

Origin, Geographical Distribution and Phylogenetic Relationships of Common Buckwheat (*Fagopyrum esculentum* Moench.)

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ABSTRACT

Fagopyrum is a genus of about 15 species, most of them indigenous to temperate eastern Asia. Common buckwheat (*Fagopyrum esculentum* Moench), the most important species in the genus, has been extensively grown in the northern hemisphere, from Eastern Europe through Japan and in the Americas, as a low-input subsistence or cash crop. It is a diploid species with an indeterminate growth habit. Flowers are hermaphroditic, heteromorphic and self-incompatible. The flourey grain is used as a cereal. Cultivation goes back to the distant past. According to archaeological data and written historical records, ancient civilizations in China and Japan used buckwheat as a staple food. This review discusses the origin and worldwide distribution of common buckwheat and some of the related plant species, using molecular genetic methods including studies of isozyme variability and modern DNA analysis. The following fields of interest are covered: botanical and genetic characteristics of common buckwheat with special regard to the heterostylic flower morphology, original birthplace, geographical distribution, diffusion of cultivation to new geographical areas, genetic relationships among remote populations, phylogenetic relations of wild and cultivated *Fagopyrum* species. Botanical description and illustration of some *Fagopyrum* species are also presented. Studies concerning phylogenetic relationships of species within the genus *Fagopyrum* were surveyed and discussed by reviewing the methods used to obtain primary data. The current view, emerging from them, is presented by naming those clades identified in the majority of the studies.

Keywords: cymosum group, domestication, heteromorphic flower morphology, molecular methods, self-incompatibility, urophyllum group, wild ancestor

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INTRODUCTION

Buckwheat is a temperate zone plant used for human nutrition since prehistoric times. It is a fast-growing annual plant with a variety of potential uses. The flourey grain of buckwheat is used in a way similar to the grains of cereals, despite that botanically buckwheat is not a member of the family *Gramineae* or *Poaceae* (“Grass” family). Buckwheat is a dicotyledonous broadleaved plant, belonging to the family *Polygonaceae*, the “smartweed” family, also called “knotweed” family or “buckwheat” family. For this reason the seed of buckwheat is rather a fruit than a grain (the botanical term is “achene”). It is often referred to as a

pseudocereal.

Although the genus *Fagopyrum* comprises several species, only two of them are of notable economic importance, these are the common (also named sweet) buckwheat (*F. esculentum* Moench) and tartary (also named bitter) buckwheat (*F. tataricum* Gaertn.), both with numerous varieties and landraces in commercial production. Globally, common buckwheat is far more important than tartary buckwheat, estimated on the smaller number of countries where this latter species is grown (mainly in the mountainous regions of China, Bhutan, Nepal and Northern India).

Buckwheat has been extensively grown in the northern hemisphere, from Eastern Europe through Japan, as a low-

input subsistence or cash crop. It is also grown in the Americas. It performs best in temperate or subtropical climate if the rainfall is reliable during the growing season. It may be grown successfully at higher elevations in the tropics (Jansen 2006). Buckwheat is adapted to poor lands. It does well on soils where most of the important cereals fail. At present the crop is hardly affected by diseases and pests, which, together with the short growing period and the low requirements for management, offers a great potential for both organic and conventional buckwheat production.

Total world production of buckwheat seed in 2008 was estimated to be 1.92 million tons from 2.46 million ha. This amount is about 25 to 30% down as compared to the amount produced 5 to 10 years earlier, and has not essentially changed since 2005 (FAOSTAT 2009). The main producers in 2008 were the Russian Federation (0.92 million tons), China (0.33 million tons), Ukraine (0.24 million tons) and France (0.12 million tons). Beside the above, Poland, Kazakhstan, Brazil and Japan also grow significant quantities of buckwheat. The grain is mainly used locally. Total world export of buckwheat was only 0.14 million tons in 2007, with China as the main exporting and Japan as the main importing countries (0.09 and 0.07 million tons, respectively).

The objective of this compilation is to review the present knowledge on the origin, geographical distribution and the taxonomy of cultivated buckwheat and the related species, based on the documented literature. The review is not intended to be exhaustive.

Fagopyrum is a genus of about 15 species, most of them indigenous to eastern Asia. The species are of different ploidy levels, and represent two types of breeding system, self-compatibility and self-incompatibility, with the economically most important species, *F. esculentum* being self-incompatible. Domesticated species are mainly cultivated in temperate and subtropical areas.

TAXONOMICAL POSITION AND BOTANICAL DESCRIPTION OF THE GENUS FAGOPYRUM

The parentage of the genus *Fagopyrum* with that of common buckwheat is shown in the taxonomic tree below (Encyclopaedia Britannica).

- Kingdom: *Plantae*
- Phylum (Division): *Magnoliophyta* (Flowering plants)
- Class: *Magnoliopsida* (Dicotyledons)
- Order: *Caryophyllales*
- Family: *Polygonaceae*
- Genus: *Fagopyrum*
- Specific epithet: *esculentum* (Moench 1794)
- Binomial (botanical) name: *Fagopyrum esculentum* Moench (also named, according to the earlier classification: *Polygonum fagopyrum* L.)

The family *Polygonaceae* comprises about 50 genera and more than 1100 species of herbs (commonly), shrubs and small trees (Flora of North America 5.44). Numerically the most important genera are *Eriogonum* (250 species), *Polygonum* (200 species), *Rumex* (200 species), *Coccoloba* (120 species) and *Calligonum* (80 species). Some well-known members include *Rumex* (sorrel), *Rheum* (rhubarb), *Polygonum* (knotgrass) and *Fagopyrum* (buckwheat), with sorrel and buckwheat as crops of economical importance. Many common and noxious weeds are found within this family. The family is present worldwide, with a few species in the tropics and the greatest biodiversity in the northern temperate regions. "The family is named for the many swollen node joints that some species have; poly means many and goni means knee or joint" (Serving History).

Buckwheat refers to several genera of the family *Polygonaceae*: the genus *Eriogonum* is native to North America, and is not closely related to the Eurasian genus *Fagopyrum* (Flora of North America 5.1). The agricultural weed "wild buckwheat" syn. "climbing buckwheat" (*Polygonum convolvulus* L. syn. *Fallopia convolvulus* L.) is also in the same family, but belongs to genus *Fallopia* (USDA, ARS, Nat-

ional Genetic Resources Program).

Scientific name of buckwheat comes from the Latin *fagus* (beech) and the Greek *pyrus* (wheat), resulting from the resemblance of the achene to a beech-nut and from the fact that it is used like wheat (Flora of North America 5.31). The word *esculentum* is of Latin origin and means edible (Dictionary of Botanical Epithets). Similarly, the English word "buckwheat" refers to beech-nut and wheat, being of Dutch origin (Online Etymology Dictionary). Synonyms in various European languages are: French wheat; saracen corn; bechwheat (English); blé noir; sarrasin (French); buchweizen; heidekorn (German); poganka (Polish); pohánka; hajdina; tatárka (Hungarian); grano saraceno (Italian); ajda (Slovenian); boekweit (Dutch); viljatatatar (Finnish); grechikha posevnaia (Russian); grano turco, trigo sarraceno (Spanish); navadna ajda (Croatian); bokhvete, bokkveite (Norwegian) (Porcher 1995).

At present it is thought that there are about 15 species and numerous subspecies, ecotypes comprised in the genus *Fagopyrum*, which implies a great genetic diversity. According to the description in Flora of North America (5.31) they are mostly annual, taprooted herbs with erect or ascending stems, glabrous or puberulous. The leaves are deciduous, cauline, alternate, petiolate (proximal leaves) or sessile (distal leaves). The ocrea is persistent or deciduous, chartaceous, with the petiole base articulated. The blade is cordate, triangular, hastate, or sagittate, with the margins entire to sinuate. Pedicels present. Inflorescences are axillary, or terminal and axillary, raceme- or panicle-like, pedunculate. Flowers are bisexual or, rarely, bisexual and staminate on the same plant, 2-6 per ocreate fascicle, heterostylous or homostylous, base stipe-like. The perianth is nonaccrescent, white, pale pink, or green, broadly campanulate, glabrous; The tepals are 5, distinct, petaloid, dimorphic, with the outer ones smaller than the inner ones. Stamens are 8, with distinct, free and glabrous filaments. The anthers are white, pink, or red, oval to elliptic. The 3 styles are reflexed, distinct, with the stigmas capitate. The achenes are strongly exserted, brown to dark brown or gray, sometimes mottled black, unwinged or essentially so, bluntly to sharply 3-gonous, glabrous. Seeds: embryo folded, $x = 8$.

Knowledge was obscure on the genetic relationships among species within the genus *Fagopyrum* until the 1980s. Perennial buckwheat [*F. cymosum* (Trev.) Meisn] was considered for long to be the putative wild ancestor of common buckwheat (Campbell 1976; Nagatomo 1984 cited in Ohnishi 1990). Research conducted during the past 20 years, coupled with the discovery of several new species, has provided new data on the origin, geographical distribution and the level of speciation, and has also revealed great part of the species relationships. Earlier phylogenetic studies were using morphological characters and isozyme markers. The development of the currently used, DNA-based molecular markers has provided a highly efficient tool to examine genetic relationships within the genus.

Common buckwheat (*Fagopyrum esculentum* Moench) is a heterostylous diploid species with an indeterminate growth habit. It is an annual broadleaved plant, with a smooth, succulent stalk, a knotted single main stem that develops lateral branches (Fig. 1). Generally, in a field population the plants only develop primary branches. The main stem is grooved, generally green, but sometimes tinged with red. Plant height varies from 30 to as much as 120 cm or more. The stems are more or less round and hollow, with a diameter of 3 to 15 mm. At the time of maturity the stems and branches turn red. The plants have a short taproot, penetrating to a depth of 30 to 50 cm in the soil, with fine lateral roots spreading to a width of 25 to 30 cm. Root architectural characteristics give buckwheat a relatively shallow rooting habit. The leaves are petiolate, positioned alternately on the opposite sides of the stem, heart shaped, ovate-triangular to triangular, 4 to 8 cm long. The blades are glabrous (hairless) (Flora of North America 5.1; Campbell 1997; Lazányi 1999; Gocs 2002; Jansen 2006).

The flowers grow terminal, densely clustered in



Fig. 1 A stand of buckwheat (*F. esculentum* Moench, cv. 'Hajnalka') near Nagykálló (North East Hungary) in 2008. (Source: I. Gondola)



Fig. 2 Flowers of common buckwheat (*F. esculentum* Moench, cv. 'Hajnalka') near Nagykálló (North East Hungary) in 2008. (Source: I. Gondola)

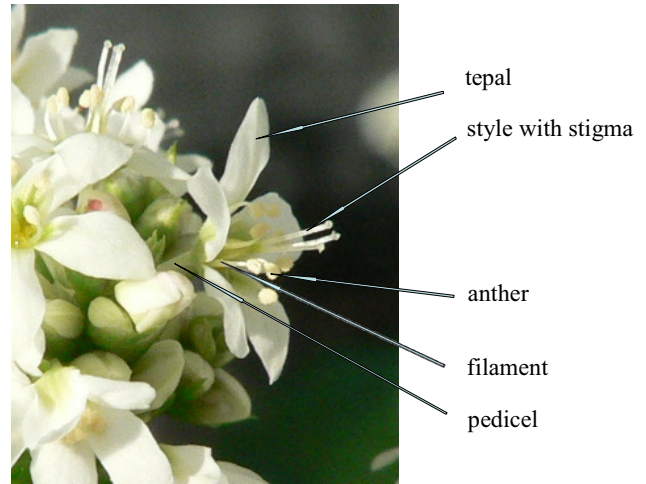


Fig. 3 Structure of pin type flower of common buckwheat (*Fagopyrum esculentum* Moench.). (Source: I. Gondola)

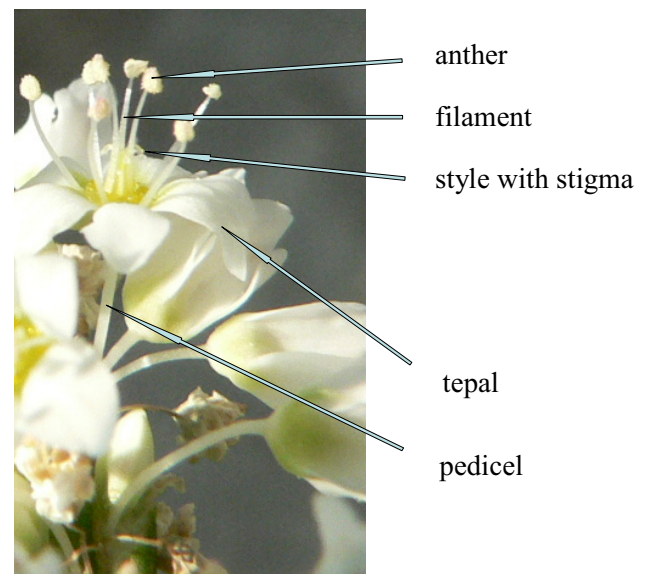


Fig. 4 Structure of thrum type flower of common buckwheat (*Fagopyrum esculentum* Moench.). (Source: I. Gondola)

racemes, light fresh in colour, and perfumed (Fig. 2). The sepals are usually white, pink or dark pink. Flowers are hermaphroditic and heteromorphic, i.e. two types of flowers are produced on separate plants (Campbell 1997).

"The existence of variation in floral structure within the same species was detected by several authors, but it was not until the publication of Hildebrand's studies in 1867 and a subsequent publication of Darwin's observations in 1877 (see Vuilleumier 1967 for review and detailed references) that a casual relation between floral variations and the prevention of self-fertilization was fully appreciated" (Frankel and Galun 1977).

In *Fagopyrum*, the heteromorphic flower morphology is associated with self-incompatibility, with the exception of three species, namely *F. pleioramosum*, *F. macrocarpum* and *F. callianthum*, which are heterostylous and self-compatible (Ohsako and Ohnishi 2000). "Heteromorphic incompatibility was reported in several ornamental plants, and is very rare in economic crops" (Frankel and Galun 1977). In buckwheat, heteromorphism is manifested in styler length and therefore the term heterostyly is preferred to heteromorphism. Common buckwheat, a distylous species, is composed of two types of plants. The pin flower has long styles with short stamens, whereas the thrum flower is of the opposite arrangement (Campbell 1997). The floral structure for the pin type is shown in Fig. 3 and for the thrum type is shown in Fig. 4. Heteromorphic incompatibility renders both self-pollination and intramorph (illegitimate) cross-



Fig. 5 Ripening fruits of common buckwheat (*F. esculentum* Moench, cv. 'Hajnalka') near Nagykálló (North East Hungary) in 2008. (Source: I. Gondola)

pollination infertile (Frankel and Galun 1977). Fertilization can only take place between pin and thrum types of flowers.

