

# The Biology of Invasive Alien Plants in Canada. 3. *Amaranthus tuberculatus* (Moq.) Sauer var. *rudis* (Sauer) Costea & Tardif

Mihai Costea<sup>1</sup>, Susan E. Weaver<sup>2</sup>, and François J. Tardif<sup>3</sup>

<sup>1,3</sup>Department of Plant Agriculture, Crop Science Building, University of Guelph, Guelph, Ontario, Canada N1G 2W1 (e-mail: <sup>1</sup>coste\_amihai@hotmail.com and <sup>2</sup>ftardif@uoguelph.ca); <sup>2</sup>Research Station, Agriculture and Agri-Food Canada, Harrow, Ontario, Canada NOR 1G0 (e-mail: weavers@agr.gc.ca).

Received 7 June 2004, accepted 21 October 2004.

Costea, M., Weaver, S. E. and Tardif, F. J. 2005. **The Biology of Invasive Alien Plants in Canada. 3. *Amaranthus tuberculatus* (Moq.) Sauer var. *rudis* (Sauer) Costea & Tardif.** Can. J. Plant Sci. **85**: 507–522. This annual dioecious weed was found in 2002 and 2003 infesting soybean fields in southwestern Ontario, and it was collected in 1992 from waste places in British Columbia. It is a major weed problem in field crops in the mid-western United States, where it has become increasingly difficult to control during the past 10 yr. Morphological differences between *Amaranthus tuberculatus* var. *rudis* and var. *tuberculatus* are presented. A review of the biological information published is provided. Plants exhibit high phenotypic plasticity and genetic variability. Emergence is prolonged, growth rapid, and female plants produce a large number of viable seeds that contribute to a persistent seed bank. *Amaranthus tuberculatus* var. *rudis* has developed multiple resistance to triazine and acetolactate synthase- and protoporphyrinogen-inhibiting herbicides. Airborne pollen can travel significant distances and *A. tuberculatus* var. *rudis* may hybridize with other noxious *Amaranthus* spp. transferring herbicide resistance or other traits.

**Key words:** *Amaranthus tuberculatus* var. *rudis*, AMATA, *Amaranthus rudis*, common waterhemp, weed biology, invasive alien

Costea, M., Weaver, S. E. et Tardif, F. 2005. **Biologie des espèces exotiques envahissantes au Canada. *Amaranthus tuberculatus* (Moq.) Sauer var. *rudis* (Sauer) Costea & Tardif.** Can. J. Plant Sci. **85**: 507–522. Cette adventice annuelle dioïque a été découverte en 2002 et en 2003 dans des champs de soja du sud-ouest de l'Ontario. On en avait déjà prélevé des spécimens en 1992, dans des endroits désolés de la Colombie-Britannique. Cette plante pose un grave problème dans les cultures du centre-ouest des États-Unis où elle est devenue de plus en plus difficile à contrôler au cours des dix dernières années. Suivent les différences morphologiques entre *Amaranthus tuberculatus* var. *rudis* et var. *tuberculatus*. L'article passe aussi en revue les données biologiques. La plante montre un phénotype d'une grande plasticité et un génotype très variable. Sa levée est prolongée, sa croissance rapide et les plants femelles produisent un grand nombre de semences viables qui concourent à créer un réservoir de graines tenace. *Amaranthus tuberculatus* var. *rudis* a acquis une résistance multiple à la triazine et à l'acétolactate synthase ainsi qu'aux herbicides inhibant le protoporphyrinogène. Le pollen véhiculé dans l'air parcourt de grandes distances et *A. tuberculatus* var. *rudis* s'hybride avec d'autres espèces nuisibles du genre *Amaranthus* pour leur transférer la résistance aux herbicides et d'autres caractères.

**Mots clés:** *Amaranthus tuberculatus* var. *rudis*, AMATA, *Amaranthus rudis*, amarante rugueuse, biologie des mauvaises herbes, plante exotique envahissante

## 1. Name and Generic Status

*Amaranthus tuberculatus* (Moq.) Sauer var. *rudis* (Sauer) Costea & Tardif (Costea and Tardif 2003b) — Synonym: *Amaranthus rudis* Sauer—**common water-hemp** (Darbyshire 2003), common waterhemp [Weed Science Society of America (WSSA) 2004]; **amarante rugueuse** (Darbyshire 2003). Bayer code: AMATA. *Amaranthus tuberculatus* (Moq.) Sauer var. *tuberculatus*—**tall water-hemp** (Darbyshire 2003), tall waterhemp (WSSA 2004); **acnide tuberculée** (Darbyshire 2003). Bayer code: AMATU. Amaranthaceae, amaranth family, Amarantacées.

The genus *Amaranthus* consists of about 70 species that are distributed worldwide. The approximately 40 species that occur in North America are mostly native, weeds or cultivated ornamentals, pseudocereals or vegetables, and only a few are introduced (Costea et al. 2001a, b). *Amaranthus*

*tuberculatus* belongs to subgenus *Acnida*, which comprises 10 dioecious species (Mosyakin and Robertson 1996). For the etymology of the generic name see Costea and Tardif (2003a). “*Tuberculatus*” refers to the fruit surface, which when dry is wrinkled and may appear as covered with tubercles. “*Rudis*” alludes to the tough nature of the plants.

The species has had nomenclatural and taxonomic complications (see Pratt and Clark 2001). Riddell (1835) was the first to name *A. tuberculatus* as *A. altissimus* and *A. miamiensis*. Regrettably, by providing two names, and by stating that these names were “temporary”, Riddell (1835) invalidated them (see Greuter et al. 2001). Later, Moquin-Tandon (1849) named the species *Acnida tuberculata*, which Sauer (1955) recircumscribed to *Amaranthus*, together with the other 10 dioecious species. *Amaranthus rudis* was initially called *Acnida tamariscina* Nuttall. Since the type speci-

men proved to be a hybrid between *A. rudis* and some undetermined amaranth, Sauer (1955) named plants with dehiscent fruits and one developed tepal *Amaranthus rudis*. Sauer (1955) recognized two water-hemp species, *A. tuberculatus* found from Indiana east to Ohio and *A. rudis* found from Nebraska south to Texas, the species being sympatric in Missouri, Illinois and Iowa. Pratt and Clark (2001) included *A. rudis* in synonymy of *A. tuberculatus* on the basis that they represent the morphological extremes of a single species continuum. Costea and Tardif (2003b) supported their treatment as a single species, but proposed their recognition at the varietal level. Historically, Uline and Bray (1895) were the first to observe that “there appears to be but one polymorphous species”, but they accepted the two species as varieties under *Acnida tamariscina* (Moq.) Wood. Taking into account the fact that seedlings in many *Amaranthus* species are more or less similar, the differences observed between the seedlings of *A. tuberculatus* var. *rudis* and var. *tuberculatus* are quite significant (see section 2b). These differences, with the other evidence from morphology (see section 2a) and ecology (see section 5c), support their recognition at varietal rank. In sympatric areas, diagnostic traits may segregate as a result of hybridization forming a unique and inseparable morphological, biological and genetic complex (Pratt and Clark 2001; Costea and Tardif 2003b).

All previously published information pertaining to *Amaranthus rudis* will be summarized below as var. *rudis*. Following Pratt and Clark (2001), some recent studies have failed to make the distinction between *A. tuberculatus* var. *rudis* (common water-hemp) and *A. tuberculatus* var. *tuberculatus* (tall water-hemp). Authors have instead referred to their plant material as “waterhemp”, *A. tuberculatus*. These studies have nevertheless been included in this review since it is very likely that they referred to var. *rudis*, which is a more troublesome weed than var. *tuberculatus*. For the sake of clarity, we therefore recommend, if possible, that authors specify in the future which *A. tuberculatus* variety they studied.

## 2. Description and Account of Variation

(a) *Description*—The following description is based primarily on observations of populations and analysis of herbarium collections from Canada and the United States made by the authors and is supplemented with information taken from the taxonomic literature (Sauer 1955; Pratt and Clark 2001; Costea and Tardif 2003b).

