports on the followings (SZABÓ & PÉNTÉK 1976/1996): “Tubers of Jerusalem artichoke were harvested in early spring or late autumn. They were eaten by children, and also fed them to pigs. Today they are only seldom collected. They are peeled and eaten uncooked. The way it appeared in our village was that around 1880 landlord Mátyás Domokos brought it and planted it along the trench of the Székelút lane. He then called it »picsóka«, but villagers said »ground apple«. Then the stream took away the roots.” This report is a good example of how information preserved in traditions on the appearance and establishment of certain introduced plants in a village, can be – and should be – recorded.

In recent times, Jerusalem artichoke has become a popular vegetable especially in France, Italy and Germany, used in a cooked or stewed form or eaten in soups and salads, but also baked, as a puree or uncooked. If eaten uncooked, its taste resembles that of hazelnuts, and when cooked it is somewhat like artichoke just that it is less tasty and sweeter. Maybe it is best as a vegetable stewed in its own juice. Consequently, Jerusalem artichoke as a human food has two types of uses: as an essential foodstuff it can substitute for potato, and on the other hand it is a food suitable for diabetic people. This is because its nutritive compounds, instead of starch, are mostly inulin and synanthrin, both of which are made up of easily digestible organic compounds (polyfructosans). Even among inulin-producing plants (*Cichorium*, *Dahlia*, *Taraxacum*, *Cirsium arvense*), Jerusalem artichoke has one of the highest inulin yields. It is recommended as one important constituent of the diet for diabetic people and for those suffering from obesity. If it is eaten, fewer calories are taken in, at the same time fulfilling the requirements of protein and mineral uptake.

The dry matter content of Jerusalem artichoke tubers is 20–25%, which can be even higher in drier years. Carbohydrate proportion, being positively correlated with dry matter content, is around an average of 13–20%, and is present in autumn mostly in the form of inulin. The protein content of tubers is highly dependent of the variety, generally ranging around 2%. Ash content is 1–2%, of which 50% is potassium, and anionic minerals are present mostly in the form of phosphates. Its mineral and trace element (manganese, zinc, copper) content is similar to or higher than those of other tuberous plants. As to its vitamins, data are incongruent. Vitamins A, B₁ and B₂ are present at higher, and vitamin C is at lower levels than in potato. The tubers also contain some vitamin H (biotin) and D.

Jerusalem artichoke is a double-use fodder crop. Its tubers are used for feeding pigs (to be rooted up by extensively kept pigs), but it can be fed to cattle, horses, sheep and other domestic animals including poultry. If dried, its stem, leaves and thinner parts are eaten by sheep, goats and rabbits. From the stems collected in early or mid-October, before the first autumn frosts, silage can be prepared. The composition of aboveground parts varies in accordance with the developmental stage of the plants. Generally, as the plants develop, lignin content grows and protein content decreases, thus both the nutritive value and tastiness of the silage declines. The smashed tuber mass (“stillage”) left from Jerusalem artichoke based alcohol-production contains sugar residues, minerals and proteins, thus it can serve as animal food with high nutritive value. In Europe, it is used also as forage for game animals; it is often grown as such in woodland or forest edge plots. The cultivated genotypes usually have higher nutritive value than that of wild types.

The potentially high tuber yield per hectare and relatively high carbohydrate content (75% when dry) make Jerusalem artichoke suitable for ethanol-production. The aboveground parts of the plant also serve as good sources of fermentable sugars. Compared with sugar beet, corn and wheat, Jerusalem artichoke tubers yield 1.7, 2.0 and 3.7 times more alcohol, respectively. It provides an equal amount of spirits with potato, and its sweetening power is 1.5 times better than that of sugar extracted from sugar beet. During ethanol production from tubers, proteins can also be extracted. The tubers themselves and the inulin, which can be recovered at industrial scales, are valuable raw materials of spirit-, sugar- and syrup production. The sweetening capacity of its high fructose-content syrups is better than that of sucrose or D-glucose. It is utilized in sweets production, and in composing feeding formulas and ersatz-coffee. Besides these major utilisation ways, its possible further uses are also being analyzed, e.g. as basis for acetone- and butanol-production, “forage fermenter”, beer, lactic acid, propionic acid, mannitol and pectine. In the autumn period, tanning substances have been observed in the tubers. About 1–2% of the dry matter of the plants is natural gum. Beyond these, stems can be used for burning when dry. Quite recently, *H. tuberosus* has been studied as a possible perennial energy-plant. In North America, there have been experiments with its production along rivers. In Poland, the removal of heavy metals from sewage-water sludge was attempted using this plant, with little success.