This complex of floral mechanism is governed by a single locus which also regulates the incompatibility rela-

tion (Bodmer 1966; Frankel and Galun 1977). The inability of selfing is explained with pollen incompatibility between the two types rather than with the heterostylic architecture of the flowers (de Nettancourt 1977; Wang *et al.* 2005b). Two sizes of pollen are associated with the heteromorphic system in common buckwheat. Large pollen grains approximately 0.16 mm in diameter are produced by thrum flowers while pin flowers produce smaller pollen grains that are approximately 0.10 mm in diameter (Campbell 1997). Hirose *et al.* (1994) reported that pollen tube in intramorphic pollination in heterostylous *Fagopyrum* species was inhibited at the stigma or style, and was shorter than that in intermorphic pollination within the same species.

Heterostyly has sporadically evolved in various phylogenetic taxa. It can be hypothesized that the genus *Fagopyrum* is entirely heterostylous. The non-heterostylous species (*F. tataricum* and *F. gracilipes*) might have arisen from the heterostylous species by the loss of heterostyly and simultaneous development of self-fertilizing mechanisms (Ohnishi 1989).

Due to heterostyly and open pollination by insects, seed set is generally low in common buckwheat. Buckwheat flower is very attractive to bees that use the nectar to produce a specially flavoured, dark honey (Campbell 1997).

The nut (so-called 'seed') has a dark brown, tough rind, enclosing the kernel or seed, and is three-sided in form, with sharp angles (Fig. 5).

As for the ploidy level, common buckwheat is a diploid plant with a chromosome number of $2n = 2x = 16$ (Darlington and Janaki Ammal 1945).

Buckwheat is a multi-purpose crop, for nearly all parts of the plant are used in a large variety of ways. The leaf provides rutin (vitamin-P), a pharmaceutical product. As a rutin – containing plant buckwheat, also named *Fagopyri herba*, has traditionally been used to brew tea to treat hypertension. The flower produces nectar for honey-bees. Buckwheat has many uses in cooking. The dehulled grains are eaten boiled. Flour can be made from the grain either entire or dehulled. The flour is prepared in various ways to make bread, pancakes and other traditional foods as well as special diets. Beer is brewed from the grain, and the grain is also distilled into spirits. Buckwheat hulls are used as filling for a variety of upholstered goods, including pillows. The straw makes good livestock feed. As a fast growing plant, buckwheat also makes good green manure even in cases when the gap period between two main crops is short (Edwardson 1996; Ihme *et al.* 1996; Campbell 1997; Jansen 2006; Brunori and Végvári 2007; Christa and Soral-Smietana 2008).

Buckwheat is neglected and underutilized at present, both as a nutritious food and as a viable alternative crop plant, particularly in the developed countries (Campbell 1997). In contrast with the important cereal crop species, only little crop improvement efforts have been focused on buckwheat during the past few decades. Today buckwheat is still mostly grown as a primitive crop, in a similar way it

was grown hundreds of years ago, with yield levels practically unchanged.

Some of the problems that are frequently encountered in the production of common buckwheat can only be solved with genetic improvement. Examples of these are:

- lack of frost tolerance (Kalinová and Moudry 2003; Jansen 2006),
- shattering of seeds (Campbell 1997; Wang *et al.* 2005a)
- lack of resistance to lodging (Campbell 1997; Jansen 2006),
- indeterminate growth habit (Ohnishi 1993c; Kreft 1998),
- low rate of seed-set (in cross-pollinated flowers). Lack of fertilization was the major cause of low seed set, rather than abortion of the embryo, in the study of Taylor and Obendorf (2001).

Because of open pollination, populations of common buckwheat are highly heterozygous and heterogeneous. Finding recessive genes for certain valuable traits (e.g. determinate growth) is a general objective of buckwheat breeders. Selection for these traits is difficult, because recessive genes are often hidden by out-crossing and are covered by dominant alleles (Kreft *et al.* 2007).

Genetic improvement of buckwheat is treated in detail in the comprehensive work by Campbell (1997).

The transfer of the self-pollinating mechanism to common buckwheat would be of particular importance, since this would reduce dependence on insect pollination, allow for increased rate of seedset which, in turn, might result in higher yields. Successful attempts have been made through hybridizing with the closely related wild species *F. homotropicum* at the diploid level.

The single gene complex that controls self-incompatibility and flower morphology segregates as a simple Mendelian factor, with two allelic states, *S* and *s*, which control the thrum (*Ss*) and the pin (*ss*) forms (Garber and Quinsberry 1927; Matsui *et al.* 2003). The pattern of segregation is shown in Fig. 6.

Matsui *et al.* (2003) reported that Sharma and Boyes (1961) regarded this gene as the *S* supergene proposed for *Primula* (Dowrick 1956). They postulated that the *S* supergene of buckwheat consists of five genes: *G*, style length; *I^S*, stylar incompatibility; *I^P*, pollen incompatibility; *P*, pollen size; *A*, anther height. Pin has small pollen and thrum has larger pollen. Pin-linked characters are recessive, and thrum-linked characters are dominant. The genotype of pin is *gi^Si^Ppa/gi^si^ppa*, and that for thrum is *GI^SI^PPA/gi^si^ppa*.

Self-compatible buckwheat lines were produced by an interspecific cross between *F. esculentum* and a closely related self-fertile, homostylous wild relative, *F. homotropicum* with embryo rescue (Campbell 1995; Aii *et al.* 1998; Woo *et al.* 1999; Matsui *et al.* 2003). The flower morphology of the self-compatible lines is long homostyle and is controlled by a single gene. The allele controlling homomorphic flowers was designated as *S^h*, and the dominance relationship of *S^h* with *S* and *s* was found to be $S > S^h > s$ (Woo *et al.* 1999). The *S^h* allele was produced by recomb-

X		gametes of the thrum parent	
		<i>S</i>	<i>s</i>
gametes of the pin parent	<i>s</i>	<i>Ss</i>	<i>ss</i>
	<i>S</i>	<i>Ss</i>	<i>ss</i>

genotypes and relative frequencies of the progeny

Fig. 6 Mendelian segregation of the single gene complex that controls self-incompatibility and heterostylous flower morphology in common buckwheat (*Fagopyrum esculentum* Moench). (Source: I. Gondola)

nation between i^S and i^P in the supergene. By studying segregation in the F_2 and BC generations, it was suggested that the self-compatible line possesses the pin type of stylar incompatibility, and thrum type of pollen incompatibility genes (Matsui *et al.* 2003). The self-compatible, long homostylous genotype was suggested to be $gi^S i^P PA/gi^S i^P PA$ ($S^h S^h$).

Wang *et al.* (2005b) proposed that homostyly and self-compatibility is controlled by a two-gene model in *F. homotropicum* and in the segregating progenies derived from interspecific crosses between *F. homotropicum* and *F. esculentum*.

ORIGIN AND DISTRIBUTION OF COMMON BUCKWHEAT AND RELATED SPECIES

Centre of origin

According to scientific evidence, the geographical areas where the ancestors of the presently cultivated plants once developed are, in many cases, located in the sunlit, dry (arid or semi-arid) table-lands and highlands of mountain ranges. The same holds true for buckwheat. There is a general consensus now among scientists that buckwheat is native to temperate East Asia, more specifically to the eastern side of the Himalayas and South-West China (Campbell 1997; Krefth 1998). The exact place of origin has been identified as Yunnan province and the mountain area between Yunnan and Sichuan provinces (Ohnishi 1995).

Vavilov, in his worldwide geographical survey, listed several centres of diversity (centres of origin), as sources of genetic variation, each characteristic of a certain group of domesticated crop plants (Vavilov 1926). Most of them are located between 20 and 40° north latitude in Eurasia. China is one of the eight centres of origin proposed by Vavilov, in fact the largest one, as regards the number of species listed.

It was found later “that some species can indeed be said to have had a single and sudden origin localised and capable of being located. With others, however, the origin is not origin at all but a gradual transformation extending over wide areas and long periods and shifting its focus in the course of time. Between the two extremes there is every gradation” (Darlington and Janaki Ammal 1945).

Research results obtained during the past two decades on the centre of origin of buckwheat, highlight Yunnan province of south-west China as a diversity hotspot for this crop plant. This is the place where the highest diversity of endemic wild relatives of common buckwheat can be found today. Several species of the genus *Fagopyrum* can be found here forming a large pool of genetic diversity (Li and Yang 1992; Ohnishi 1995). The region is dominated by rugged mountainous topography, climatic variability and a biologically diversified ecosystem (Chen and Dao 2001).

Beside south-west China, common buckwheat is also widely cultivated in mountainous regions of temperate Asia in Nepal, India, China, and also in Japan and Korea. It is also cultivated in the regions with cooler climate such as northern China. Cultivation of common buckwheat dates back to the Jomon era (1000 BCE) in Japan, several hundred years BCE in northern China and more than 2000 years in eastern Tibet (Ohnishi 1985; Murai and Ohnishi 1995). The spread of buckwheat cultivation to European countries is rather recent (Campbell 1976; Ohnishi 1985, 1989).

Tartary buckwheat (*F. tataricum*), a homostylous, self fertilizing diploid species, with cleistogamous flowers (pollination occurs before the flowers open), is the other domesticated food plant in the genus. Since this species carries a relatively high level of frost-tolerance, it is cultivated most extensively in the Himalayan region of India, Nepal and Bhutan, particularly in the areas of high altitude, 2000 m above sea level and higher. It is one of the most important crops in these areas. Cultivation of tartary buckwheat is also of importance in southern China. In other places it is only occasionally cultivated. In many cases it is a weed in buckwheat fields (Ohnishi 1989).

A case study on Yunnan, South West China in 2001 (Chen and Dao 2001), listed nine wild species of *Fagopyrum* as endemic to this province, each species given a vernacular name: golden *Fagopyrum* (*F. cymosum*), rock *Fagopyrum* (*F. gilesii*), thin cauli wild *Fagopyrum* (*F. gracilipes*), tooth-alar wild *Fagopyrum* (*F. gracilipes* var. *odontopterum*), small wild *Fagopyrum* (*F. leptopodum*), sparse stachys small *Fagopyrum* (*F. leptopodum* var. *grossii*), linear leaf wild *Fagopyrum* (*F. lineare*), bolting *Fagopyrum* (*F. stative*) and hard twig ten thousand-year *Fagopyrum* (*F. urophyllum*).

The centres of origin can also be defined as the region where domestication of the particular plant first took place and where the wild ancestor and the derived cultivated species co-exist (De Candolle 1883; Molina-Cano *et al.* 1999).

Archaeological data and written historical records indicate that buckwheat was extensively cultivated and used as a staple food by ancient Chinese as early as the 5th-3rd centuries BC and thereafter (Li and Yang 1992), thus ancient Chinese were the earliest nation to discover and utilize buckwheat. Not only was buckwheat cultivated, but it was highly appreciated as a crop that contributed to overcome famine and disaster. The health protecting abilities of foods made of buckwheat were first recognized and documented around 600 CE. According to Li and Yang (1992), Yunnan province possesses 11 species of the genus, nearly three-quarters of the total of 15 species known in the early 1990's. These are:

1. Sweet (common) buckwheat (*F. esculentum* Moench 1794)
2. Bitter buckwheat (*F. tataricum* Linn. ((Gaertner)) 1791)
3. *F. cymosum* (Trev) Meisn. 1832
4. *F. gilesii* (Hemsley) Hedberg 1946
5. *F. gracilipes* (Hemsley) Dammer ex Diels (1918)
6. *F. leptopodum* (Diels) Hedberg (1944)
7. *F. grossii* (Levl) H. Gross 1913 (Variant)
8. *F. odontopterum* Gross 1913 (Variant)
9. *F. lineare* (Samuelss) Haraldson 1978
10. *F. stative* (Levl) H. Gross 1913
11. *F. urophyllum* (Bur. et Franch) H. Gross 1913.

Shapes of root systems for wild buckweats can be classified into perennial globular or tuber root, and annual fibrous root. The cultivated species only develop fibrous root. Beside the occurrence of wild species in Yunnan, a great variability also exists among accessions of cultivated common buckwheat in morphological traits like colour and architecture of flowers, fruit shape, fruit coat colour, and length of growing period (Li and Yang 1992; Chen and Dao 2001).

The authors conclude that the typical evolutionary trend can be clearly detected based on shapes of Yunnan buckwheat: perennial wild species → annual wild species → annual cultivated species.

Cultivation of buckwheat was step by step spreading from the place of origin to other parts of the world: to South East Asia, India, Minor Asia in the 8th century, to Siberia and Russia in the 13th century, to Europe in the 15th century, to the Americas in the 17th century, and later to Africa (Li and Yang 1992). An important part of the spread might have occurred via transmission on the silk-road.

Despite that common buckwheat has been cultivated since ancient times in several Asian countries including China, Korea and Japan, the place of origin and the process of expansion of cultivation remained obscure for long.

Buckwheat was thought for a long time to have its origin in northern China or the area of the river Amur (De Candolle 1883; Ohnishi 1993b). In the late 19th century and in the first half of the 20th century, the discovery of a large number of wild relatives of common buckwheat by several investigators in southern China suggested that the theory of De Candolle on buckwheat's origin in northern China or the area of the river Amur was false (Bretschneider 1898; Gross 1913; Steward 1930; Ohnishi 1990).