Plants are annual, with a taproot, and reproduce only by seeds. The hypocotyl of seedlings is 2.5–5 cm long, glabrous. Cotyledons are variably shaped, ovate to linear-lanceolate, 12–14 long and 2–4 mm wide. The first leaves are ovate-lanceolate, oblong to oblong-elongate, with 2–4 pairs of secondary veins. Stems of mature plants are erect, (5–) 20–200 (–300) cm in height, glabrous or with sparse hairs. Leaves are long petioled, ovate, rhombic-oblong to lanceolate-oblong, 2–10 long and 1–3 cm wide; the upper leaves are reduced and narrow. Male and female flowers occur on separate plants (dioecious). They are grouped in axillary cymes, which are further arranged in terminal indeterminate and dense inflorescences (thyrses). Terminal inflorescences are usually 10–20 cm long, unbranched, or with numerous paniced branches,

leafy or leafless. Bracts of male flowers are 1.5–2 mm long, with midrib extended into an acuminate apex, those of female flowers are 1.5–2.5 mm long, with a more prominent midrib. Male flowers have five unequal tepals (i.e., sepals and petals are not differentiated); the outer 3 tepals are ca. 3 mm long, acuminate, with conspicuous, excurrent midveins; the inner tepals, ca. 2.5 mm long, obtuse or emarginate. Female flowers with 1 or 2 tepals, one rudimentary and one ca. 2 mm long, narrow-lanceolate, acuminate. Fruit about 1.5 mm long, transversal (circumscissile) dehiscent at the middle, rugose, often reddish. Seeds ca. 1 mm long, elliptic to obovate, with a prominent, conical hilum, dark reddish-brown.

Grant (1959) reported a chromosome count of  $2n = 32$  for *A. tuberculatus* var. *rudis* from Iowa. From the same population, a female plant was triploid ( $2n = 48$ ). The dioecious condition is apparently not associated with heteromorphic chromosomes (Grant 1959).

(b) *Distinguishing Features*—*Amaranthus tuberculatus* is the only dioecious *Amaranthus* species in Canada and it can be easily distinguished at maturity from the monoecious species by the presence of only unisexual flowers on an individual plant. During the vegetative stage, it can be recognized by the usually narrower leaves compared to *A. retroflexus* L., *A. powellii* S. Watson and *A. hybridus* L. An identification key of *Amaranthus* spp. from Canada can be found in Costea and Tardif (2003b).

*Amaranthus tuberculatus* var. *rudis* can be distinguished from var. *tuberculatus* as follows:

Seedlings with the hypocotyl 2.5–5 mm long; cotyledons variable in shape and size, 12–14 × 2–4 mm, ovate to linear-lanceolate; first leaves ovate-lanceolate, oblong or oblong-elongate 15–20 × 5–8 mm (Fig. 1 E1). Female flowers with 1 or 2 tepals, lanceolate or linear (Figs. 1A, 2D). Fruit is dehiscent. (Figs. 1B, 2A) .....*A. tuberculatus* var. *rudis*  
 Seedlings with the hypocotyl 0.5–1.5 mm long; cotyledons uniform, 6–8 × 2.5–3 mm, ovate-elliptic; first leaves ovate to elliptic 12–18 × 9–12 mm (Fig. 1E2). Female flowers without tepals. Fruit is indehiscent. ....*A. tuberculatus* var. *tuberculatus*

(c) *Intraspecific Variation*— The dioecious condition allows an even higher level of polymorphism compared to monoecious amaranths (see Costea et al. 2004).

*Amaranthus tuberculatus* var. *rudis* exhibits extensive morphological variation at both the population and individual levels, including variation in the overall size of plants, the pattern of stem branching and its colour (from green to red), the shape of leaves, and the shape and colour of inflorescences.

(d) *Illustrations*—Colour photographs of entire plants are available online at <http://www.wssa.net> and <http://www.weedscience.org>. The plant, seedlings, details of flowers, fruits and seeds are illustrated in Figs. 1, 2 and 3.

## 3. Economic Importance and Environmental Impact

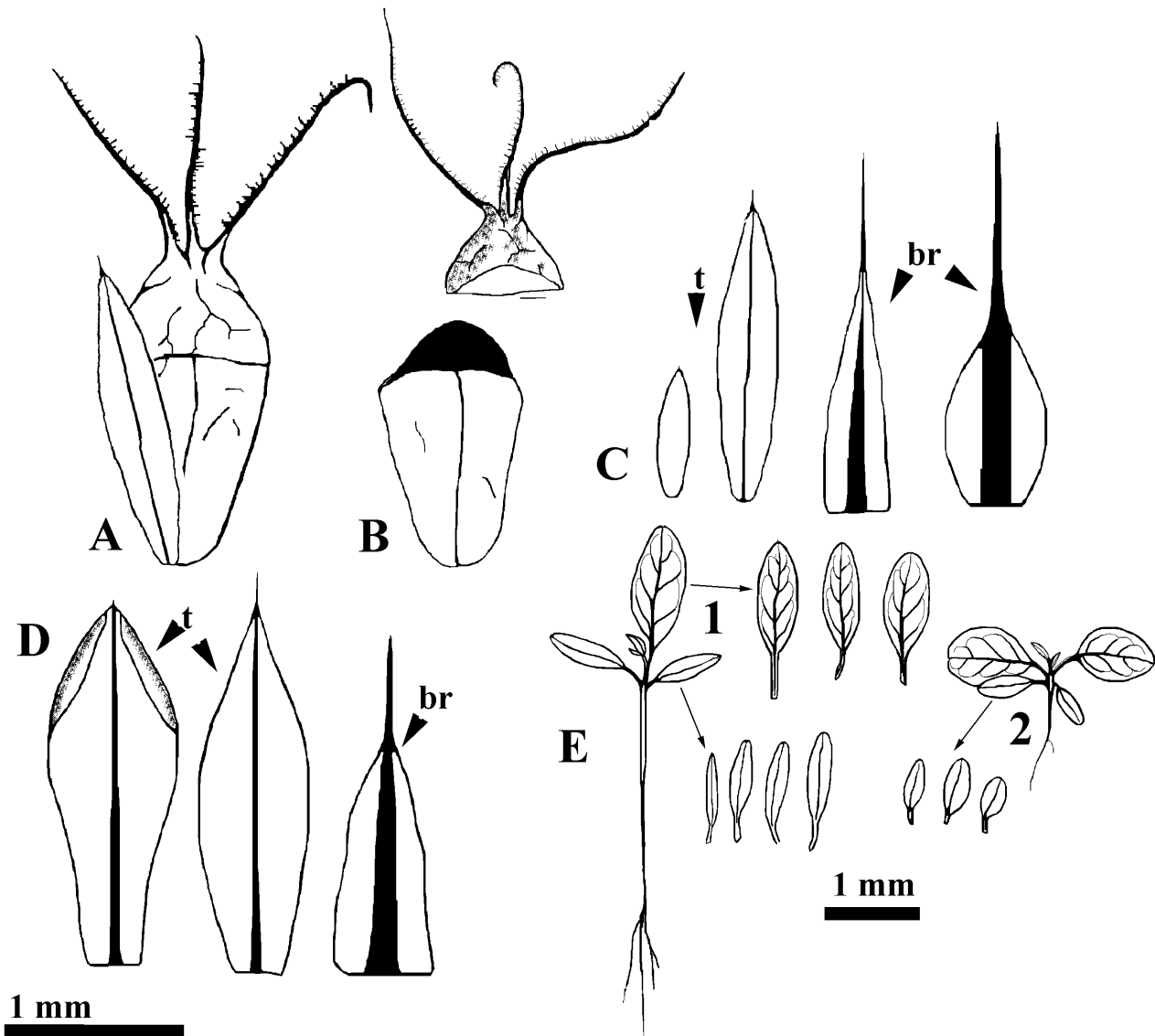
(a) *Detrimental*—There are relatively few crop loss studies available, but these findings suggest that yield losses in soybean [*Glycine max* (L.) Merr.] and corn (*Zea mays* L.) from



Fig. 1. *Amaranthus tuberculatus* var. *rudis*. A. Lower part of plant, B. Inflorescence of female plant. Both scale bars = 4 cm.

*A. tuberculatus* var. *rudis* interference are similar to or greater than those produced by other weedy *Amaranthus* spp. (reviewed by Costea et al. 2004). In Illinois, dense populations of *A. tuberculatus* var. *rudis* (89 to 360 plants  $m^{-2}$ ) that emerged at the soybean unifoliolate stage reduced soybean yield by an average of 43% if they remained all season, and by 13% if they were removed 4 wk after emergence (Hager et al. 2002b). In Kansas, estimated soybean yield

losses from similar densities of *A. tuberculatus* var. *rudis* varied from 27 to 63%, depending on year and location (Bensch et al. 2003). Despite its later time of emergence, *A. tuberculatus* var. *rudis* caused greater yield losses than *A. retroflexus*, but was not as competitive as *A. palmeri* (Bensch et al. 2003). Comparable results were reported from Iowa, Illinois and Missouri (Battles et al. 1998; Jones et al. 1998; Pfeifer et al. 2001, respectively).