Wild *Helianthus* species are possible genetic sources for sunflower and Jerusalem artichoke breeding, thus for example *H. paradoxus* might be a suitable genetic resource for improving the salt tolerance of sunflower, and *H. pauciflorus* for influencing its cytoplasmic male sterility. Wild Jerusalem artichoke flowering in late summer or early autumn, and the early types of cultivated Jerusalem artichoke blooming in late summer serve as pollen and nectar sources late in the season. Several species and hybrids

of the *Helianthus* genus are ornamental plants, especially *H. annuus*, *H. debilis* subsp. *cucumerifolius*, *H. ×laetiflorus*, *H. pauciflorus* and *H. ×multiflorus*. Among these, the most frequently grown one is the cheerful sunflower (*H. ×laetiflorus*) flowering almost into the first frosts.

As seen from those written above, almost all of the economic uses regard cultivated *H. tuberosus*. However, there is no such information available about wild Jerusalem artichoke, the invasively spreading weed. Nevertheless, this species is very similar to the already mentioned plant called *helianthi* or *salsifis* grown in Europe in the first half of the 20th century, the cultivation of which was given up because its characteristics were worse in several respects than that of the cultivated Jerusalem artichoke and only some of its features were better.²⁵ It is an interesting fact that the Austrian JANCHEN wrote about *helianthi* or *salsifis* in 1975: it is a forage plant and vegetable just like Jerusalem artichoke, but it is much rarer. Quite possibly, wild Jerusalem artichoke could be suitable as an animal feed and for human consumption too. However, such propaganda should be carefully thought in order to prevent the possibility of some people starting to propagate the existing populations in riversides.

Damages

Several of the sunflower species occur in their North-American native distribution areas as weeds, such as *H. annuus*, *H. petiolaris*, *H. maximiliani* and *H. tuberosus* in the northern-central states of the USA. The latter acts as a weed in wet farm-lands, verges, roadsides, and once established it becomes an annoying weed mostly in arable fields. Its eradication in segetal habitats has been dealt with extensively in literature. In Canada's weed checklist there are sunflower species, too; in some states Jerusalem artichoke is listed among dangerous weeds. The sunflowers *H. lenticularis*, *H. petiolaris*, *H. ciliaris*, *H. californicus* and *H. rigidus* (*H. pauciflorus* subsp. *rigidus*) were listed among quarantine weeds in the former USSR. From the point of view of riverbank protection, the fact that rodents or larger animals keep digging for wild Jerusalem artichoke tubers and thus break up the loose bank can be quite disadvantageous. These weakness zones can become the starting points of greater riverbank erosion caused by the power of floods. According to WIERSEMA & LEÓN (1999) *H. tuberosus* can be toxic to certain mammals. The pollen-allergic effect of *H. annuus* is known from literature; wild Jerusalem artichoke should also be analyzed from this aspect.

NATURE CONSERVATION SIGNIFICANCE

It is not the rare garden escapee sunflowers (pl. *H. ×laetiflorus*, *H. pauciflorus*) or the cultivated varieties of Jerusalem artichoke (*H. tuberosus* sensu stricto) that cause nature conservation problems in Europe, but the taxa having been dealt with above as wild Jerusalem artichoke (*H. tuberosus* sensu lato, incl. wild forms, *H. decapetalus* auct. eur. centr. non L.). Stiff sunflower and cheerful sunflower (*H. pauciflorus*, *H. ×laetiflorus*) have been found in ruderal areas mostly, because they are usually thrown away with garden waste, so its normally small populations are limited to the areas of disposal. In the autumn of 2000, though, stands of *H. pauciflorus* and *H. ×laetiflorus* were found colonizing the reed bed near the city of Győr, Győr-Moson-Sopron county.

H. tuberosus is regarded as an adventive species in the northern central states of the USA, acting as a weed in wet forests. It is listed in the checklist of invasive species compiled by the European and Mediterranean Plant Protection Organization (EPPO). Wild Jerusalem artichoke as a typical ecological weed occurring in (semi)natural vegetation causes nature conservation problems. Having naturalized and spreading intensively mostly in floodplains of rivers and streams, it has become a significant invasive plant throughout Europe. In Hungary it is one of the characteristic representatives of invasive plants aggressively spreading in alluvial communities. By means of its strong vegetative reproduction and shading, it often forms extensive and dense, homogenous stands. Strongly assisted by its allelopathic effect too, it inhibits the establishment (germination and further growth) of other plants on surfaces that are re-opened by floods, and has negative effect on the natural colonization of native shrubs and trees. Its

25 Cf. writings by GASS, GRÁBNER, GRAEBNER, GYÁRFÁS, HÉRICS-TÓTH, OSZTROVSZKY, MÁNDY and WITTMACK.

extremely homogenous stands cause that vegetation becomes monotonous, leading in turn to the depletion of the fauna. It must be noted here that the author has not recorded any evidence of that the cultivated Jerusalem artichoke (*H. tuberosus* s. str.) spreading or showing considerable invasion as a weed of nature conservation concern in Hungary, therefore any actions against the cultivation of Jerusalem artichoke (*H. tuberosus* s. str.), an important vegetable in reform foods, is viewed as unjustified.

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