All the written evidence we now have (geographical distribution of *Fagopyrum* species, allozyme variability

between southern China and the Himalayan region) suggest that both common and tartary buckwheat were born in southern China, and diffused westward along the southern slopes of the Himalayas together with two wild species also born in southern China (Ohnishi 1992). One of them is tetraploid perennial buckwheat (*F. cymosum* Meissn.) that grows wild in temperate Himalayas and is commonly found around habitation areas and farms. It is utilized in certain regions as forage and also as a medicinal plant. This species extends its distribution southward to the northern part of the Indochinese Peninsula, southern part of China, and westward to the Himalayan region of Nepal and India as far as Karakoram and the Hindukush. It is also found in eastern parts of Tibet (Ohnishi 1993a). The flowering pattern resembles that of *F. esculentum* in that both are heterostylous outcrossing species and produce pin and thrum plants with white flowers. *F. cymosum* is, however, cytologically and morphologically distinct and stands out as a separate taxon (Tahir and Farooq 1989). The other wild species born in southern China is *F. gracilipes* Hemsl., a self-fertilizing tetraploid weedy plant in farmer's fields. It is distributed widely, covers almost the whole of China, except Tibet. Bhutan is the western limit of its distribution. This species is the most successful colonizer, and has the widest distribution in China among *Fagopyrum* species (Ohnishi 1992). Most of the other wild *Fagopyrum* species have a narrow endemic distribution in southern China.

An overview of buckwheat production and genetic diversity of *Fagopyrum* species in the Himalayan region is given by Arora *et al.* (1995). The region includes the mountain ranges of Pakistan, India, Nepal and Bhutan. The area is very diverse in topography, climate and agro-ecology. Cultivation of buckwheat provides here a security for the traditional subsistence farmers. Diverse ethnic communities grow this crop for grain and as a leafy vegetable, besides using it as animal feed and as a medicine. The crop is well adapted to marginal lands and harsh environments and is cultivated under low input conditions. Common buckwheat and tartary buckwheat are grown under diverse cropping patterns and cultural practices in different seasons, depending on the climate and particularly the altitude. While common buckwheat is adapted to both lowlands and uplands and grows between 400-4200 m, tartary buckwheat is not grown in plains, and is confined to mid-hills and high-hills. Companion crops on higher elevations are barley, wheat, potato, amaranth, foxtail millet, proso millet and *Brassicaceae*. Rice, soybean, finger millet and maize are the rotating crops in the low hills and in the intermediate zone. Also, because of vertical crop zonation related to altitude, common buckwheat is grown as a winter crop in plains, while tartary buckwheat is grown as a spring crop in mid-hills. Several hundreds of known landraces make a large diversity of the cultivated species, common buckwheat and tartary buckwheat. They are maintained, characterised and evaluated in germplasm collections using some 30 descriptors, supported by international and national programs for the conservation of plant genetic resources. Part of the landraces is utilized in cultivation by native farmers and also in crop improvement programs by scientists. The Himalayan region is rich in genetic resources. Beside the two cultivated species that have been grown here since the distant past, numerous wild species also contribute to the gene pool of *Fagopyrum* in the region. These are *F. cymosum*, *F. gracilipes* and *F. megacarpum*, which are mainly perennial, late maturing and indeterminate types. In contrast with earlier knowledge (Steward 1930) *F. gilesii* cannot be found in the region of the northwestern Himalayas, it can only be found in Yunnan province and eastern Tibet (Ohnishi 2001).

Diffusion routes on the studies of allozyme variability

The diffusion routes of cultivated common buckwheat in Eurasia were followed by studying allozyme variability as a marker. The amount of allozyme variability in Korean,

Japanese and European populations was revealed to be less than the average of the annual plant species (Hamrick 1979; Gottlieb 1981), and this was particularly true for the European populations (Ohnishi 1983, 1985). Since buckwheat is a completely outcrossing species due to heterostyly, and the usual population size is large, more than 10^4 - 10^6 , we can expect a large amount of genetic variability in populations. Therefore, there must be an explanation for the low allozyme variability i.e. the loss of genetic variability in buckwheat populations in Japan and Europe. A possible reason is that populations in these regions may be considered to be marginal populations that have lost several variant alleles during the spread of cultivation to these regions.

European common buckwheat populations came from northern China long ago, based on allozyme analysis (Ohnishi 1986, 1993c). According to archaeological evidence (Li and Yang 1992), buckwheat cultivation diffused to Europe almost immediately after its spread from the place of birth in Yunnan province to northern China (2nd-1st centuries BCE), but cultivation only became popular in the Middle Ages, in the 14th and 15th centuries and afterwards. Buckwheat was first cultivated in Russia, Ukraine and Germany, and from here it diffused southwards to the Mediterranean region and further to the western part of Europe (Ohnishi 1993c).

Within Europe, allozyme studies show greater genetic variability among samples from the northern regions (Russia, Poland, Hungary, Finland) than among samples from southern regions (Ohnishi 1993c). Further, a new morphological variant is present in samples of southern European landraces, grey buckwheat with a grey husk rather than the usual brown husk. This variant is not present in the samples of the silk-road. Another variant allele frequently found in southern Europe is the determinant inflorescence gene. This is a recessive gene also present in some Russian varieties, but apparently its frequency is much higher in southern Europe (Ohnishi 1993c).

Similar increase or decrease of allozyme frequency was observed by Ohnishi (1993c) at other loci of southern European populations, and also in populations from Kashmir, India. As postulated by Ohnishi (1993c), the changes in genetic frequencies in these cases are probably due to random genetic drift during the course of diffusion, rather than the systematic selection against particular alleles. Both the western parts of India and southern Europe contain marginal buckwheat populations, i.e. populations that are the closest to the geographical terminus of the diffusion route. In these populations random events such as founder and bottleneck effects might have taken place more frequently than elsewhere. Such events are less likely to occur in other areas, where migration pressure from adjacent areas is strong enough to annihilate local differentiation of allele frequencies. The same reasoning can be applied to explain the relatively low average heterozygosity and low percentage of polymorphic loci in European populations, as found by Ohnishi (1993c).

Calculation of genetic distance in these studies with the use of allele frequencies between populations revealed that European populations are most closely related to the populations of the silk-road and to the Chinese populations and least related to the Kashmirian populations. The silk-road populations, again, have almost the same genetic constitution as Chinese populations. It follows from this, that European common buckwheat came from northern China through the silk road in very ancient times (1st or 2nd century or earlier). The introduction might have been repeated later, possibly also introducing tartary buckwheat as a weed, but the buckwheat from the Himalayan region has never been introduced into Europe. Migration pressure between the silk-road and northern China is still acting, but European populations are isolated geographically from Asian populations because the geographical gap between the Silk Road and Europe is great. After the introduction to Europe, local populations have changed considerably within a relatively short period, i.e. the last 500 years (Ohnishi 1993c).

In the light of the above, there should be more allozyme variability within populations in southern China and the Himalayan region, which are closer to, or are in fact, the centre of origin.

The gene frequencies at polymorphic loci did not vary so much among the 15 Nepali populations but they were quite different from those in the two Kashmirian (Indian) populations studied (Ohnishi 1985). There was no distinct local differentiation in allozyme frequency among the populations in Nepal, and the Nepali populations maintained as much allozyme variability as other outcrossing annual plant species. The two Kashmirian populations had almost the same genetic constitution, however, they showed several distinct characters from the Nepali populations. They were monomorphic at loci for which the Nepali populations were polymorphic. The average genetic distance between the Kashmirian populations and the Nepali populations was 0.0043, compared with genetic distance between the two Kashmirian populations of 0.00011, and the average of the distances between any two of the Nepali populations of 0.00098. The Kashmirian populations seem to have lost variation at certain loci (ADH, 6-PGDH-1, PGM-2) probably during the spread of the cultivation in this area. It seems reasonable to consider that Kashmirian common buckwheat came from the Nepali Himalayan region and lost variability at certain loci during the spreading process. The reason for the loss of variability is not clear, but accidental losses by random drift including the founder principle may be more likely than the loss by any selective pressure on the alleles involved. No attempt to improve buckwheat has ever been made in this region, and farmers grow buckwheat from the seeds they harvested the previous season. Thus, according to Ohnishi (1985), the low level of allozyme variability in Kashmirian populations may be interpreted by the loss of genetic variability during the spread of cultivation.

The area of Karakoram and Hindukush (northern Pakistan) is the western terminus of buckwheat cultivation along the diffusion route south of the Himalayas (Ohnishi 1994). Both common and tartary buckweats are cultivated here. Agricultural activity is limited to the valleys of the river Indus, river Kunar and their tributaries. In most of these valleys the climate allows two crops a year while at higher elevations only one crop is possible. Buckweats are cultivated as summer crops, after either barley or wheat as winter crop, in the belt just below the one crop zone. Allozyme variability showed long genetic distance between the Pakistan and Tibetan populations of common buckwheat. At the same time, no drastic changes in gene frequency were observed in Karakoram, which is in contrast with the expectations of marginal populations. The lack of differentiation at isozyme loci can be explained by the large population size hence the stable genetic constitution in populations of Karakoram (Ohnishi 1994). As for tartary buckwheat, there are three distinct groups found in northern Pakistan. These are, as listed by Ohnishi (1994), the cultivated, the wild and the weedy forms of tartary buckwheat. Cultivated tartary mainly diffused along the southern hills of the Himalayas, while the natural populations of the wild tartary (*F. tataricum* ssp. *potanini* Batalin) diffused from its original birthplace, Sichuan province of China, to eastern Tibet then to the Yalutsangpu river valley in Tibet (Ohnishi 1993a). If this is true, the wild tartary buckwheat in Karakoram and Hindukush must have come from Tibet, probably via Ladakh, through the old trading routes. As regards the weedy tartary, it has never been reported anywhere else. This form has wild characters such as shattering habit and strong dormancy, yet morphologically similar to cultivated tartary buckwheat. It is hypothesized by Ohnishi (1994) that the weedy form originated from the hybridization of the wild form and the cultivated form in northern Pakistan after the two forms had come here from the common place of birth in different routes of diffusion.

The same author reported he was unable to find the wild species perennial buckwheat (*F. cymosum*) in Karakoram and Hindukush, probably because the climate, and particu-

larly the dry land does not allow the distribution of *F. cymosum* in this area.

A worldwide survey was conducted on allozyme variability in common buckwheat in the hope to find, as Vavilov proposed, a centre of allozyme diversity which might represent the original place of domestication of this crop (Ohnishi 1993b). By comparing allozyme variability in cultivated populations from different parts of the world, the author gave a clue to understand the genetic processes of domestication and subsequent diffusions of buckwheat to remote geographical areas. The following conclusions were drawn from the survey.

- At all loci, allele frequency does not vary much among the populations from a wide range of Asian countries, from Japan through Nepal. The large population size and the complete panmixis of each population by insect pollination may have led to the uniformity of gene frequency among cultivated populations over wide areas in Asia, along with enough migration among populations (migration pressure nullifies the local differentiation of cultivated populations).
- Cultivated buckwheat has much more genetic variability based on allozyme studies, than the natural populations of the wild ancestor species (*F. esculentum* ssp. *ancestrale* Ohnishi), with both average heterozygosity and average number of alleles per locus being higher. In this study, average heterozygosity was found = 0.15, and 50% of the loci were polymorphic in common buckwheat, compared to values of 0.1 and 26% for the wild ancestor, respectively. Since the two species are intercrossable, allozyme variants in wild populations of the ancestral species may have contributed to the high level of variability in cultivated populations, partially explaining the above observation. Further, the large population size together with the outcrossing breeding system may also have played a role. The case is the opposite for tartary buckwheat, a self-fertilizing species, with wild populations being genetically more variable than the cultivated populations. Apparently, population size is of less importance in case of an inbreeding species.
- Most of the evolutionary events which might have taken place during the spread of buckwheat cultivation are the losses of variant alleles probably by random genetic drift, including founder effects. These events are more likely to occur in marginal populations with relatively small population size, as it is frequently the case when colonizing to new areas. Drastic changes in allele frequency, including losses, have only been observed in marginal populations that is Kumaun, Garwhal hills and Kashmir in India and in southern Europe.

The final conclusion drawn by Ohnishi (1993b) is that the high genetic variability over wide geographical areas will not make Vavilov's theory applicable to buckwheat. Vavilov suggested a close relationship between the original place of domestication and geographical genetic variability. This principle does not hold on buckwheat, mainly because of its botanical nature, and the outcrossing breeding system. As pointed out earlier by Hutchinson (1965 in Ohnishi 1993b) "It now appears that the classical Vavilov type of distribution of variability in a crop plant, with a progressive decline in diversity from centre of origin to periphery, is associated with the development of self-pollination." Buckwheat, a complete outcrossing species, became widely dispersed without any local differentiation due to strong migration pressure between populations and between distinct regions. Buckwheat is a monocentric crop in the sense that it has a definable centre of origin and wide dispersal, without a secondary centre. In another sense, however, it is a non-centric crop because it has a pattern of variation that suggests domestication over a wide geographical area. This theory is supported by the fact that there is no archaeological evidence of buckwheat cultivation at the original birthplace in Yunnan.

The case of buckwheat contradicts to Vavilov's theory:

centre of origin \neq centre of diversity \neq centre of domestication.

Diffusion routes on the studies of DNA-based markers

DNA-based molecular markers have been used to reveal diffusion routes of buckwheat cultivation in Asia, and the results are in accordance with those of earlier studies on allozymes. RAPD markers among 29 landraces from Asia were compared in order to clarify major routes of diffusion of buckwheat cultivation (Murai and Ohnishi 1995). The results, a dendrogram written by the unweighted pair group (UPG) method and the neighbour joining (NJ) method, clearly indicated that cultivated common buckwheat diffused to two major directions. One major route is southern China \rightarrow northern China \rightarrow Korean peninsula \rightarrow Japan. The other major direction is the Himalaya region, mainly through the southern slopes of the Great Himalayas, with the exact route of southern China \rightarrow Bhutan \rightarrow Nepal \rightarrow Kashmir \rightarrow Karakoram, Hindukush. As expected, the amount of RAPD marker variability sharply decreased as the cultivation of buckwheat diffused from the centre of origin to peripheral parts of the distribution. This shows that the total amount of variability maintained in each population decreased as the diffusion of cultivated buckwheat progressed. This finding is not in contradiction with the high genetic variability over wide geographical areas observed in Asian populations.

ORIGINAL BIRTHPLACE OF CULTIVATED COMMON BUCKWHEAT

The theory that *F. cymosum* is the putative ancestor of common buckwheat was holding until quite recently (Campbell 1976). In 1990 a new, unfamiliar wild buckwheat species was found in Yongsheng-xiang of Yunnan province (Ohnishi 1990). It was very closely related to common buckwheat, and it was identified, based on its morphology, as the wild ancestor of *F. esculentum*. The newly discovered species was growing in the wild on rocky cliffs and on roadsides.