**Fig. 2.** A–D. Morphology of fruit and flowers of *Amaranthus tuberculatus* var. *rudis*. A. Female flower, B. Fruit, C. Tepals (t) and bracts (br) of female flowers, D. Tepals (t) and bracts (br) of male flowers, E. Seedlings of: 1. *A. tuberculatus* var. *rudis*, 2. *A. tuberculatus* var. *tuberculatus*. Longer scale bar (= 1 mm) for A, B, C, D; shorter scale bar (=1 mm) for E only.

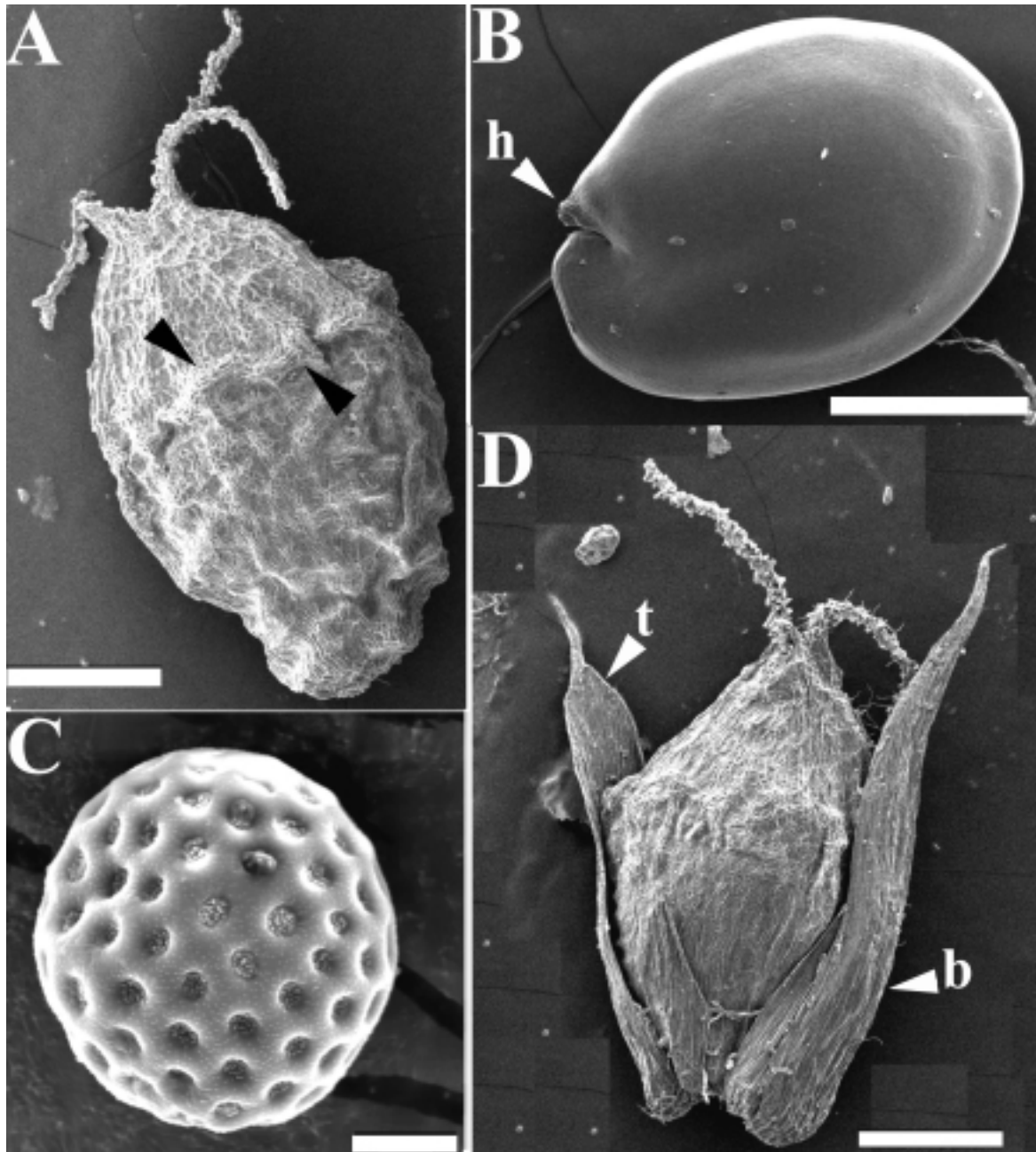
In corn, season-long interference from dense populations of *A. tuberculatus* var. *rudis* (60 to 300 plants  $m^{-2}$ ) reduced yield in Illinois by 74% in 2 yr of the study, and 11% in the third year (Steckel and Sprague 2004). *Amaranthus tuberculatus* var. *rudis* removed before corn had reached the 6-leaf growth stage, or emerging after the corn 10-leaf stage, caused no yield loss. Steckel and Sprague (2004) found that *A. tuberculatus* var. *rudis* interference increased with moisture stress, and Cordes and Johnson (2003) suggested that *A. tuberculatus* var. *rudis* competes strongly with corn for nitrogen and soil moisture.

Pollen grains are strongly allergenic (Lewis et al. 1983). Although there are no reports of cattle poisoning following ingestion, this is a possibility since *Amaranthus* spp. are known to accumulate nitrates and oxalates under certain

conditions (Costea and Tardif 2003c; Costea et al. 2004). The same may be true about the allelopathic effects that have been documented for other *Amaranthus* spp. [reviewed by Costea and Tardif (2003c), Costea et al. (2004)].

(b) *Beneficial*—Beneficial uses of this plant have not been explored. Potentially, some of the uses of other *Amaranthus* spp., as forage, vegetables, phytoremediation of contaminated sites, etc. (Costea and Tardif 2003c; Costea et al. 2004), may apply to *A. tuberculatus* var. *rudis* as well.

(c) *Legislation*—There is no official designation in Canada or the United States (Invaders Database System 2003), and this issue should probably be addressed by the competent institutions.



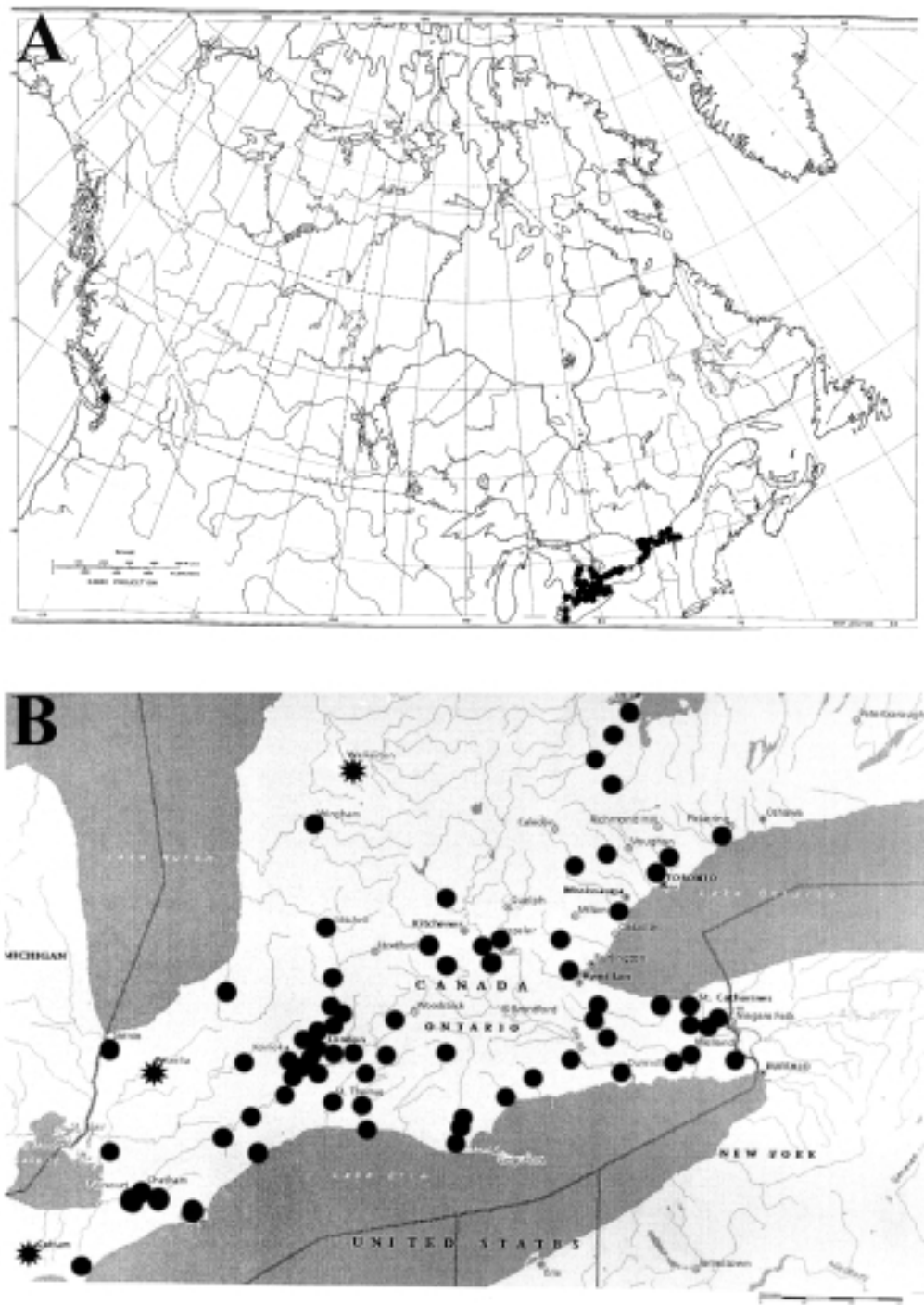
**Fig. 3.** *Amaranthus tuberculatus* var. *rudis*. A. Fruit (arrows indicate dehiscence line, scale bar = 0.5 mm), B. Seed (scale bar = 0.5 mm), C. Pollen grain (scale bar = 10  $\mu$ m), D. Flower (scale bar = 0.5 mm). h = hilum, t = tepal, b = bract

#### 4. Geographical Distribution

The geographical distribution in Canada (Fig. 4) is based on field surveys and herbarium material. *Amaranthus tuberculatus* is native to North America (Sauer 1955). Although *A. tuberculatus* var. *tuberculatus* is most likely native to southern Ontario and western Québec, var. *rudis* has probably been introduced in Canada from the United States. This is supported by the fact that *A. tuberculatus* var. *rudis* has so far been found only in agricultural fields from Petrolia (Lambton Co.), Cottam (Essex Co.) and Walkerton (Huron Co.) in south-

western Ontario in 2002 and 2003. In addition, a few specimens were collected in 1992 from waste places in Burnaby, British Columbia (Costea and Tardif 2003b), where apparently it has not persisted, since it was not mentioned by Douglas et al. (1998). *Amaranthus tuberculatus* var. *tuberculatus* occurs in Canada only on riverbanks, on the margins of lakes and ponds; it has not been collected from ruderal or agricultural fields.

In the United States, *A. tuberculatus* var. *rudis* occurs in 35 states, being notably absent from the western region



**Fig. 4.** Distribution of *Amaranthus tuberculatus* in Canada. [ACAD, ALTA, BH, BRS, DAO, HAM, MMMN, MT, MTMG, NSPM, OAC, OTT, QFA, QK, QUE, SASK, SFS, TRTE, TUP, UAC, UBC, USAS, UWO, UWPG, V, WAT, WIN and WIS; herbarium abbreviations according to Holmgren et al. (1990)] A. General distribution in Canada, B. Distribution in southern Ontario. Dots represent *A. tuberculatus* var. *tuberculatus*, and star-shapes *A. tuberculatus* var. *rudis*.

(Sauer 1955; Sauer 1972; USDA NRCS 2004), where it is likely to spread in the future. It has also been introduced to Europe (Aellen 1959; Joel and Liston 1986; Costea 1996).

### 5. Habitat

(a) *Climatic Requirements*—*Amaranthus tuberculatus* var. *rudis* occurs over a wide climatic range. The ecological

preferences of this taxon for temperature, water, light and nitrogen content of the soil can be summarized as follows: thermophyte, hygrophyte to mesophyte, heliophyte and nitrophilous.

(b) *Substratum*—*Amaranthus tuberculatus* var. *rudis* can tolerate a broad range of soil types and textures, but it prefers those that are well-drained and rich in nutrients, e.g., nitrophilous alluvial sands or substrates that are suitable for many field vegetables or row crops. The range of acceptable soil pH varies from 4.5 to 8. The plant can easily tolerate the anaerobiosis produced by temporary flooding (USDA, NRCS 2004). It has no salinity tolerance, and CaCO<sub>3</sub> tolerance is said to be moderate (USDA, NRCS 2004). *Amaranthus tuberculatus* var. *rudis*, growing naturally on conserved prairies in South Dakota, occurred only on dry potholes with a substrate that contained on average: 14.6 kg ha<sup>-1</sup> nitrate, 139 kg ha<sup>-1</sup> phosphorus and 1041.7 kg ha<sup>-1</sup> potassium (Umbanhowar 1992).

(c) *Communities in which the Species Occurs*—Similar to *A. tuberculatus* var. *tuberculatus*, var. *rudis* occurs on the margins of fresh waters, rivers, lakes, ponds, marshes, and bogs. However, unlike the former, var. *rudis* also grows in disturbed habitats, such as roadsides, railroads, cultivated fields and gardens. In Canada, it has been encountered only in the latter type of habitats. In a soybean field near Petrolia, in southwestern Ontario, its density reached 100–220 plants m<sup>-2</sup>. Other weed species with much lower densities observed at the site were: *Chenopodium album* L., *A. retroflexus*, *A. powellii* and *Polygonum persicaria* L. In Iowa, *A. tuberculatus* var. *rudis* reached a density of 346 plants m<sup>-2</sup> in corn and soybeans, when no herbicides were applied and represented up to 51% of the total weed population consisting of *Ambrosia artemisiifolia* L., *Asclepias syriaca* L., *Chenopodium album*, *Coryza canadensis* (L.) Cronq., *Cyperus esculentus* L., *Hibiscus trionum* L., *Setaria faberi* Herrm., *S. glauca* (L.) Beauv., *Sida spinosa* L., *Solanum carolinense* L., *S. pycnanthum* Dun., and *Polygonum pennsylvanicum* L. (Felix and Owen 1999).

## 6. History

Herbarium vouchers attest the presence of *A. tuberculatus* var. *tuberculatus* in Ontario and Québec from the end of the 19th and the beginning of the 20th century. For example, in Ontario: London 1880 (DAO, ROM), Thames River 1887; Komoka 1890 (DAO), Ottawa 1892 (DAO); in Québec: St. Amélie 1890 (MT), Saint Laurent 1909 (MT). In contrast, except for a few collections from Burnaby, British Columbia, there are no herbarium records of *A. tuberculatus* var. *rudis* in Canada. Its recent occurrence in agricultural fields from southern Ontario suggests that this weed has been recently introduced from the United States.

## 7. Growth and Development

(a) *Morphology*—*Amaranthus tuberculatus* var. *rudis* has the attributes of an invasive successful weed: ecological plasticity, rapid growth, production of numerous seeds over a prolonged period of time, and seed dormancy (see section 8c).

Plants have an indeterminate growth habit. Stem morphology (length, diameter, orientation and branching pattern) is extremely variable depending on environmental conditions and the response of plants to injury. Under unfavorable conditions, the shoot may not exceed 0.1 m, whereas in favorable circumstances, it may reach 3 m in length. Mechanical factors, such as trampling or cutting, determine formation of secondary axes, and in the former case, plants may adopt a prostrate habit. Plants can regenerate from axillary buds if they are cut above the cotyledons. Cole and Holch (1941) reported that roots of *A. tuberculatus* var. *tuberculatus* growing in a fine silt loam soil in Nebraska, reached about 70 cm in depth and spread laterally for more than 2 m.

The secondary structure of roots and the base of stems of *A. tuberculatus* var. *rudis* is characterized by the development of successive, concentric and centrifugally developing cambial zones (Costea and DeMason 2001). These generate a complex structure consisting of hundreds of collateral bundles as evidenced in ground tissue. The leaves and bracts have C<sub>4</sub> anatomy (Costea 1998; reviewed by Costea and Tardif 2003c). The average density of stomata in mature leaves is 120 stomata mm<sup>-2</sup> in the lower epidermis and 95 stomata mm<sup>-2</sup> in the upper epidermis (Costea 1998). The morphology and structure of the small fruits (Costea et al. 2001c) and seeds facilitate dispersal by water, animals or birds, and to a lesser extent by wind (see section 8b). Embryology is similar to other *Amaranthus* spp. (see Costea and Tardif 2003c; Costea et al. 2004).

(b) *Perennation*—*Amaranthus tuberculatus* var. *rudis* plants are summer annuals and overwinter as seeds on or below the surface of the soil.