The ancestral species differs from common buckwheat in having a fragility of premature seeds, strong seed dormancy, longer growth period and branching at lower nodes. In other respects the two species are similar and are intercrossable. This discovery, combined with the observation of the richest distribution of wild *Fagopyrum* species in southern China, indicates that the birthplace of cultivated common buckwheat is southern China, probably Yunnan province. This finding is in accordance with earlier isozymes analysis by Ohnishi (1983, 1990). It had been pointed out that *F. cymosum* is only distantly related to either *F. esculentum* or *F. tataricum*. Allozyme studies also pointed out, that there is a high level of allozyme variability in any cultivated population of common buckwheat (Ohnishi 1988, 1990). This finding supports the idea that common buckwheat has never suffered from a bottleneck effect during its domestication. The improvement of common buckwheat from the wild ancestor was probably an evolutionary process, since most of the allozymes present in *F. esculentum* are also present in the ancestor species. The wild ancestor of cultivated buckwheat (*F. esculentum* ssp. *ancestrale* Ohnishi) was classified as subspecies of the cultivated species (*F. esculentum* ssp. *esculentum* Moench) because they differ only in dormancy and shattering habit as key distinguishing characters (Ohnishi and Matsuoka 1996).

The discovery of the wild ancestor (*F. esculentum* ssp. *ancestrale* Ohnishi) of common buckwheat provided the first scientific evidence of the probable birthplace of common buckwheat (*F. esculentum* ssp. *esculentum* Moench). A conclusive evidence for a wild species to be the ancestor of a crop species is based on morphological, cytological and genetic comparisons and on the study of crossability (Konishi *et al.* 2005).

According to earlier studies, the wild subspecies (*F.*

esculentum ssp. *ancestrale* Ohnishi) is the most closely related to cultivated common buckwheat among the presently discovered wild *Fagopyrum* species, as regards morphology, allozyme variability and RFLP of cpDNA (Ohnishi and Matsuoka 1996), and the nucleotide sequence of the *rbcl-accD* region of cpDNA and the ITS region of nuclear rRNA gene (Yasui and Ohnishi 1998a, 1998b). Also this wild subspecies is able to cross with the cultivated subspecies and produces fertile hybrids (Ohnishi 1999; Konishi *et al.* 2005). Perennial buckwheat (*F. cymosum* Meisn.) has now been shown to be only distantly related to common buckwheat (Kishima *et al.* 1995; Ohnishi and Matsuoka 1996; Yasui and Ohnishi 1998a, 1998b). The cross between *F. cymosum* and *F. esculentum* was quite difficult to accomplish (Woo *et al.* 1999).

The wild ancestor having been identified, the question to be answered is which part of the distribution area is the original birthplace of cultivated common buckwheat. Recurrent expeditions revealed that natural populations of the wild ancestor of common buckwheat can also be found in the Three Rivers Area (Ohnishi 1998a, 1998b; Tsui *et al.* 1999; Konishi and Ohnishi 2001; Ohnishi 2001). The Three Rivers Area (San Jiang Area) of southern China is bordering the provinces of Yunnan and Sichuan and also eastern Tibet (Ohnishi 2004). Populations of the wild ancestor were found here on mountain slopes, along big rivers, and deep in mountain areas, however the climate here is rather hot and less humid. The "San Jiang (Three Rivers) area" is a key area for the study on the origin of cultivated common buckwheat (Ohnishi 2004).

AFLP analysis was performed to reveal genetic relationships among cultivated populations of the crop species *F. esculentum* ssp. *esculentum* and natural populations of the wild ancestor subspecies *F. esculentum* ssp. *ancestrale* in order to locate the original birthplace within the distribution area (Konishi *et al.* 2005). A phylogenetic tree was constructed by the neighbour-joining method based on genetic distance estimated from the gene frequencies. The natural populations of the ancestral subspecies from the San Jiang area were more closely related to cultivated populations than natural populations from other regions including populations from Yunnan and Sichuan. As for the AFLP variations within a population, both cultivated and natural populations have retained high level of diversity. On average, 78.8% of the detected loci were polymorphic with average heterozygosity (H) of 0.293 for the cultivated populations. The corresponding values for the natural wild populations were 0.921 and 0.349, respectively. The approximately equal amount of genetic variations in cultivated and natural populations agrees well with the results on allozyme variations (Ohnishi 1998b). It may be inferred again that common buckwheat might not have suffered from strong bottleneck effect during the domestication process. It can be concluded from the study, that natural populations of wild common buckwheat from the San Jiang river area are the most closely related to cultivated common buckwheat, hence they are the strong candidate of the direct wild ancestral population. This leads to an assertion that the original birthplace of cultivated common buckwheat is the San Jiang river area.

This finding of Konishi *et al.* (2005) was confirmed by Ohnishi (2007), who surveyed 11 natural populations of the wild ancestor (*F. esculentum* ssp. *ancestrale* Ohnishi) from various parts of Yunnan, Sichuan and Tibet for their allozyme variations at 19 loci, together with 12 cultivated populations of common buckwheat from the "San Jiang (Three Rivers) area". In this study again, the natural populations from the "San Jiang" area were most closely related with the cultivated populations. This study allows us to get closer to the putative birthplace of the wild ancestor itself within this area. Among the populations surveyed, the Dongyi and Yiji populations had the highest allozyme variations for this subspecies. "Since diploid *F. cymosum*, the putative ancestor of the wild ancestor of common buckwheat (Yamane *et al.* 2003), grows in the Dongyi river valley, we may con-

sider that the Dongyi river valley is the center of genetic diversity of the wild ancestor, and the valley is probably the original birthplace of the wild ancestor itself" (Ohnishi 2007).

WILD FAGOPYRUM SPECIES

Classification of *Fagopyrum* species has been modified several times by the discovery of new species. In the 1980s there were only seven wild species known, beside the two cultivated species, in the genus *Fagopyrum*. With the discovery of several new species in southern China, the number of known wild species increased to about fifteen in the 1990s, as summarized by Ohnishi (1995, 2001). The newly discovered species were *F. capillatum* Ohnishi, *F. callianthum* Ohnishi, *F. pleioramosum* Ohnishi and *F. homotropicum* Ohnishi, as well as the subspecies *F. esculentum* ssp. *ancestrale* Ohnishi. The majority of the species was found in two hotspots of differentiation of *Fagopyrum*. One of them is the northwest corner of Yunnan province and the other is the upper Min river valley in Sichuan province of China. The two hotspots have no common wild species. This implies that speciation in *Fagopyrum* might have taken place in those places independently (Ohnishi 1995). All the newly discovered species have a narrow endemic distribution, probably because the environmental factors restrict their distribution to a narrow territory. Exceptions are the widely distributed *F. cymosum* (perennial buckwheat, 4x), *F. tataricum* ssp. *potanini* and *F. gracilipes*. These species extend their distribution to the Himalayan hills and the Tibetan plateau. Also, some new species were occasionally found in between the two hotspots (e.g. *F. leptopodium*). Morphological classification of the known species is given by Ohnishi (1995).

According to Wang *et al.* (2007), "the distribution of wild buckwheat resources in Sichuan is relatively centralized", with two main distribution centres. One of them is the Southwest and the other is the North of Sichuan. The south-west Sichuan centre is the distribution area of all known buckwheat species in this area, with 7 species, 2 varieties and 2 subspecies: *F. cymosum*, *F. urophyllum*, *F. lineare*, *F. gracilipes*, *F. statice*, *F. leptopodium*, *F. gilesii*, *F. gracilipes* var. *odontopterum*, *F. leptopodium* var. *grossi*, *F. tataricum* ssp. *potanini* and *F. esculentum* ssp. *ancestrale*. In the centre of North there are 4 species, 2 varieties and 2 subspecies: *F. cymosum*, *F. urophyllum*, *F. gracilipes*, *F. leptopodium*, *F. gracilipes* var. *odontopterum*, *F. leptopodium* var. *grossi*, *F. tataricum* ssp. *potanini* and *F. esculentum* ssp. *ancestrale*. The 3 most widely spread species are *F. gracilipes*, *F. gracilipes* var. *odontopterum* and *F. cymosum*. They are growing under varying environmental conditions across the two centres. *F. gracilipes* and *F. gracilipes* var. *odontopterum* are major weeds in corn, vegetable and potato fields. "The reasons are self-pollination, high rate of seed setting, easy to drop, small seed size, convenient to spread and fast in breeding." "*F. cymosum* is mainly growing on shady and wet hillside, field side, stone heap, shore of crub, often accompanied with perennial herbs or scrubs."

The wild ancestor of both cultivated species had been discovered by the mid-1990s, with the ancestor of common buckwheat (*F. esculentum* ssp. *ancestrale*) coming from Yunnan, and that of tartary buckwheat (*F. tataricum* ssp. *potanini*) coming from Sichuan. This may indicate the independent origin of the two species.

F. homotropicum, a homostylous, self-fertilizing wild species, has natural populations both in northern Yunnan and southern Sichuan, with plants from different locations showing different morphology. Both diploid and tetraploid cytotypes of *F. homotropicum* are distributed in Yunnan and Sichuan provinces, whereas all the samples from eastern Tibet were tetraploid (Konishi and Ohnishi 2001). After the discovery of *F. esculentum* ssp. *ancestrale* and *F. homotropicum*, it became clear from subsequent analysis on phylogenetic relationship that both species are closely related to cultivated common buckwheat, both are intercrossable with

it, hence they are the most probable candidate of the wild ancestor. Since the direction from a self-incompatible outbreeder to a self-compatible self-fertilizing species is a general trend of evolution in the plant kingdom, *F. homotropicum* has been eliminated as a candidate. This has led to the conclusion, that *F. esculentum* ssp. *ancestrale* is the wild ancestor of cultivated common buckwheat. This also asserts the place of origin of buckwheat cultivation. It is probably the northwest corner of Yunnan province, judging from the distribution of the wild ancestor species in nature (Ohnishi 1995).

Wild tartary buckwheat (*F. tataricum* ssp. *potanini* Batalin) is distributed in the northwest part of Yunnan, south-western part of Sichuan and eastern Tibet. Wild tartary buckwheat grows on disturbed barren lands, roadsides, occasionally within barley or rape fields. The populations of wild tartary buckwheat are not so large, usually consisting of 10 to 500 individuals (Ohnishi 2001). A putative progenitor for tartary buckwheat, with heterostylic self-incompatible pollination mechanism has not yet been found (Ohnishi 1995).

Since the Three Rivers Area is considered to be the original birthplace of common and tartary buckwheat, intensive research was focused on it in the 1990s to search for natural populations of wild *Fagopyrum* species (Ohnishi 2004). As described by Ohnishi (2004), rice is the major crop produced here by farmers in the lower, warmer areas, whereas maize production takes the place of rice in the higher and cooler areas. Buckwheat and millets are mainly found on the mountain slopes. Of the two buckwheat species, common buckwheat is produced at a greater extent than tartary buckwheat. At elevations higher than 3000 m cultivation of barley is dominant. Two additional wild species were found to be growing wild in the Three Rivers Area: these are *F. gracilipes* and *F. cymosum*. The high mountains in the Three Rivers Area appear to have been a critical barrier for the distribution of *Fagopyrum* species. Only two species, *F. gracilipes* and *F. cymosum* appear to have overcome this barrier and distributed further westward, as it was discussed above.

A new species (*F. jinshaense* Ohsako *et* Ohnishi) was discovered and registered. This species was found to be morphologically similar to *F. gilesii* and *F. leptopodium*. However, it was shown by molecular phylogenetic analysis that *F. jinshaense* was related to *F. gilesii* and *F. leptopodium* in nuclear DNA, but was related to *F. urophyllum* in their chloroplast DNA (Nishimoto *et al.* 2003; Ohnishi 2004).

Plant mating systems play a crucial role in shaping the genetic composition of populations and determine the distribution of allozyme variation within and among populations. Most of the wild species in the genus *Fagopyrum* have a distylous self-incompatibility system with some species being distylous but self-fertilizing and some others homostylous, self-compatible. The question arises whether predominantly outcrossing species maintain higher levels of intrapopulation genetic diversity than do predominantly inbreeding species? The genetic diversity parameters (the percentage of polymorphic loci, mean number of alleles per locus, mean number of alleles per polymorphic locus, total genetic diversity, genetic diversity within populations and among populations) were evaluated using enzyme electrophoretic markers, in four *Fagopyrum* species (Huh *et al.* 2001). Genetic diversity was higher for *F. leptopodium* (heterostylous, outcrossing species) than for *F. gracilipes* (homostylous, self-fertilizing species), and again higher for *F. esculentum* than for *F. tataricum*. This observation in *Fagopyrum* is consistent with the general knowledge that predominantly out-crossing species maintain higher levels of genetic variation than predominantly inbreeding species.

Tetraploid forms of shrubby perennial buckwheat (*F. cymosum*) have a wider distribution than diploid forms. An interesting observation is that certain tetraploid populations in Indochina and India completely lack thrum plants, and only consist of pin plants. These populations are sterile, and can only propagate and diffuse by vegetative organs (Ohni-

shi 1989; Tahir and Farooq 1992). The possibility was suggested that the thrum-lacking population of *F. cymosum* is an intermediate evolutionary step from the diploid species to the fertile tetraploid species (Ohnishi 1989).

PHYLOGENIC RELATIONSHIPS OF *FAGOPYRUM* SPECIES

There have been numerous efforts to determine the phylogenetic relations and possible speciation in *Fagopyrum*. The studies not only differ in the particular approach to obtain and analyze data, but also in the sampling strategy. The number of samples varied by accessions/species and also by locations for both wild and cultivated populations. The method used may have a significant influence on the branching of the phylogenetic tree obtained. As for the present work, there would be no sense in trying to synthesize the phylogenetic trees from different studies in one single tree. However, phylogenetic relationships in *Fagopyrum* can be presented by naming those clades identified in the majority of the studies and by citing the appropriate papers for support.

The first attempts to uncover phylogenetic relations in *Fagopyrum* were based on different morphological classifications by Steward (1930) and Hedberg (1946), and later some other studies were published (Ye and Guo 1992; Hirose *et al.* 1994, 1995; Ohnishi and Matsuoka 1996; Ohsako and Ohnishi 1998; Ohsako *et al.* 2002). The key characters for a new morphological classification in *Fagopyrum* were described in Ohnishi and Matsuoka (1996). Meanwhile, several new molecular genetic methods have been developed giving the opportunity of combining their power to construct the phylogenetic tree which is able to represent the true relationships among *Fagopyrum* species.