(c) *Physiological Data*—*Amaranthus* spp. have the C<sub>4</sub> pathway of photosynthesis (see Costea and Tardif 2003c; Costea et al. 2004), and exhibit the characteristic Kranz anatomy in leaves, cotyledons (see Costea et al. 2004) and bracts (Costea and Tardif 2003d). Although there are few physiological studies on *A. tuberculatus*, it may be assumed that var. *rudis* has traits similar to other weedy *Amaranthus* spp.: high photosynthetic rates at high temperatures and light intensity, reduced photorespiration, low CO<sub>2</sub> compensation point, greater water use efficiency, and increased nitrogen use efficiency (see Costea and Tardif 2003c; Costea et al. 2004).

In a greenhouse study by Guo and Al-Khatib (2003), *A. tuberculatus* var. *rudis* biomass, height and root volume measured at 4 wk after emergence were higher at 25/20°C and 35/30°C than at 15/10°C. Plants died 9 d after being exposed to 45/40°C. Rubisco activity was greater at 15/10°C than at 25/10 or 35/10°C, whereas the chlorophyll content and fluorescence varied inversely.

Horak and Loughin (2000) conducted a 2-yr field study in Kansas comparing the growth rates of four *Amaranthus* spp. in the absence of competition. Growth parameters recorded for *A. tuberculatus* var. *rudis* were: rate of height increase of 0.11 to 0.16 cm per growing degree day; maximum relative growth rate of 0.31 g g<sup>-1</sup> d<sup>-1</sup>; net assimilation rate of 3.9 mg cm<sup>-2</sup> d<sup>-1</sup>; specific leaf area of 160 to 205 cm<sup>2</sup> g<sup>-1</sup>; plant volume of 1 127 162 to 3 946 463 cm<sup>3</sup>; and dry weight of 222 to 742 g plant<sup>-1</sup>. Based on these parameters, *A. tuberculatus*

var. *rudis* ranked second after *A. palmeri* and ahead of *A. retroflexus* and *A. albus* L. In a similar experiment undertaken in Missouri, *A. tuberculatus* var. *rudis* ranked after *A. palmeri*, *A. retroflexus* and *A. hybridus*, based on dry weight measured at the end of the season (Sellers et al. 2003).

Similar to other *Amaranthus* spp., *A. tuberculatus* var. *rudis* plants exhibit a facultative short-day flowering response. Under short-day conditions, flowering is initiated very early, at the cost of reduced vegetative growth and lower seed production. Under long-day conditions, plants grow larger, flower later, and produce more seeds if sufficient time is available (see section 7d). Steckel et al. (2003) in Illinois reported that growth of female plants of var. *rudis* depended on time of emergence and light availability. Plants grown under full sun accumulated 720 g plant<sup>-1</sup> when they emerged in late May and 350 g plant<sup>-1</sup> when they emerged in late June. Under 40 and 68% shading, plants produced 550 and 370 g plant<sup>-1</sup>, respectively, when emerged in May, and 220 and 170 g plant<sup>-1</sup>, respectively, when emerged in June. Furthermore, under shaded conditions, more biomass was partitioned to the leaves at the cost of reproductive structures, resulting in higher leaf area ratios (up to 1.5-fold, 2.2-fold and 2.8-fold increase under 40, 68 and 99% shade levels, respectively).

(d) *Phenology*—*Amaranthus tuberculatus* var. *rudis* is a summer annual that emerges in southern Ontario from the beginning of June to August. In Iowa, emergence began in late May and continued through early August (Hartzler et al. 1999). In Missouri, *A. tuberculatus* var. *rudis* emerged 7 to 10 d later than *A. hybridus* and *A. albus*, and 10–12 d later than *A. retroflexus* (Sellers et al. 2003). Flower initiation depends on photoperiod. Plants grown under short-day conditions (8 h) require 14–16 d to initiate flowering, whereas plants grown under long-day conditions (16 h) need approximately 45 d. These data are in agreement with those for other *Amaranthus* spp. (reviewed by Costea et al. 2004). Flowering and seed set continue until the first frost, which in southern Ontario coincides with the end of October or the beginning of November.

(e) *Mycorrhiza*—Although Amaranthaceae have traditionally been considered non-mycorrhizal, vesicular-arbuscular mycorrhizae have been observed under certain conditions in several other *Amaranthus* spp. (reviewed by Costea et al. 2004).

## 8. Reproduction

(a) *Floral Biology*—The inflorescence of *Amaranthus* spp. is fairly complex (reviewed by Costea et al. 2004). Flowers are unisexual (diclinous), and in the dioecious species, male and female flowers occur on separate plants. Steinau et al. (2003) observed that a hybrid between *A. tuberculatus* var. *rudis* and *A. hybridus* had predominantly female flowers, but also a small male inflorescence making such plants monoecious. The flowers of both male and female plants develop in numerous dense cymes, which are further arranged in spikes (spiciform branches). Although Murray's (1940) results indicated that an equal number of male and

female seeds are produced in dioecious species, Lemen (1980) found that the proportion of male plants in a population of *A. tuberculatus* var. *rudis* from Illinois was 0.33, which significantly deviates from the normal 1:1 sex ratio. The ratio of males to females in Ontario field populations in 2003 and when grown from seed in the greenhouse was very close to 1:1 (Weaver, unpublished data). Menalled et al. (2004) reported a marginally higher male to female ratio in plants grown from seed receiving compost-amended treatments compared with compost-free treatments ( $P = 0.061$ ).

Flowers are small, wind-pollinated and plants are necessarily outcrossing. Male flowers have five stamens; anthers open longitudinally, and their volume is about 0.157 mm<sup>3</sup> (Lemen 1980). The pollen grain is spherical, 18–25 µm in diameter, with 90–110 sunken apertures uniformly distributed on its surface (Fig. 2C) (Costea 1998; Franssen et al. 2001b). The number of apertures is twice that found in monoecious species (Costea 1998; Franssen et al. 2001b). These are extreme aerodynamic adaptations for wind pollination. The numerous, uniformly distributed apertures generate a layer of turbulent air that decreases the friction between the pollen grain and the air, maximizing the distance pollen grains can be wind-dispersed (Franssen et al. 2001b). The pollen grain is covered with granules that ensure the adherence to stigma hairs.

The perianth of female flowers is reduced to one or two short tepals, and therefore the gynoecium is more exposed than in other dioecious (e.g., *A. palmeri*) or some monoecious species (e.g., *A. retroflexus*), which have five tepals that are longer than the gynoecium. The gynoecium does not have a style and consists of two or three united carpels (Costea et al. 2001c). The two or three stigma are significantly longer than in monoecious species (stigmas of 3.2–4.3 mm in *A. tuberculatus* var. *rudis*, versus stigmas of 0.9–2.1 mm in *A. hybridus*, *A. powellii* and *A. retroflexus*; Costea 1998). The stigmas are covered with 2–4 rows of receptive hairs (Costea et al. 2001c). Stigmas of unfertilized female flowers can persist indefinitely until pollen reaches them, consistent with observations on another dioecious species, *A. cannabinus* (Quinn et al. 2000). After fertilization, the stigmas dry out.

In two populations from Illinois, female plants had at least one male plant within 1 to 6 m distance (Lemen 1980). However, the maximum distance that pollen can travel is much further. We determined the downwind distance of pollen transfer with the following equation (Kyaw Tha Paw and Hotton 1989):

$$L = UH/V_{\text{set}} \quad (1)$$

where  $L$  is the downwind distance of pollen transfer (m);  $U$  is mean wind speed (m s<sup>-1</sup>);  $H$  is the height at which pollen is released (m); and  $V_{\text{set}}$  is the settling velocity (m s<sup>-1</sup>). After their release, pollen grains fall towards the ground with a certain settling velocity ( $V_{\text{set}}$ ), which is determined by the aerodynamics of the pollen grain and gravity. Settling velocities can be determined using the equation of Stokes (Gregory 1973):



$$V_{\text{set}} = 2/9 (\rho_p - \rho_a) d^2/\mu \quad (2)$$

where  $\rho_p$  is pollen density ( $\text{g cm}^{-3}$ );  $\rho_a$  is atmospheric density;  $d$  is pollen diameter; and  $\mu$  is dynamic viscosity (approximately  $1.8 \times 10^{-4} \text{ g cm}^{-1} \text{ s}^{-1}$ ). Assuming that pollen grains are spherical, without any ornamentation, and that pollen density is  $1 \text{ g cm}^{-3}$  (Kyaw Tha Paw and Hotton 1989), the calculated value of  $V_{\text{set}}$  for *A. tuberculatus* var. *rudis* would be between 0.0185 and  $0.021 \text{ m s}^{-1}$ , depending on pollen size.

Based on Eq. 1, if male plants were 0.5 m tall, and the wind velocity  $10 \text{ km h}^{-1}$ , pollen grains could reach a distance of 35–50 m. If plants were 1 m tall and the wind velocity  $40 \text{ km h}^{-1}$ , pollen grains could travel 300–325 m. These estimates do not take into account the effect of the plant canopy, which is likely to significantly reduce the distance of pollen transfer, or the aerodynamic ornamentation of pollen grains, which is likely to increase the distance of pollen transfer. These simple estimations show that pollen can be carried significant distances. However, isolated female plants will not form seeds, and this may be viewed as a significant cost of dioecism.

Inbreeding is often considered a specialization of annual weeds and pioneer species (e.g., Baker and Stebbins 1965). In the case of *Amaranthus* spp., some dioecious species, like *A. tuberculatus* var. *rudis* and *A. palmeri*, are just as successful as monoecious species, such as *A. retroflexus*, *A. powellii*, and *A. hybridus*. The recombination potential of dioecious amaranths appears to outweigh the costs of dioecism, especially when the large number of seeds produced by a single plant renders irrelevant the fact that initial colonization cannot start from a single seed (see section 8b). Indeed, colonization by *A. tuberculatus* var. *rudis* has to begin with several plants (a micropopulation), and not with single plants as in the case of monoecious amaranths. Although this may be regarded as a disadvantage, after initial establishment, its spread will progress as fast as in monoecious species.

(b) *Seed Production and Dispersal*—Unlike the monoecious amaranths, only female plants of *A. tuberculatus* var. *rudis* produce seeds, and therefore seed production at the population level may be lower than in the former species. However, female plants of dioecious species may have a greater capacity for seed production because they do not partition resources to male flowers as in monoecious amaranths (see Costea et al. 2004). Comparison of rates of increase of populations of dioecious and monoecious amaranths deserves further attention. A single female plant of *A. tuberculatus* var. *rudis* normally produces between 35 000 and 1 200 000 seeds (Stevens 1932; Sellers et al. 2003; Steckel et al. 2003; Hartzler et al. 2004). Fecundity declines, along with biomass and height, as time of emergence is delayed (Steckel et al. 2003; Hartzler et al. 2004; Nordby and Hartzler 2004). Female plants emerging with soybean at four sites in central Iowa produced on average 300 000 seeds  $\text{plant}^{-1}$ , whereas those emerging 50 d after planting produced 3000 seeds  $\text{plant}^{-1}$  (Hartzler et al. 2004). In corn, in Iowa the earliest emerging *A. tuberculatus* var. *rudis* plants produced 48 400 seeds, whereas those emerging at the

corn 6-leaf stage produced 950 seeds  $\text{plant}^{-1}$ , and plants emerging after the corn 8-leaf stage failed to reproduce (Nordby and Hartzler 2004). Seed production by plants emerging in late May in Illinois declined from over 1 million seeds per plant in full sunlight, to 401 200 seeds  $\text{plant}^{-1}$  under 68% shade and 8 seeds under 99% shade (Steckel et al. 2003). Seeds from North Dakota and Illinois weigh 0.19–0.27 g per 1000 seeds (Stevens 1932; Lemen 1980; Sellers et al. 2003). The size and weight of the seeds are likely to vary among different populations, among individuals within populations and even from the same plant (see Costea et al. 2004).

Seed dispersal is accomplished by water, farm machinery, spreading of manure and compost, birds, animals, and to a lesser extent by wind, as with other *Amaranthus* spp. (Costea et al. 2004). Dispersal by water (streamlets produced on the soil by rain, surface irrigation, and rivers) may be significant since both fruits and seeds float, and plants prefer the proximity of water. There is no information regarding the survival capacity of seeds in the digestive tract of animals or during composting. Nevertheless, judging by the similar structure of the seed coat, it can be speculated that these values are comparable to those observed in other *Amaranthus* spp. (see Costea et al. 2004). For example, seeds of *A. retroflexus* survived digestion by 10-mo-old lambs, rumen digestion by cattle (27–45% of the seeds survived), ensiling followed by rumen digestion (1–6% of the seeds survived), and a small percentage of seeds (3.5%) survived after 2 wk of windrow composting at temperatures of 55–65°C (reviewed by Costea et al. 2004).

(c) *Seed Banks, Seed Viability and Germination*—Seeds of *A. tuberculatus* var. *rudis* have a high (>80%) initial viability (Leon et al. 2004; Steckel et al. 2004), and are likely to form a persistent seed bank, similar to other *Amaranthus* spp. (Costea and Tardif 2003c; Costea et al. 2004). Burnside et al. (1996) reported that 1–3% of *A. tuberculatus* var. *rudis* seeds germinated after 17 yr of burial at a soil depth of approximately 20 cm in Nebraska (viability of remaining seeds was not determined). Buhler and Hartzler (2001) found that 11% of seeds maintained their viability after 4 yr of burial in the upper 5 cm of soil in Iowa. In Iowa, *Amaranthus tuberculatus* var. *rudis* was one of the dominant species appearing on land brought back into crop production after 8 yr under the conservation reserve program (Felix and Owen 1999).

The seed bank of *A. tuberculatus* var. *rudis* in agricultural fields from Iowa ranged in size from 1910 to 64 160 seeds  $\text{m}^{-2}$ , and comprised up to 90% of the total seed bank (Buhler et al. 2001). Comparatively, seed banks of *A. tuberculatus* var. *rudis* from natural prairie wetlands in Iowa were much lower, averaging 181 seeds  $\text{m}^{-2}$  (Galatowitsch and van der Valk 1996). The size of the seed bank is influenced by numerous factors: the tillage system, various cultural practices, including weed management practices, and crop rotation, which in turn affect the number of seed produced, their vertical distribution in the soil profile, and the probability of seed survival and germination. Buhler et al. (2001) characterized the size and depth of the seed bank of *A. tubercula-*

*tus* var. *rudis* in a field in central Iowa throughout a 5-yr crop rotation consisting of legume/grass hay → corn → soybean → corn → oat. The seed bank was greatest during the hay/oat phases, but declined rapidly during the corn and soybean phases. They attributed the decline in corn and soybeans to moldboard plowing, which distributed the seeds over a greater soil depth, and inter-row cultivation, which reduced *A. tuberculatus* var. *rudis* survival and seed return, and the increase in hay and oat crops, to its ability to emerge after harvest and produce numerous seeds that remained concentrated near the soil surface in the absence of plowing. Comparable results have been reported for other *Amaranthus* spp. (reviewed by Costea et al. 2004).

The fraction of the *A. tuberculatus* var. *rudis* seed bank emerging in a single year in central Iowa varied from 1 to 22%, and was greater in years of higher rainfall and temperature (Hartzler et al. 1999; Buhler and Hartzler 2001). Common water-hemp emergence begins later and occurs over a more prolonged period of time compared to most annual weeds (Hartzler et al. 1999). Most seedlings emerge from near the soil surface, probably because the hypocotyl can elongate only 0.5–3.5 (–5) cm. Seedling emergence was 102% greater in areas marked by tractor wheel traffic than in untracked areas (Jurik and Zhang ShuYu 1999).

The minimum temperature for germination was 10°C for populations from Iowa (Leon et al. 2004), over 15/10°C for populations from Kansas (Guo and Al-Khatib 2003), and 15 to 20°C for populations from Illinois (Steckel et al. 2004). The optimum temperature was 33–35°C, above which germination declined (Guo and Al-Khatib 2003; Leon et al. 2004). Approximately 20% of seeds germinated at 45/40°C and no seeds germinated at 50/45°C (Guo and Al-Khatib 2003). Alternating temperatures increased germination compared to constant temperatures, and the greater the temperature variation the larger the increase in germination, with the optimum amplitude 18°C (Leon et al. 2004; Steckel et al. 2004).

Seeds of *Amaranthus* spp. shed on the soil surface or buried at different depths, undergo cyclical changes in dormancy, regulated primarily by seasonal variation in temperature (reviewed by Costea et al. 2004). Most freshly harvested *A. tuberculatus* var. *rudis* seeds are dormant but will germinate after wet stratification at 4°C for 12 wk (Leon and Owen 2003; Leon et al. 2004). Seed dormancy and germination are regulated by phytochrome. Germination is stimulated by exposure to red light and the effect is reversible by treatment with far-red light (Leon and Owen 2003). Temperature influences light sensitivity, and high temperatures (36°C) promoted germination of chilled seeds even after they were treated with far-red light (Leon and Owen 2003). These results are in agreement with those reported for other *Amaranthus* spp. (Costea and Tardif 2003c; Costea et al. 2004).