A strange characteristic of the work was the recurrent need to repeatedly redraw the intra- and interspecific phylogenetic relationships enforced by frequent discovery and description of new *Fagopyrum* species in the late 1990's (Ohnishi 1998a, 1998b; Ohsako and Ohnishi 1998) and even in the following decade (Ohsako *et al.* 2002).

Before discussing the phylogenetic relationships, a short survey is given on the methods used to obtain the primary data.

Methods of phylogenetic studies

1. Isozyme variability

Studies of isozyme variability in buckwheat were based on electrophoretic analyses of 12 enzymes, representing 19 loci, described in Ohnishi and Nishimoto (1988). The enzymes such as alcohol dehydrogenase (Adh, EC 1.1.1.1), glutamate dehydrogenase (Gdh, EC 1.4.1.2), fumarase (Fum, EC 4.2.1.2), isocitrate dehydrogenase (Idh, EC 1.1.1.42) and leucine aminopeptidase (Lap, EC 2.6.1.1) are determined by one locus. Phosphoglucosyltransferase (Pgm, EC 2.7.5.1), 6-phosphogluconate dehydrogenase (6-Pgdh, EC 1.1.1.44) and shikimate dehydrogenase (Sdh, EC 1.1.1.25) are determined by two loci. At least two loci are involved in diaphorase (Dia, EC 1.6.4.3), three in tetrazolium oxidase (Tox, superoxide dismutase EC 1.15.1.1) and glutamate-oxaloacetate transaminase (Got, EC 2.6.1.1), probably five (or more) in NAD-dependent malate dehydrogenase (Mdh, EC 1.1.1.37), respectively. Seed samples were used to assay the *Adh*, *Fum*, *Gdh*, *Got-1*, *Idh*, *Lap*, *Mdh-1*, *Mdh-5*, *Pgm-1*, *Pgm-2*, *6-Pgdh-1*, *6-Pgdh-2*, *Tox-1* and *Tox-2* loci, while the first or second foliage leaves were used to assay the remaining loci, such as *Dia-1*, *Dia-2*, *Got-2*, *Lap*, *Mdh-3* and *Sdh-1* (Ohnishi and Nishimoto 1988). Assignment of genotypes was based on the observed bandmorphs at the polymorphic loci as well as on the known linkage relationships between isozyme loci.

When isozyme variability is used for analysis, genotypes are deduced from protein data. Due to the lower variability of coding regions, particularly allele differences

detectable at the protein level, the power of the technique to supply detailed genetic information lags behind the power of modern PCR based methods or proper sequence information. The obtained molecular information is suitable for phylogenetic studies at interspecific taxonomic levels. Despite the limitation of this method, several studies on population genetics of buckwheat were published before the PCR era (Ohnishi 1985, 1988, 1993b; Ohnishi and Nishimoto 1988), and this method was also used to determine phylogenetic relationship between eleven *Fagopyrum* species (Ohnishi and Matsuoka 1996).

2. Use of nuclear DNA sequences

One of the most popular sequences for phylogenetic inference at the generic and infrageneric levels in plants is the internal transcribed spacer (ITS) region of the 18S-5.8S-26S nuclear ribosomal cistron. The ITS region is a suitable target to investigate plant phylogenetic relationship among closely related genera or species because of its rapid evolution (Baldwin 1992; Baldwin *et al.* 1995) and homogenization among repeat units through concerted evolution (Arnheim 1983). It was observed that the sequences of the 5.8S subunit are conserved at the same level as other coding regions, while the sequences of ITS are much more variable.

However, there are some complications for phylogenetic inference of sequence data of the ITS region in many plant genomes because extensive sequence variations may derive from ancient or recent array duplication events, genomic harboring of pseudogenes in various states of decay, and/or incomplete intra- or inter-array homogenization. These phenomena separately and collectively create a network of paralogous sequence relationships potentially confounding accurate phylogenetic reconstruction (Alvarez and Wendel 2003).

DNA sequence data of internal transcribed spacer (ITS) region of the rRNA gene were obtained from different buckwheat species and used for phylogenetic analyses. The ITS region contains the complete ITS1, ITS2 sequences and the 5.8S subunit of the rRNA gene. The region could be obtained by PCR amplification of a short (700 bp) fragment, and its sequence can be determined directly from PCR product or after its cloning. The sequences of ITS1 and ITS2 were about 3-7 times more variable than the sequence of the 5.8S subunit of the rRNA gene (Yasui and Ohnishi 1998b). ITS sequence information were used for phylogenetic analyses in the identification of several new *Fagopyrum* species (Ohsako and Ohnishi 1998).

Despite the near-universal usage of ITS sequence data in plant phylogenetic studies, its complex and unpredictable evolutionary behavior reduces its utility for phylogenetic analysis. It is suggested that more robust insights are likely to emerge from the use of single-copy or low-copy nuclear genes.

Low-copy nuclear genes in plants are a rich source of phylogenetic information. They hold a great potential to improve the robustness of phylogenetic reconstruction at all taxonomic levels. Low-copy nuclear genes, however, remain underused in plant phylogenetic studies due to practical and theoretical complications in unraveling the evolutionary dynamics of nuclear gene families. The lack of the universal markers or universal PCR primers of low-copy nuclear genes has also hampered their phylogenetic utility. It has become clear that low-copy nuclear genes are particularly helpful in resolving close interspecific relationships and in reconstructing allopolyploidization in plants (Sang 2002).

Two floral homeotic genes, *FLORICAULA/LEAFY* (*FLO/LFY*) and *AGAMOUS* (*AG*), thought to be single/low-copy genes in *Fagopyrum*, were used to analyze phylogenetic relationships in the Urophyllum group (Nishimoto *et al.* 2003). Conserved regions of *FLO/LFY* have been used previously for phylogenetic analyses at higher taxonomic levels (Himi *et al.* 2001), while the long intronic sequence of *AG* contributed to its phylogenetic utility at lower taxonomic levels.

3. DNA fingerprinting

Random amplified polymorphic DNA (RAPD) is a PCR based fingerprinting method which provides molecular data in an efficient, simple and inexpensive way. Although this method has been employed in many plants for both taxonomic and phylogenetic studies, there are only a few studies concerning buckwheat. RAPD was used for phylogenetic studies of cultivated landraces and natural populations of tartary buckwheat (Tsuji and Ohnishi 2000, 2001a) and for determination of relationship among 14 species and two sub-species of *Fagopyrum* (Sharma and Jana 2002).

Amplified fragment length polymorphism (AFLP) is a powerful method to detect polymorphisms, however, for researchers wanting to use AFLP, this molecular technique is difficult and time-consuming to adapt to the species of interest. This might be a reason why AFLP has been employed so rarely for phylogenetic studies of buckwheat species. The AFLP technique was used to investigate phylogenetic relationships among cultivated landraces and natural populations of wild subspecies of tartary buckwheat (Tsuji and Ohnishi 2001b; Park *et al.* 2006) as well as among cultivated and natural populations of common buckwheat at the individual level (Konishi *et al.* 2005).

Restriction fragment length polymorphism (RFLP), a rather old DNA fingerprinting technique was used to analyze chloroplast genome DNA (cpDNA) in *Fagopyrum*. The molecular size of the total chloroplast genome was found to be approximately 155 kbp in all the buckwheat species examined (Kishima *et al.* 1995) which is small enough to visualize band patterns obtained by electrophoretic separation of fragments following restriction digestions with different enzymes (Ohnishi and Matsuoka 1996). Although this technique is very simple and combines the advantage of using chloroplast in determining phylogenetic relationship (non-meiotic and uniparental inheritance), it became anachronistic by the technical simplicity of obtaining detailed sequence information.

4. Use of chloroplast DNA sequences

Chloroplast genome sequences are extremely informative about species-interrelationships owing to its non-meiotic and often uniparental inheritance over generations. The complete chloroplast genome sequence of the wild ancestor of cultivated buckwheat, *Fagopyrum esculentum* ssp. *ancestrale* has been reported recently (Logacheva *et al.* 2008). The gene content and order in buckwheat chloroplast genome was found to be similar to *Spinacia oleracea* with some unique structural differences in buckwheat, such as the presence of an intron in the *rpl2* gene, a frameshift mutation in the *rpl23* gene and extension of the inverted repeat region to include the *ycf1* gene. Phylogenetic analysis of 61 protein-coding gene sequences from 44 complete plastid genomes (representing all major lineages of angiosperms) provided strong support for the sister relationships of *Caryophyllales* (including *Polygonaceae*) to Asterids (Logacheva *et al.* 2008).

The size of the chloroplast genome of *F. esculentum* ssp. *ancestrale* is composed of 159599 nucleotide bases, and it exceeds the average size of flowering plant's chloroplast genomes ~155 kbp. The observed increase in size is due to the expansion of the inverted repeat (IR) region. The inverted repeats (IRa and IRb) separate the genome into small (SSC) and large (LSC) single-copy regions. It was shown that the expansion was not only a characteristic of *Fagopyrum* but it was also found in some other related genera and this may represent a common feature in *Polygonaceae*. Comparative analysis of the various sequences derived from buckwheat species revealed minor variations in the fine structure of the IR/SSC borders (Logacheva *et al.* 2008). Further studies of the fine structure of IR/SSC borders can be of utility to illustrate phylogenetic relationships within *Fagopyrum*.

There are a number of studies in which sequence infor-

mation from different regions of the chloroplast genome were used to reveal phylogenetic relationships among *Fagopyrum* species. Some advantages come from the combination of using single-copy genes and the features of non-meiotic and uniparental inheritance of the chloroplast genome. All three regions, used in the different studies, are located in the large single-copy region (LSC) of the chloroplast genome. The nucleotide substitution rate of plant chloroplast DNA (cp-DNA) is lower than that of nuclear DNA (Wolfe *et al.* 1987) but sequences of coding and intergenic spacer regions can be used together for phylogenetic analyses.

The sequences of the *rbcL* gene, which encodes the large subunit of ribulose-1,5-bisphosphate carboxylase/oxidase, have been used widely to construct plant phylogenies. However, these phylogenetic studies have been limited at taxonomic levels above subfamilies, because the *rbcL* gene has a slow base substitution rate (Doebley *et al.* 1990). In *Fagopyrum* and related genera of *Polygonaceae*, analyses of the DNA sequences of *rbcL* were successful to separate *Fagopyrum* from other related genera of *Polygonaceae* and to classify major groups of *Fagopyrum* (Yasui and Ohnishi 1996). To obtain sequence information suitable for studying phylogenetic relationship at lower taxonomic levels, the sequenced region was extended downstream from *rbcL* into the 5' region of the next gene, *accD*, in the chloroplast genome. The 5' coding region of the *accD* gene, which encodes one of the subunits of acetyl-CoA carboxylase, and the intergenic region between the two genes differ greatly from species to species (Nagano *et al.* 1991). Phylogenetic analyses of the genus *Fagopyrum*, based on nucleotide sequence of the *rbcL-accD* coding and their intergenic region in cp-DNA, has been reported (Yasui and Ohnishi 1998a; Oshako *et al.* 2001).

Another region in the chloroplast genome, used in phylogenetic studies, is the intron of the *trnK* (UUU) gene, including the *matK* gene. The *trnK* intron comprises three regions: the *matK* gene, which is an intron-internal open reading frame that is thought to encode a maturase-like protein (Neuhaus and Link 1987), and two non-coding regions flanking both sides of the *matK* gene. Phylogenetic relationships of new *Fagopyrum* species based on *trnK* intron sequences (Oshako *et al.* 2002), as well as studies on intra-specific polymorphisms and interspecific divergence of the *trnK/matK* region within and between two wild *Fagopyrum* species (Oshako and Ohnishi 2001) have been reported.

Nucleotide sequences in the intragenic spacer between *trnC*(GCA) and *rpoB* genes of cp-DNA have also been used in several phylogenetic studies. Due to the higher nucleotide variation in this region, intra- and interspecific phylogenetic relationships can be determined. Molecular phylogeny based on *trnC-rpoB* spacer region sequences was applied to verify the existence of two distinct groups in natural populations of *F. urphyllum* (Kawasaki and Ohnishi 2006).

The certainty to reveal true phylogenetic relationships among species could be increased by using molecular data from two or three regions of the cp-DNA simultaneously. In *Fagopyrum*, using sequence information of the *trnK* intron and *trnC-rpoB* spacer regions (Oshako and Ohnishi 2000), as well as nucleotide sequences of the *rbcL-accD*, *trnK* intron and *trnC-rpoB* spacer regions (Nishimoto *et al.* 2003; Yamane *et al.* 2003), have been reported.

Combination of two or more methods mentioned above can increase further the certainty of the revealed phylogenetic relationships.

Results of phylogenetic studies

1. Current view on phylogenetic relations based on the above studies

Phylogenetic relations of *Fagopyrum* species have been inferred from morphological data as well as molecular information obtained by using one or more of the methods reviewed above. There are several well-known, accepted methods to analyze the data to reveal relationships at both

intra- and interspecific taxonomic levels and usually presented in a form of a phylogenetic tree. Phylogenetic trees from different studies greatly vary as they are influenced by several factors, such as sampling strategy, the method used to obtain and analyse data.

None of the studies have questioned the general view that species in genus *Fagopyrum* fall into two major monophyletic groups, namely the cymosum group and the urophyllum group.

2. Phylogeny within the cymosum group

Three clades can be recognized within the cymosum group. The *F. esculentum*-*F. homotropicum* clade comprises two subspecies of *F. esculentum*, notably the cultivated ssp. *esculentum* (Moench) and its wild ancestor ssp. *ancestrale* (Ohnishi) grouped together and separated from the closely related *F. homotropicum* (Ohnishi) (Ohnishi and Matsuoka 1996; Yasui and Ohnishi 1998a, 1998b). The majority of the studies revealed a strong relationship between *F. cymosum* (Meisn.) and the two *F. tataricum* subspecies, the cultivated ssp. *tataricum* (Gaertn.) and its wild relative ssp. *potanini* (Batalin). These three species were considered as the second clade of the cymosum group (Ohnishi and Matsuoka 1996; Yasui and Ohnishi 1998a; Nishimoto *et al.* 2003). The inclusion of several accessions of *F. cymosum* in the studies resulted in dividing this clade into two clades (Yasui and Ohnishi 1998b). The phylogenetic relationships within *F. cymosum* coincide with geographic locations of the accessions. The Tibet-Himalayan clade included both *F. tataricum* subspecies, the Yunnan-Sichuan clade only consisted of *F. cymosum* accessions. It was suggested that *F. tataricum* speciated from *F. cymosum* in the Tibet-Himalayan area (Yamane *et al.* 2003). It was shown that *Fagopyrum giganteum* (a hybrid species between *F. tataricum* and *F. cymosum*), *F. pilus* and *F. cymosum* clustered together (Sharma and Jana 2002).

3. Phylogeny within the urophyllum group

The results of the numerous studies addressing phylogenetic relationships within the urophyllum group of genus *Fagopyrum* are not congruent. The results of a recent study by Kawasaki and Ohnishi (2006) are presented here and compared to findings of other studies.

The species *F. urophyllum* was divided into two distinct groups, the Dali group and the Kunming group, based on morphological characteristics, and the classification was verified by molecular phylogeny. It is suggested that the two groups should be handled as subspecies or two distinct species on the basis of their reproductive isolation. These two groups were recognized also in previous studies (Ohnishi and Matsuoka 1996; Yasui and Ohnishi 1998a, 1998b; Ohsako and Ohnishi 2000). Clades within the urophyllum group are (Kawasaki and Ohnishi 2006):

F. leptopodum – *F. statice*

F. gracilipes – *F. rubifolium* – *F. gracilipedoides* – *F. capillatum*

F. macrocarpum – *F. pleioramosum* – *F. callianthum*

F. gillessii

Kunming group of *F. urophyllum* – *F. jinshaense*

Dali group of *F. urophyllum* – *F. lineare*.

The Kunming group of *F. urophyllum* and *F. jinshaense* formed a sister clade, and a sister clade was also formed by the Dali group of *F. urophyllum* and *F. lineare* (Kawasaki and Ohnishi 2006). The *F. leptopodum* – *F. statice* clade was supported by additional studies (Yasui and Ohnishi 1998a; Ohsako and Ohnishi 1998, 2000, 2001; Ohsako *et al.* 2001, 2002). The existence of the *F. gracilipes* – *F. rubifolium* – *F. gracilipedoides* – *F. capillatum* clade had also been previously revealed by Ohsako *et al.* (2002) and Nishimoto *et al.* (2003), while the close relationships between *F. gracilipes* and *F. capillatum* was recognized in the majority of the studies (Ohnishi and Matsuoka 1996; Ohsako and Ohnishi 1998; Yasui and Ohnishi 1998a; Sharma and Jana

2002). *F. rubifolium* was added to this clade later (Ohsako and Ohnishi 2000; Ohsako *et al.* 2001). The *F. macrocarpum* – *F. pleioramosum* – *F. callianthum* clade, where the first two species were close relatives, was reported in some of the studies (Ohsako and Ohnishi 1998, 2000; Ohsako *et al.* 2001, 2002; Nishimoto *et al.* 2003). *F. gillessii* was not usually clustered together with any of the clades (Ohsako *et al.* 2001, 2002; Sharma and Jana 2002) except with *F. jinshaense* (Nishimoto *et al.* 2003). The sister clade composed by *F. jinshaense* and the Kunming group of *F. urophyllum* could be seen in Nishimoto *et al.* (2003). Phylogenetic analysis revealed that the debated *F. megacarpum* should be excluded from genus *Fagopyrum* (Ohsako *et al.* 2001).

BOTANICAL DESCRIPTION OF SOME SELECTED FAGOPYRUM SPECIES WITH BOTANICAL NAMES AND SYNONYMS

This section and information contained herein is based on information from eFloras 2008 (www.eFloras.org; Missouri Botanical Garden, St. Louis, MO and Harvard University Herbaria, Cambridge, MA).

Cymosum group

1. *Fagopyrum esculentum* Moench, Methodus. 290. 1794.

“Hook.f., l. c. 55; D. A. Webb in Tutin *et al.*, Fl. Europ. 1: 81. 1964; Kitamura, Pl. Afg. and W. Pak. 43. 1964; Rech. f. and Schiman-Czeika, l. c. 83; R.R. Stewart, l. c. 202; Bhopal and Chaudhri in Pak. Syst. 1(2): 87. 1977; Grierson and D. G. Long, Fl. Bhutan 1(1): 171. 1983; Munshi and Javeid, Syst. Stud. Polygon. Kashm. Himal. 83. 1986.

Polygonum fagopyrum L., Sp. Pl. 364. 1753; *Fagopyrum sagittatum* Gilib, Exerc. Phyt. 2: 435. 1792 - nom. illegit.; *Polygonum emarginatum* Roth, Catalect. B. 1: 48. 1797; *Fagopyrum vulgare* T. Nees, Gen. Pl. Fl. Germ. Monochlam. 53. 1835.”

English: Common buckwheat

French: Sarrasin commun

“Annual, up to 1 m tall herb, glabrous or young parts rarely minutely papillose. Stem ribbed, reddish. Leaves petiolate, petiole 0.5-2 cm long, grooved lower leaves with long petiole, upper ones sessile; lamina triangular or sagittate, cordate, basal lobes rounded to acuminate, 1.5-10 × 1-8 cm. Ochrea 2-3 (-5) mm long, hyaline, pubescent near the base. Inflorescence axillary and terminal, pedunculate, many-flowered corymbose cyme. Flowers pink or red, pedicelled, c. 1 mm across. Perianth segments 5-partite, ovate or oblong-ovate c. 3 × 2 mm broad. Stamens 8, unequal, alternating with glands, c. 1.5 mm long. Ovary 3-angled; styles 3, as long as ovary. Nuts deeply 3-angled, angles acute, brown, smooth, narrowed at both the ends, 4-8 × 2.5-5 mm broad.” $2n = 16$.

Flowering: June-August. Fruiting: July – September.

Flowers are chasmogamous, heterostylous. Obligate out-croser.

Habitat in Asia.

Illustration:

http://efloras.org/object_page.aspx?object_id=44793&flora_id=5

2. *Fagopyrum tataricum* (L.)

“Gaertn., Fruct. Sem. Pl. 2: 182. t. 119, f. 6. 1791; Hook. f., l. c. 55; Losinsk. in Kom., Fl. URSS 703. 1936; D. A. Webb in Tutin *et al.*, Fl. Europ. 1: 81. 1964; Kitamura, l. c.; Rech. f. and Schiman-Czeika, l. c. 83; R. R. Stewart, l. c. 202; Bhopal and Chaudhri in Pak. Syst. 1(2): 88. 1977; Munshi and Javeid, l. c. 84; Grierson and D. G. Long, l. c.”

Polygonum tataricum Linnaeus, Sp. Pl. 1: 364. 1753.

“Annual, glabrous, commonly green herb, up to 1 m tall, stem glabrous or slightly pubescent. Leaves petioled, petiole 0.5-6 cm long, the upper short and lower long petioled; lamina broadly triangular-cordate, triangular-hastate or

sagittate-cordate, acuminate, 2-8 × 1.2-5 cm. Ochrea hyaline, slightly truncate, 5-7 mm long, brown. Inflorescence axillary and terminal, pedunculate, corymbose cyme. Flowers white or pink. Perianth segments 5-partite, subequal, oblong-ovate, obtuse, entire, 1.3-1.7 × c. 0.5-1. Stamens 8, alternating with rounded glands, filaments unequal with dorsifixed anthers. Ovary 3-angled; styles 3, free, half the length of the ovary; stigmas capitate. Nuts deeply 3-angled, angles rounded in the upper part, and wrinkled and somewhat crenate in the lower part, blackish-brown, 4-6 mm long, 1.5-2 mm broad, narrowed above." $2n = 16$.

Flowering: May – September. Fruiting: June – October.

Flowers are cleistogamous, homostylous. Self-fertilization.

Habitat: Central Asia.

Illustration:

http://efloras.org/object_page.aspx?object_id=50735&flora_id=2.

3. *Fagopyrum dibotrys* (D. Don)

"Hara, Fl. E. Himal. 69. 1966; 2: 22. 1971; Hara in Hara *et al.*, Enum. Fl. Pl. Nep. 3: 174. 1982; Munshi & Javeid, l. c. 82; Grierson and D. G. Long, l. c.

Polygonum dibotrys D. Don, Prod. Fl. Nep. 73. 1825; *Polygonum cymosum* Trev. in Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. 13: 177. 1826; *Fagopyrum cymosum* (Trev.) Meisn. in Wall., Pl. As. Rar. 3: 63. 1832; Hook. f., l. c. 55; R. R. Stewart, Ann. Cat. Vasc. Pl. Pak. Kashm. 201. 1972; Bhopal & Chaudhri, l. c. 88.

F. megaspartanium Q. F. Chen; *F. pilus* Q. F. Chen; *P. acutatum* Lehmann; *P. labordei* H. Léveillé & Vaniot; *P. tristachyum* H. Léveillé; *P. volubile* Turczaninow.

Herbs perennial. Rhizomes black-brown, stout, ligneous. Stems erect, green or brownish, 40-100 cm tall, much branched, striate, glabrous. Petiole 2-10 cm; leaf blade triangular, 4-12 × 3-11 cm, both surfaces papillate, base nearly hastate, margin entire, apex acuminate; ochrea brown, 5-10 mm, membranous, oblique, apex truncate, not ciliate. Inflorescence terminal or axillary, corymbose; bracts ovate-lanceolate, ca. 3 mm, margin membranous, apex acute, each 4-flowered, rarely 6-flowered. Pedicels equaling bracts, articulate at middle. Perianth white; tepals narrowly elliptic, ca. 2.5 mm. Stamens included. Styles free; stigmas much exceeding persistent perianth, capitate, opaque. Achenes blackish brown, dull, broadly ovoid, 6-8 mm, trigonous, sometimes narrowly winged, angles smooth to repandous, apex acute." $2n = 16, 32$.

Flowering: April – October. Fruiting: May – November.

Flowers are heterostylous. Cross-fertilization.

"Moist valleys, grassy slopes, 300-3200 m. It is considered to be a good fodder plant. The leaves are used as vegetable. The grains are used in stomach disorders; Distribution: India, China and Pakistan."

Illustration:

http://efloras.org/object_page.aspx?object_id=7504&flora_id=5.

Urophyllum group

1. *Fagopyrum urophyllum* (Bureau & Franchet)

"H. Gross, Bull. Acad. Int. Géogr. Bot. 23: 21. 1913.

Polygonum urophyllum Bureau & Franchet, J. Bot. (France) 5: 150. 1891; *Fagopyrum mairei* (H. Léveillé) H. Gross; *P. mairei* H. Léveillé.

Subshrubs. Stems suberect, 60-90 cm tall, much branched; branches ligneous, bark red-brown, exfoliating, simple, herbaceous, green striate. Petioles 2-5 cm, shortly pubescent; leaf blade greenish abaxially, green adaxially, sagittate or ovate-triangular, 2-8 × 1.5-4 cm, both surfaces shortly pubescent along veins, base broadly sagittate, margin entire, apex long acuminate or caudate; ochrea brown, 4-6 mm, membranous, oblique. Inflorescence terminal, paniculate, 15-20 cm; branches spreading, lax; bracts greenish,

narrowly funnel-shaped, 2-2.5 mm, apex acute, each 3- or 4-flowered. Pedicels longer than bracts, 3-3.5 mm, slender, apex articulate. Perianth white; tepals elliptic, 2-3 mm. Stamens included. Styles free; stigmas capitate. Achenes exceeding persistent perianth, black-brown, shiny, broadly ovoid, sharply trigonous, 3-4 mm." $2n = 16$.

Flowering: April – September. Fruiting: May – November.

Flowers are heterostylous. Cross-fertilization.

"Grassy or gravelly slopes, thickets in valleys; 900-2800 m. Sichuan, Yunnan (China)".

Illustration:

http://efloras.org/object_page.aspx?object_id=50736&flora_id=2

2. *Fagopyrum gilesii* (Hemsl.)

"Hedberg, in Svensk. Botanisk. Tidskrift. 40(4):390. 1946.

Polygonum gilesii Hemsl. in Hook. Icon Pl. t. 1756, 1887-88; Rech., f. and Schiman.-Czeika in Rech. f., Fl. Iran. 56: 55. 1968; R. R. Stewart, l. c. 206.

Erect, 25-60 cm high, branched, glabrous - pubescent, perennial herb. Stem circular, glabrous, woody, branched, leaves very few, internodes quite long. Lower leaves 10-15 × 8-15 mm, ovate-orbicular, obtuse, entire, long petiolate, petiole 1-3 cm long, upper leaves 4.0-8.0 × 2.5-6.0 mm, ovate, obtuse, entire, petiole 1-2 mm long. Ochrea minute, 1-2 mm long, lanceolate, acuminate, oblique. Inflorescence axillary - terminal, 2-5 mm long, few flowered, capitulate or fasciculate raceme. Flowers up to 1.5 mm across, pedicel c. 0.5 mm. Ochreolae 1-2 mm long, lanceolate, margin membranous. Perianth segments 5, parted to base, 2.0-2.5 × 1.25-1.5 mm, oblanceolate - obovate, obtuse, entire, unequal. Stamens 8, filaments short, unequal, anthers basifixed. Ovary small, 0.75-1.0 × c. 0.5 mm, lanceolate, trigonous, with three styles and capitate stigmas. Nuts trigonous, glabrous, brown." $2n = 16$.

Flowering: July-August. Fruiting: August-September.

Flowers are heterostylous. Cross-fertilization.

Grassy slopes, valleys; 2200-4000 m. Sichuan, Yunnan (China), Pakistan.

Illustration:

http://efloras.org/florataxon.aspx?flora_id=5&taxon_id=242100053

3. *Fagopyrum leptopodum* (Diels)

"Hedberg, Svensk Bot. Tidskr. 40: 390. 1946.

Herbs annual. Stems 6-30 cm tall, slender, glabrate, branched at base, leafless above. Petiole 1-1.5 cm, slender; leaf blade triangular or triangular-ovate, abaxially papillate along veins, adaxially scabrous, midvein slightly prominent abaxially, base sagittate or nearly truncate, margin entire, apex acute; ochrea white or brownish, membranous, oblique, apex acute. Inflorescence racemose, dense or very lax, several racemes together large and panicle-like; bracts membranous, oblique, apex acute, each 2- or 3-flowered. Pedicels longer than bracts, ca. 3 mm, slender, apex articulate. Perianth white or pinkish; tepals elliptic, 1.5-2.5 mm. Stamens included. Styles filiform, free; stigmas capitate. Achenes exceeding persistent perianth, yellow-brown, ovoid, trigonous, 2-2.5 mm." $2n = 16$.