(d) *Vegetative Reproduction*—*Amaranthus tuberculatus* var. *rudis* does not reproduce vegetatively.

## 9. Hybrids

Natural hybrids have been reported between *A. tuberculatus* var. *rudis* and other dioecious species from the subgenus

*Acnida*, as well between var. *rudis* and monoecious species from the subgenus *Amaranthus* (Thellung 1914; Wetzel et al. 1999b; Franssen et al. 2001a; Costea and Tardif 2003b; Steinau et al. 2003; Costea et al. 2004). First generation hybrids between *A. tuberculatus* (variety unspecified) and *A. hybridus* were dioecious (Trucco et al. 2004). Natural hybridization rates between *A. tuberculatus* (variety unspecified) and *A. hybridus* were as high as 5.9% when the former species was used as the male parent, and 0.7% when it was used as a female parent (Trucco et al. 2004). Franssen et al. (2001b) found that the number of apertures on the pollen grains of a hybrid between *A. tuberculatus* var. *rudis* and *A. palmeri* was intermediate between the parents. Other morphological characters may not be intermediate between the two parents (Steinau et al. 2003), as has also been reported for hybrids between monoecious species of the section *Amaranthus* (Costea and Tardif 2003b; Costea et al. 2004). The presence of morphological characteristics absent in parent species may be explained by the formation of polymorphic DNA fragments resembling transposon-like elements (Wetzel et al. 1999b; Steinau et al. 2003). First generation hybrids between dioecious and monoecious, or between monoecious *Amaranthus* species, have reduced fertility, low vigor and slow growth, distorted leaves, abnormally shaped inflorescences, and numerous, densely packed bracteoles. Such characters, together with the presence of parent species in the field may serve as a preliminary identification method for hybrids. Two molecular datasets, restriction enzyme polymorphisms within the internal transcribed spacers (ITS) of the ribosomal DNA (Wetzel et al. 1999a) and amplified fragment length polymorphism (AFLPs) (Wetzel et al. 1999b), have not proven useful for identification of *Amaranthus* hybrids. In contrast, DNA content analysis has been successfully used to distinguish between *A. hybridus* and *A. tuberculatus* (Tranel et al. 2002; Jeschke et al. 2003). F<sub>1</sub> hybrids exhibited nuclear DNA contents equal to the mean of the two parents (e.g., *A. hybridus* 1.04 pg and *A. tuberculatus* 1.34 pg) (Tranel et al. 2002; Jeschke et al. 2003).

*Amaranthus* spp. often grow in large mixed populations of two or three species. As a consequence of hybridization, introgression occurs and hybrid swarms result. When hybrids between *A. tuberculatus* and *A. hybridus* were backcrossed to *A. hybridus*, the progeny include both monoecious and dioecious types and their DNA contents were intermediate (Tranel et al. 2004). From a practical point of view, hybridization is one route by which resistance to herbicides can be transferred between different *Amaranthus* spp. Such transfers of herbicide resistance have been documented from *A. palmeri* to *A. tuberculatus* var. *rudis* (Wetzel et al. 1999b; Franssen et al. 2001a), and from *A. hybridus* to *A. tuberculatus* var. *rudis* (Tranel et al. 2002).

## 10. Population Dynamics

Because of its late emergence, *A. tuberculatus* var. *rudis* is likely to produce only one generation per year. The plant rapidly invades disturbed areas because of copious seed production and the formation of persistent seed banks that build up very quickly in the absence of control. During the past decade, *A. tuberculatus* var. *rudis* has gradually emerged as

a dominant weed species in corn and soybeans throughout the mid-western United States. An increase in the frequency and severity of infestations of *A. tuberculatus* var. *rudis* has been caused by changes in cultural practices and weed management, and by the rapid development of herbicide-resistant biotypes (see sections 11 and 12).

Comparative growth studies in Kansas, suggested that *A. tuberculatus* var. *rudis* is competitively inferior to *A. palmeri*, but superior to *A. retroflexus* (Horak and Loughin 2000). In Missouri, *A. tuberculatus* var. *rudis* ranked after *A. palmeri*, *A. retroflexus*, and *A. hybridus* in terms of dry weight gain and height, but had more efficient seed production (by 2.0-, 1.4- and 1.4-fold greater, respectively) (Sellers et al. 2003). Triazine-resistant *A. tuberculatus* var. *rudis* plants in Nebraska were less competitive than triazine-susceptible plants at densities of 50, 100 and 150 plants m<sup>-2</sup>, while at 300 plants m<sup>-2</sup> they were equally competitive (Anderson et al. 1996b).

## 11. Response to Herbicides and Other Chemicals

*Amaranthus tuberculatus* var. *rudis* is susceptible to many selective and non-selective herbicides available for the control of broad-leaved weeds in crop and non-crop areas. However, management of *A. tuberculatus* (both varieties) with herbicides is complicated by its prolonged emergence pattern, genetic variability within and between populations, and the ability of the species to rapidly develop resistance after repeated exposure (Patzoldt et al. 2002).

*Amaranthus tuberculatus* var. *rudis* emerges after most crops have been planted, so herbicides applied before planting are not an effective control measure, unless they have residual soil activity. Herbicides with residual activity applied to the soil at planting will control emerging *A. tuberculatus* var. *rudis* for at least part of the season. Foliar-applied postemergence herbicides will control growing weeds, but in the absence of residual activity, repeated applications must be made to control new flushes. In many crops, a soil-applied herbicide followed by a postemergence herbicide is required for season-long control. Broadcast herbicide treatments controlled *A. tuberculatus* var. *rudis* better than band treatments (Felix and Owen 1999).

In a number of studies in the mid-western United States, the most effective soil-applied herbicide for control (97–98%) of *A. tuberculatus* var. *rudis* in soybeans was sulfentrazone (Krausz et al. 1998; Dirks et al. 2000b; Hager et al. 2002a; Nolte and Young 2002b; Krausz and Young 2003). Other preemergence herbicides reported to control *A. tuberculatus* var. *rudis* are flumioxazin, dimethenamid, S-metolachlor, pendimethalin, acetochlor, linuron, imazethapyr, metribuzin, flufenacet plus metribuzin, and flumetsulam plus metolachlor (Sweat et al. 1998; Niekamp and Johnson 2001; Steckel et al. 2002). Preemergence herbicides should be applied as close to planting as possible, to maximize the duration of activity (Hager et al. 2002a). By 56 d after planting, sequential herbicide applications usually provide better control than single treatments.

Postemergence control of *A. tuberculatus* var. *rudis* up to 10 cm in height can be achieved in soybeans by the diphenylether herbicides lactofen, fomesafen and acifluor-

fen. These herbicides provided 75–90% control of *A. tuberculatus* var. *rudis* in Illinois, with lactofen and fomesafen more effective than acifluorfen (Hager et al. 2003). Control by all three herbicides declined with time after treatment, as some plants re-grew from lower leaf nodes and new seedlings germinated. Sweat et al. (1998) and Mayo et al. (1995) reported that *A. tuberculatus* var. *rudis* could also be controlled postemergence by imazamox, imazethapyr, chlormuron and thifensulfuron, provided the populations were not resistant to herbicides that inhibit the enzyme acetolactate synthase (ALS). Wide-spread resistance to ALS-inhibitors now makes these herbicides ineffective on many *A. tuberculatus* var. *rudis* populations.

In corn from Nebraska, preemergence application of S-metolachlor plus atrazine provided season-long control (Nolte and Young 2002a). Other preemergence herbicides reported to provide control of *A. tuberculatus* var. *rudis* in corn are pendimethalin, dimethenamid, isoxaflutole, and mesotrione (Steckel et al. 2002; Peter Sikkema, University of Guelph, unpublished data). Sequential applications and the addition of atrazine generally improved the level of control (but see triazine resistance below). Postemergence control can be achieved with atrazine, primisulfuron, dicamba, prosulfuron plus dicamba, 2,4-D plus atrazine, diflufenzopyr plus dicamba, and mesotrione (Anderson et al. 1996a; Peter Sikkema, University of Guelph, unpublished data).

In sugarbeets in Minnesota, season-long *A. tuberculatus* var. *rudis* control required three sequential applications of desmedipham alone or in combination with triflusaluron-methyl, clopyralid and methylated seed oil, or metolachlor or dimethenamid (Roehl et al. 2001).