Flowering: May-October. Fruiting: June-November.

Flowers are heterostylous. Cross-fertilization.

Mountain slopes, valleys; 1000-3000 m. Sichuan, Yunnan.

Illustration:

http://efloras.org/object_page.aspx?object_id=50734&flora_id=2

4. *Fagopyrum gracilipes* (Hemsley)

"Dammer ex Diels, Bot. Jahrb. Syst. 29: 315. 1900.

Polygonum gracilipes Hemsley, J. Linn. Soc., Bot. 26: 340. 1891; *Fagopyrum bonatii* (H. Léveillé) H. Gross; *F.*

odontopterum H. Gross; *P. bonatii* H. Léveillé; *P. gracilipes* var. *odontopterum* (H. Gross) Samuelsson; *P. odontopterum* (H. Gross) H. W. Kung.

Herbs annual. Stems erect, 20-70 (-80) cm tall, branched at base, striate, sparsely shortly strigose. Petiole 1-3 cm, shortly strigose; leaf blade ovate-triangular, 2-4 × 1.5-3 cm, both surfaces sparsely shortly strigose, base cordate or hastate, apex acuminate; ocrea 4-5 mm, membranous, shortly strigose, oblique, apex acute. Inflorescence axillary or terminal, racemose, interrupted, pendulous, very lax, 2-4 cm, slender; bracts green, funnel-shaped, margin membranous, each 2- or 3-flowered. Pedicels longer than bracts, slender, apex articulate. Perianth pinkish; tepals elliptic, unequal, 2-2.5 mm, with conspicuous green veins. Stamens included. Stigmas capitate. Achenes exceeding persistent perianth, shiny, broadly ovoid, ca. 3 mm, sharply trigonous, sometimes narrowly winged along angles."

$$2n = 4x = 32.$$

Flowering: June-October. Fruiting. July-November.

Flowers are homostylous. Self-fertilization.

"Grassy slopes, wet valleys, field margins; 300-3400 m. S Gansu, Guizhou, Henan, Hubei, Shanxi, Sichuan, Yunnan (China)."

Illustration:

http://efloras.org/object_page.aspx?object_id=50736&flora_id=2.

FUTURE PERSPECTIVES

Common buckwheat is unique in the sense that after cultivating the species for so many centuries in different parts of the world, diffusion routes can still be traced with molecular markers in populations currently grown. One reason why cultivated populations of common buckwheat reflect the evolutionary processes that occurred during the spread of cultivation might be that buckwheat has been given little attention by scientists to alter the existing cultivars until recently. The large gene pool and the out-crossing breeding habit always provided a sufficiently high genetic variation for breeders to use the local germplasm for the improvement of the crop in the past. Subsistence farming and local use of the products also favour the preservation of the genetic constitution of local populations.

As discussed in this review, the total amount of variability maintained in each population decreased during the spread of cultivation from the centre of origin to the peripheral parts. The loss of variant alleles in populations close to the geographical terminus of the diffusion route is probably due to random genetic drift during the course of diffusion, rather than to systematic selection. In future, systematic selection is likely to play a major role in forming the genetic constitution of populations. The recent discovery of new *Fagopyrum* species (a process that may not have come to an end) and the identification of phylogenetic relationships within the genus may further provide breeders with potential sources of economically valuable genes. Common buckwheat is of fast life cycle, easy to manage *in vitro*, which may support interspecific cross breeding without the need to use gene transfer.

Although buckwheat is not likely to globally become a staple food crop in the future, land area planted to this crop may be expanded in some particular regions. Growing interest in buckwheat as a functional food and as a nutraceutical generates more research efforts to improve the existing cultivars. Cross-border exchange of germplasm, whether importing a cultivar or a breeding material (including wild *Fagopyrum* species), may substantially change the distribution and frequencies of genes and may even cause the loss of local populations and landraces on the short term, at least if we place this process in the evolutionary time scale.

Besides, new breeding objectives may also be originated from the appearance of new pathogens and pests if larger expanses of land are used in a smaller geographical area.

Molecular methods, adapted so far to determine phylogenetic relationships of both the *Fagopyrum* genus itself and

species within the genus, were sufficient to clarify major issues and complement morphological observations. However, more sequence based information is needed to further refine the picture. It is hard to predict when, but it is undoubtedly that decreasing cost of the highly efficient new generation sequencing methods and the increasing interests in buckwheat breeding will result in determination of the sequence of the entire buckwheat genome. Using routinely sequences of the complete chloroplast and/or large regions of the genomes from different *Fagopyrum* species will enhance our capabilities to finalize answers for evolutionary and phylogenetic questions as well as promote efficient buckwheat breeding.

REFERENCES

- Aii J, Nagano M, Penner GA, Campbell CG, Adachi T (1998) Identification of RAPD markers linked to the homostylar (*Ho*) gene in buckwheat. *Breeding Science* **48**, 59-62
- Arora RK, Baniya BK, Joshi BD (1995) Buckwheat genetic resources in the Himalayas: their diversity, conservation and use. In: Matano T, Ujihara A (Eds) *Current Advances in Buckwheat Research, Proceedings of the 6th International Symposium on Buckwheat*, Shinshu, Japan, Shinshu University Press, Nagano, Japan, pp 39-45
- Alvarez I, Wendel JF (2003) Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* **29**, 417-434
- Arnheim N (1983) Concerted evolution of multigene families. In: Nei M, Koehn RK (Eds) *Evolution of Genes and Protein*, Sinauer Assoc., Sunderland, MA, pp 38-61
- Baldwin BG (1992) Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the Compositae. *Molecular Phylogenetics and Evolution* **1**, 3-16
- Baldwin BG, Sanderson MJ, Porter JM, Wojciechowski MF, Campbell CS, Donoghue MJ (1995) The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* **82**, 247-277
- Bodmer WF (1966) The genetics of homostyly in populations of *Primula vulgaris*. *Philosophical Transactions of the Royal Society Series B* **242**, 517-519
- Bretschneider E (1898) *History of European Botanical Discoveries in China*, Press Imprimerie of the Russian Academy of Sciences, St Petersburg
- Brunori A, Végvári G (2007) Rutin content of the grain of buckwheat. *Acta Agronomica Hungarica* **53** (3), 265-272
- Campbell CG (1976) Buckwheat. In: Simmonds NW (Ed) *Evolution of Crop Plants*, Longman, London, pp 235-237
- Campbell CG (1995) Inter-specific hybridization in the genus *Fagopyrum*. In: Matano T, Ujihara A (Eds) *Current Advances in Buckwheat Research, Proceedings of the 6th International Symposium on Buckwheat*, Shinshu, Japan, 1995, Shinshu University Press, Nagano, Japan, pp 255-263
- Campbell CG (1997) Buckwheat. *Fagopyrum esculentum* Moench. Promoting the conservation and use of underutilized and neglected crops. 19. Institute of plant genetics and crop plant research, Gatersleben/International Plant Genetics Resources Institute, Rome, Italy
- Chen A-G, Dao Z-L (2001) Managing agricultural resources for biodiversity conservation. Case study Yunnan, South-west China. A study commissioned by Environmental Liaison Center International, pp 1-23
- Christa K, Soral-Smietana M (2008) Buckwheat grains and buckwheat products – nutritional and prophylactic value of their components – a review. *Czech Journal of Food Sciences* **26**, 153-162
- Darlington CD, Janaki Ammal EK (1945) *Chromosome Atlas of Cultivated Plants*, George Allen and Unwin Ltd., London, 397 pp
- Darwin C (1877) *The Different Forms of Flowers on Plants of the Same Species*, John Murray, London
- De Candolle A (1883) *L'Origine des Plantes Cultivées*, Librairie Germer Baillière et C^{ie}, Paris
- de Nettancourt D (1977) *Incompatibility in Angiosperms*, Springer-Verlag, Berlin, 230 pp
- Dictionary of Botanical Epithets
(<http://www.winternet.com/~chuckg/dictionary.html>)
- Doebley J, Durbin M, Golenberg EM, Clegg MT, Ma DP (1990) Evolutionary analysis of the large subunit of carboxylase (*rbcL*) nucleotide sequence among the grasses (Gramineae). *Evolution* **44**, 1097-1108
- Dowrick VPJ (1956) Heterostyly and homostyly in *Primula obconica*. *Heredity* **10**, 219-236
- Encyclopaedia Britannica (<http://www.britannica.com>)
- Edwardson S (1996) Buckwheat: Pseudocereal and nutraceutical. In: Janick J (Ed) *Progress in New Crops*, ASHS Press, Alexandria, VA, pp 195-207
- FAOSTAT (2009) FAO Statistical Database (<http://faostat.fao.org/>)
- Flora of North America **5**, 31. *Fagopyrum* (www.eFloras.org)
- Flora of North America **5**, 1. *Eriogonum* (www.eFloras.org)
- Flora of North America **5**, 44. *Polygonaceae* (www.eFloras.org)
- Frankel R, Galun E (1977) Pollination mechanisms, reproduction and plant

- breeding. In: Frankel R, Gall GAE, Grossman M, Linskens HF, de Zeeuw D (Eds) *Monographs on Theoretical and Applied Genetics 2*, Springer-Verlag, Berlin, 281 pp
- Garber RJ, Quisenberry KS** (1927) The inheritance of length of style in buckwheat. *Journal of Agricultural Research* **34**, 181-183
- Gocs L** (2002) Buckwheat. In: Lazányi J (Ed) *Crop Species Developed and Maintained in the Research Institutes of the University of Debrecen, Centre of Agricultural Sciences* (2nd Edn), University of Debrecen, pp 188-191 (in Hungarian)
- Gottlieb LD** (1981) Electrophoretic evidence and plant populations. *Progress in Phytochemistry* **7**, 1-46
- Gross MH** (1913) Remarques sur les Polygonées de l'Asie Orientale. *Bulletin de Géographie Botanique* **23**, 7-32
- Hamrick JL** (1979) Genetic variation and longevity. In: Solbrig O, Jain SK, Johnson GB, Raven PH (Eds) *Topics in Plant Population Biology*, Columbia University Press New York, pp 84-113
- Hedberg O** (1946) Pollen morphology in the genus *Polygonum* L. s. lat. and its taxonomical significance. *Svensk Botanisk Tidskrift* **40**, 371-404
- Himi S, Sano R, Nishiyama T, Tanahashi T, Kato M, Ueda K, Hasebe M** (2001) Evolution of MADS-box gene induction by FLO/LFY genes. *Journal of Molecular Evolution* **53**, 387-393
- Hirose T, Ujihara A, Kitabayashi H, Minami M** (1994) Interspecific cross-compatibility in *Fagopyrum* according to pollen tube growth. *Breeding Science* **44**, 307-314
- Hirose T, Ujihara A, Kitabayashi H, Minami M** (1995) Pollen tube behavior related to self-incompatibility in interspecific crosses of *Fagopyrum*. *Breeding Science* **45**, 65-70
- Hutchinson JB** (1965) Crop plant evolution: A general discussion. In: Hutchinson J (Ed) *Essays on Crop Plant Evolution*, Cambridge University Press, London, pp 166-181
- Huh MK, Huh HW, Ohnishi O** (2001) Genetic diversity and ecological characteristics in four buckwheat species. *Fagopyrum* **18**, 15-19
- Ilme N, Kiesewetter H, Jung F, Hoffmann KH, Birk A, Müller A, Grütznert KI** (1996) Leg oedema protection from a buckwheat herb tea in patients with chronic venous insufficiency: a single-centre, randomised, double-blind, placebo-controlled clinical trial. *European Journal of Clinical Pharmacology* **50**, 443-447
- Jansen PCM** (2006) *Fagopyrum esculentum* Moench. In: Brink M, Belay G (Eds) *PROTA 1: Cereals and Pulses/Céréales et Légumes Secs*. [CD-Rom]. PROTA, Wageningen, Netherlands.
- Kalinová J, Moudry J** (2003) Evaluation of frost resistance in varieties of common buckwheat (*Fagopyrum esculentum* Moench). *Plant Soil and Environment* **49**, 410-413
- Kawasaki M, Ohnishi O** (2006) Two distinct groups of natural populations of *Fagopyrum urophyllum* (Bur. et Franch.) Gross revealed by the nucleotide sequence of a non-coding region in chloroplast DNA. *Genes and Genetic Systems* **81**, 323-332
- Kishima Y, Ogura K, Mizukami K, Mikami T, Adachi T** (1995) Chloroplast DNA analysis in buckwheat species: phylogenetic relationships, origin of the reproductive systems and extended inverted repeats. *Plant Science* **108**, 173-179
- Konishi T, Ohnishi O** (2001) Wild *Fagopyrum* species in eastern Tibet. *Breeding Research* **3** (Supplement 1), 165 (in Japanese)
- Konishi T, Yasui Y, Ohnishi O** (2005) Original birthplace of cultivated common buckwheat inferred from genetic relationships among cultivated populations and natural populations of wild common buckwheat revealed by AFLP analysis. *Genes and Genetic Systems* **80**, 113-119
- Kreft I** (1998) A genetic basis for buckwheat breeding. In: Campbell C, Przybylski R (Eds) *Advances in Buckwheat Research. Proceedings of the 7th International Symposium on Buckwheat*, Winnipeg, Manitoba, Canada 1998, International Buckwheat Research Association, pp 255-264
- Kreft I, Chrunghoo NK, Devadasan N, Licen M, Chai Y, Wang Z, Zhang Z, Lin R, Ikeda S, Ikeda K, Wieslander G, Norbäck D, Fabjan N, Germ M** (2007) Perspectives of breeding buckwheat for high quality. In: Yan C, Zongwen Z (Eds) *Advances in Buckwheat Research. Proceedings of the 10th International Symposium on Buckwheat*, Yangling, Shaanxi, China, 2007, Northwest A&F University Press, pp 1-6
- Lazányi J** (1999) Buckwheat. In: Lazányi J, Dobránszki J (Eds) *Agricultural Research in Nyírség Region*, Research Centre of Debrecen Agricultural University, Nyíregyháza, pp 91-92
- Li QY, Yang MX** (1992) Preliminary investigation on buckwheat origin in Yunnan. In: Lin R, Zhou M, Tao Y, Li J, Zhang Z (Eds) *Proceedings of the 5th International Symposium on Buckwheat*, Taiwan, China 1992, Agricultural Publishing House, pp 44-46
- Logacheva MD, Samigullin TH, Dhingra A, Penin AA** (2008) Comparative chloroplast genomics and phylogenetics of *Fagopyrum esculentum* ssp. *ancestrale* – A wild ancestor of cultivated buckwheat. *BMC Plant Biology* **8**, 59
- Matsui K, Tetsuka T, Nishio T, Hara T** (2003) Heteromorphic incompatibility retained in self-compatible plants produced by a cross between common and wild buckwheat. *New Phytologist* **159**, 701-708
- Moench C** (1794) *Methodus plantarum horti botanici et agri Marburgensis: a staminum situ describendi / auctore Conrado Moench. Marburgi Cattorum*. Officina Nova Libraria Academiae, Missouri Botanical Garden Library Online Catalogue
- Molina-Cano JL, Moralejo M, Igartua E, Romagosa I** (1999) Further evidence supporting Morocco as a center of origin of barley. *Theoretical and Applied Genetics* **98**, 913-918
- Murai M, Onishi O** (1995) Diffusion routes of buckwheat cultivation in Asia revealed by RAPD markers. In: Matano T, Ujihara A (Eds) *Current Advances in Buckwheat Research, Proceedings of the 6th International Symposium on Buckwheat*, Shinshu, Japan 1995, Shinshu University Press, Nagano, Japan pp 163-173
- Nagano Y, Matsuno R, Sasaki Y** (1991) Sequence and transcriptional analysis of the gene cluster *trnQ-zfpA-psaI-ORF231-petA* in pea chloroplasts. *Current Genetics* **20**, 431-436
- Nagatomo T** (1984) Soba-no-Kagaku (Scientific considerations on buckwheat), Shincho-sha, Tokyo (in Japanese)
- Neuhaus H, Link G** (1987) The chloroplast rRNAlys(UUU) gene from mustard (*Sinapis alba*) contains a class II intron potentially coding for a maturase-related polypeptide. *Current Genetics* **11**, 251-257
- Nishimoto Y, Ohnishi O, Hasegawa M** (2003) Topological incongruence between nuclear and chloroplast DNA trees suggesting hybridization in the urophyllum group of the genus *Fagopyrum* (Polygonaceae). *Genes and Genetic Systems* **78**, 139-153
- Ohnishi O** (1983) Isozyme variation in common buckwheat *Fagopyrum esculentum* Moench., and its related species. In: Nagatomo T, Adachi T (Eds) *Proceedings of the 2nd International Symposium on Buckwheat*, Miyazaki, Japan, 1983, Organizing Committee, pp 39-50
- Ohnishi O** (1985) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. IV. Allozyme variability in Nepali and Kashmirian populations. *The Japanese Journal of Genetics* **60**, 293-305
- Ohnishi O** (1986) Evaluation of world buckwheat varieties from the viewpoints of genetics, breeding and the origin of buckwheat cultivation. In: *Proceedings of the 3rd International Symposium on Buckwheat*, Pulawy, Poland Part I, 1986 International Symposium on Buckwheat Committee, pp 198-213
- Ohnishi O** (1988) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. VII. Allozyme variability in Japan, Korea and China. *The Japanese Journal of Genetics* **63**, 507-522
- Ohnishi O** (1989) Cultivated buckwheat species and their relatives in the Himalaya and southern China. In: *Proceedings of the 4th International Symposium on Buckwheat*, Orel, USSR, pp 562-571
- Ohnishi O** (1990) Discovery of the wild ancestor of common buckwheat. *Fagopyrum* **11**, 5-10
- Ohnishi O** (1992) Buckwheat in Bhutan. *Fagopyrum* **12**, 5-13
- Ohnishi O** (1993a) A memorandum on the distribution of buckwheat species in Tibet and the Himalayan hills: has buckwheat crossed the Himalayas? *Fagopyrum* **13**, 3-10
- Ohnishi O** (1993b) Population genetics of cultivated common buckwheat *Fagopyrum esculentum* Moench. IX. Concluding remarks on worldwide survey of allozyme variability. *The Japanese Journal of Genetics* **68**, 317-326
- Ohnishi O** (1993c) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. VIII. Local differentiation of landraces in Europe and the silk road. *The Japanese Journal of Genetics* **68**, 303-316
- Ohnishi O** (1994) Buckwheat in Karakoram and the Hindkush. *Fagopyrum* **14**, 17-25
- Ohnishi O** (1995) Discovery of new *Fagopyrum* species and its implication for the studies of evolution of *Fagopyrum* and of the origin of cultivated buckwheat. In: Matano T, Ujihara A (Eds) *Current Advances in Buckwheat Research, Proceedings of the 6th International Symposium on Buckwheat*, Shinshu, Japan, 1995, Shinshu University Press, Nagano, Japan, pp 175-190
- Ohnishi O** (1998a) Search for the wild ancestor of buckwheat I. Description of new *Fagopyrum* (Polygonaceae) species and their distribution in China and the Himalayan hills. *Fagopyrum* **15**, 18-28
- Ohnishi O** (1998b) Search for the wild ancestor of Buckwheat III. The wild ancestor of cultivated common buckwheat, and of tartary buckwheat. *Economic Botany* **52** (2), 123-133
- Ohnishi O** (1999) Non-shattering habit gene (*sh1*), chlorophyll-deficient and other detrimental genes concealed in natural populations of the wild ancestor of common buckwheat. *Fagopyrum* **16**, 23-28
- Ohnishi O** (2001) Recent progress of the study on wild *Fagopyrum* species. In: Ham SS, Choi YS, Kim NS, Park CH (Eds) *Advances in Buckwheat Research, Proceedings of the 8th International Symposium on Buckwheat*, Chunchon, Korea 2001, Kangwon National University Press, Chunchon, Korea, pp 218-224
- Ohnishi O** (2004) Wild buckwheat species in the Sang Jiang (Three Rivers) area of southwestern China. In: Faberová I (Ed) *Advances in Buckwheat Research, Proceedings of the 9th International Symposium on Buckwheat*, Prague, 2004, Research Institute of Crop Production, pp 226-232
- Ohnishi O** (2007) Natural populations of the wild ancestor of cultivated common buckwheat, *Fagopyrum esculentum* ssp. *ancestrale* from the Dongyi River Valley – their distribution and allozyme variations. In: Chai Y, Zhang Z-W (Eds) *Advances in Buckwheat Research, Proceedings of the 10th International Symposium on Buckwheat*, Yangling, Shaanxi, China, 2007, Northwest A&F University Press, pp 13-18
- Ohnishi O, Matsuoka Y** (1996) Search for the wild ancestor of buckwheat. II. Taxonomy of *Fagopyrum* (Polygonaceae) species based on morphology, iso-

- zymes and cpDNA variability. *Genes and Genetic Systems* **71**, 383-390
- Ohnishi O, Nishimoto T** (1988) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. V. Further studies on allozyme variability in the Indian and Nepali Himalaya. *The Japanese Journal of Genetics* **63**, 51-66
- Ohsako T, Ohnishi O** (1998) New *Fagopyrum* species revealed by morphological and molecular analyses. *Genes and Genetic Systems* **73**, 85-94
- Ohsako T, Ohnishi O** (2000) Intra- and interspecific phylogeny of wild *Fagopyrum* (Polygonaceae) species based on nucleotide sequences of non-coding regions in chloroplast DNA. *American Journal of Botany* **87**, 573-582
- Ohsako T, Ohnishi O** (2001) Nucleotide sequence variation of the chloroplast *trnK/matK* region in two wild *Fagopyrum* (Polygonaceae) species, *F. leptopodum* and *F. stictice*. *Genes and Genetic Systems* **76**, 39-46
- Ohsako T, Fukuoka S, Bimbj HP, Baniyaj BK, Yasui Y, Ohnishi O** (2001) Phylogenetic analysis of the genus *Fagopyrum* (Polygonaceae), including the Nepali species *E. megacarpum*, based on nucleotide sequence of the *rbcl-accD* region in chloroplast DNA. *Fagopyrum* **18**, 9-14
- Ohsako T, Yamane K, Ohnishi O** (2002) Two new *Fagopyrum* (Polygonaceae) species, *F. gracilipedoides* and *F. jinshaense* from Yunnan, China. *Genes and Genetic Systems* **77**, 399-408
- Online Etymology Dictionary**
(<http://www.etymonline.com/index.php?term=buckwheat>)
- Park BJ, Lee JK, Shin JH, Park JI, Kim NS, Park CH** (2006) Genetic diversity of cultivated and wild Tartary buckwheat (*Fagopyrum tataricum* Gaert.) accessions by AFLP analyses. *Korean Journal of Genetics* **28**, 91-98
- Porcher Michel H** (1995-2020) Sorting *Fagopyrum* Names. *Multilingual Multiscript Plant Name Database*. School of Agriculture and Food Systems. Faculty of Land & Food Resources. The University of Melbourne. Australia, <http://gmr.landfood.unimelb.edu.au/Plantnames/Sorting/Fagopyrum.html>
- Sang T** (2002) Utility of low-copy nuclear gene sequences in plant phylogenetics. *Critical Reviews in Biochemistry and Molecular Biology* **37**, 121-147
- Serving History** (www.servinghistory.com/topics/Polygonaceae)
- Sharma KD, Boyes JW** (1961) Modified incompatibility of buckwheat following irradiation. *Canadian Journal of Botany* **39**, 1241-1246
- Sharma TR, Jana S** (2002) Species relationships in *Fagopyrum* revealed by PCR-based DNA fingerprinting. *Theoretical and Applied Genetics* **105**, 306-312
- Steward AN** (1930) The polygonaceae of eastern Asia. *Contributions from the Gray Herbarium* **88**, 1-129
- Tahir I, Farooq S** (1989) Grain and leaf characteristics of perennial buckwheat (*Fagopyrum cymosum* Meissn.). *Fagopyrum* **9**, 41-43
- Tahir I, Farooq S** (1992) Buckwheat research in Kashmir. In: Lin R, Zhou M-D, Tao Y-R, Li J-Y, Zhang Z-W (Eds) *Proceedings of the 5th International Symposium on Buckwheat*, Taiwan, China 1992, Agricultural Publishing House, pp 83-87
- Taylor DP, Obendorf RL** (2001) Quantitative assessment of some factors limiting seed set in buckwheat. *Crop Science* **41**, 1792-1799
- Tsuji K, Ohnishi O** (2000) Origin of cultivated tartary buckwheat (*Fagopyrum tataricum* Gaertn.) revealed by RAPD analyses. *Genetic Resources and Crop Evolution* **47**, 431-438
- Tsuji K, Ohnishi O** (2001a) Phylogenetic position of east Tibetan natural populations in tartary buckwheat (*Fagopyrum tataricum* Gaert.) revealed by RAPD analyses. *Genetic Resources and Crop Evolution* **48**, 63-67
- Tsuji K, Ohnishi O** (2001b) Phylogenetic relationships among wild and cultivated Tartary buckwheat (*Fagopyrum tataricum* Gaert.) populations revealed by AFLP analyses. *Genes and Genetic Systems* **76**, 47-52
- Tsui K, Yasui Y, Ohnishi O** (1999) Search for *Fagopyrum* species in eastern Tibet. *Fagopyrum* **16**, 1-6
- USDA, ARS, National Genetic Resources Program**. National Germplasm Resources Laboratory, Beltsville, Maryland
<http://www.ars-grin.gov/cgi-bin/npgs/html/taxon>
- Vavilov N** (1926) *Centers of Origin of Cultivated Plants*, The Institute of Applied Botany and Plant Breeding 16(2), Leningrad
- Vuilleumier BS** (1967) The origin and evolutionary development of heterostyly in Angiosperms. *Evolution* **21**, 210-226
- Wang A-H, Xia M-Z, Cai G-Z, Ren Y-H** (2007) Investigation and study on the geographical distribution of wild buckwheat resources in Sichuan. In: Chai Y, Zhang Z-W (Eds) *Proceedings of the 10th International Symposium on Buckwheat*, 2007, Xian, pp 41-45
- Wang Y, Scarth R, Campbell C** (2005a) Inheritance of seed shattering in interspecific hybrids between *Fagopyrum esculentum* and *Fagopyrum homotropicum*. *Crop Science* **45**, 693-697
- Wang Y, Scarth R, Campbell C** (2005b) S^h and S^c – Two complementary dominant genes that control self-compatibility in buckwheat. *Crop Science* **45**, 1229-1234
- Wolfe KH, Li W-H, Sharp PM** (1987) Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. *Proceedings of the National Academy of Sciences USA* **84**, 9054-9058
- Woo SH, Adachi T, Jong SK, Campbell CG** (1999) Inheritance of self-compatibility and flower morphology in an interspecific buckwheat hybrid. *Canadian Journal of Plant Science* **79**, 483-490
- Yamane K, Yasui Y, Ohnishi O** (2003) Intraspecific cpDNA variations of diploid and tetraploid perennial buckwheat, *Fagopyrum cymosum* (Polygonaceae). *American Journal of Botany* **90**, 339-346
- Yasui Y, Ohnishi O** (1996) Comparative study of *rbcl* gene sequences in *Fagopyrum* and related taxa. *Genes and Genetic Systems* **71**, 219-224
- Yasui Y, Ohnishi O** (1998a) Interspecific relationships in *Fagopyrum* (Polygonaceae) revealed by the nucleotide sequences of the *rbcl* and *accD* and their intergenetic region. *American Journal of Botany* **85**, 1134-1142
- Yasui Y, Ohnishi O** (1998b) Phylogenetic relationships among *Fagopyrum* species revealed by the nucleotide sequences of the ITS region of the nuclear rRNA gene. *Genes and Genetic Systems* **73**, 201-210
- Ye NG, Guo GQ** (1992) Classification, origin and evolution of genus *Fagopyrum* in China. In: Lin R, Zhou M-D, Tao Y-R, Li J-Y, Zhang Z-W (Eds) *Proceedings of the 5th International Symposium on Buckwheat*, Taiwan, China 1992, Agricultural Publishing House, pp 19-28