Herbicide-resistant crops provide an opportunity to control *A. tuberculatus* var. *rudis* up to 30 cm in height with the non-selective herbicides glyphosate or glufosinate (Coetzer et al. 2002; Hoss et al. 2003). However, these products have no residual activity, and consistent, season-long control (>80%) of *A. tuberculatus* var. *rudis* in corn in Missouri required two applications of glyphosate or glufosinate in combination with residual herbicides (Hellwig et al. 2003). Single applications were much less effective, unless combined with a residual herbicide, such as atrazine in corn, or sulfentrazone in soybeans (Bradley et al. 2000; Dirks et al. 2000a; Johnson et al. 2000; Beyers et al. 2002; Nolte and Young 2002a, b). Control with single glyphosate applications in soybeans increased as row spacing decreased from 76 to 19 cm (Young et al. 2001).

Throughout the mid-western United States, *A. tuberculatus* var. *rudis* populations have developed resistance to herbicides that inhibit photosystem II (Group 5, e.g., triazines), ALS-inhibitors (Group 2, e.g., sulfonyleureas) and herbicides that inhibit protoporphyrinogen oxidase (PPO, Group 14, e.g., diphenylethers) (Heap 2004). Resistance to triazine herbicides was first reported in Nebraska in 1990 (Anderson et al. 1996b), and has since been discovered in Missouri, Kansas, Iowa, Illinois and Ontario (Heap 2004). Resistance to ALS-inhibiting herbicides was confirmed in 1993, and now occurs in Iowa, Missouri, Oklahoma, Kansas, Illinois, Ohio, and Ontario (Horak and Peterson 1995; Peterson 1999; Heap 2004). In Ontario, multiple resistance to

imazethapyr (Group 2) and atrazine (Group 5) was first reported from soybean fields in 2002 (Heap 2004). Resistance to the PPO (protoporphyrinogen oxidase)-inhibiting herbicides lactofen, acifluorfen, fomesafen and sulfentrazone was observed in a biotype in Kansas in 2001, after 4 yr of repeated exposure to acifluorfen (Shoup et al. 2003). This biotype also had a high level of resistance to the ALS herbicides imazethapyr and thifensulfuron. Resistance to acifluorfen and lactofen was reported in two soybean fields in Missouri (Li et al. 2004b). Falk et al. (2004) conducted a survey of northeastern Kansas, and found PPO resistance in half of the sampled fields, and ALS resistance in most *A. tuberculatus* var. *rudis* populations. Other cases of multiple resistance to triazines, ALS or PPO inhibitors have been reported in Illinois (Heap 2004). Although true resistance to glyphosate has not yet been reported in any of the varieties of *A. tuberculatus*, populations exhibit a wide range of response to this herbicide, and appear to vary in tolerance (Li et al. 2004a; Patzoldt et al. 2004).

*Amaranthus tuberculatus* (variety unspecified) populations differ in the mechanism of resistance to the various herbicide classes and in the pattern of cross-resistance to other herbicides within the same chemical family. In most weed species, triazine resistance is conferred by a mutation at the site of action in the chloroplast, and is maternally inherited. Patzoldt et al. (2003) surveyed *A. tuberculatus* (variety unspecified) populations in Illinois and found that some segregated for triazine resistance and that the trait was nuclear encoded and not maternally inherited. These populations had a lower level of resistance and less cross-resistance to triazines other than atrazine compared to populations that were uniformly resistant and possessed target site resistance. Patterns of cross-resistance to herbicides that inhibit the ALS enzyme also vary from one population to another, indicating different single point mutations (Lovell et al. 1996; Hinz and Owen 1997; Sprague et al. 1997a, b). Foes et al. (1998) found that a tryptophan to leucine substitution at position 574 of the ALS gene conferred broad cross-resistance to ALS-inhibiting herbicides, i.e., more than 10-fold resistance to sulfonylureas, imidazolinones and triazolopyrimidines. On the other hand, a substitution from serine to asparagine or threonine at position 653 of the ALS gene resulted in resistance to imidazolinones, but not sulfonylureas or triazolopyrimidines (Tranel and Wright 2002). The physiological basis for resistance to the PPO-inhibitor herbicides acifluorfen and lactofen in Missouri *A. tuberculatus* var. *rudis* populations involves reduced accumulation of protoporphyrin IX (Li et al. 2004b).

Genetic variation within and between populations in response to various herbicides (Patzoldt et al. 2002), and interspecific hybridization, and gene flow between monoecious (Tranel et al. 2002) and dioecious *Amaranthus* species (Wetzel et al. 1999b; Franssen et al. 2001a), probably contribute to the rapid spread of herbicide resistance in these species.

## 12. Response to Other Human Manipulations

*Amaranthus tuberculatus* var. *rudis* populations increase under no-tillage or reduced tillage cropping systems, because seeds remain near the soil surface, which promotes germination and emergence (Hager et al. 1997; Hager 1998;

Felix and Owen 1999). Survival, plant height, biomass, and seed production all decline when *A. tuberculatus* var. *rudis* emergence is delayed relative to a crop (Hartzler et al. 2004; Nordby and Hartzler 2004). Nitrogen application at 120 kg ha<sup>-1</sup> early in the season provided a competitive advantage to corn in Nebraska, and reduced growth of *A. tuberculatus* var. *rudis* and *Abutilon theophrasi* Medic. (Evans et al. 2003). Results obtained in Iowa have shown that composted swine manure applied at rate of 4000 or 8000 kg C ha<sup>-1</sup> reduced the emergence of *A. tuberculatus* var. *rudis* and other weeds, but increased their overall competitive ability (Menalled et al. 2004).

## 13. Response to Herbivory, Disease and Higher Plant Parasites

The response of *A. tuberculatus* var. *rudis* to various herbivores, diseases, and higher plant parasites is unknown. However, it is very likely that *A. tuberculatus* var. *rudis* is affected more or less by the same nematodes, viruses, fungi and bacteria as other *Amaranthus* weed species (Costea and Tardif 2003c; Costea et al. 2004).

### (a) Herbivory:

(i) *Mammals*—No data.

(ii) *Birds and other vertebrates*—No data.

(iii) *Insects*—Preliminary studies on post-dispersal seed predation done at Boone, Iowa (van der Laet and Owen, personal communication) have indicated that more or less the same insects associated with other *Amaranthus* spp. (Costea et al. 2004) fed on the seeds of *A. tuberculatus* var. *rudis* as well. The most important post-dispersal seed predators observed were: *Amara aeneopolita* Casey, *Anisodactylus rusticus* Say, *Stenolophus comma* (F.), *Gryllus pennsylvanicus* Burmeister, and *Harpalus pennsylvanicus* De Geer. Among these, the latter two species had the highest populations (van der Laet and Owen, personal communication).

(iv) *Nematodes*—No data.

### (b) Diseases:

(i) *Fungi*—Canada—No records. United States: *Albugo bliti* (Biv.-Bern.) Kuntze: Minnesota (Preston and Dostall 1955); Oklahoma (Preston 1945); North America (Wilson 1908); *Phymatotrichum omnivorum* (Duggar) Hennebert: Texas (Anonymous 1960). Additionally, var. *tuberculatus* was reported to be a host of *Albugo bliti*: Iowa, Kansas and Wisconsin (Anonymous 1960); *Cercospora acnidae* Ellis & Everh.: Wisconsin (Greene 1945; Anonymous 1960); and *Phyllosticta amaranthi* Ellis & Kellerm: New York (Anonymous 1960).

*Biocontrol*—Preliminary tests using *Microsphaeropsis amaranthi* (Ellis & Barthol.) Heiny & Mintz (= *Aposphaeria amaranthi* Ellis & Barthol.) concluded that this fungus has potential as a bioherbicide for the control of

*A. tuberculatus*. The fungal pathogen caused foliar and stem necrosis resulting in the mortality of *A. tuberculatus* (variety unspecified) plants under optimal conditions (Smith and Hallett 2004a). Tank mixtures of the fungus conidia and glyphosate had reduced efficacy (Smith and Hallett 2004b).

(ii) *Bacteria*—No data.

(iii) *Viruses*—No data.

(c) *Higher Plant Parasites*—No information was located.

#### 14. Prognosis

The presence of *A. tuberculatus* var. *rudis* as a weed of arable fields represents a threat to crop production in Eastern Canada, particularly where soybeans and corn are grown. The recent range expansion throughout the mid-western United States and its ability to rapidly develop herbicide resistant biotypes have caused an increase in the frequency and severity of infestations. It spread from southern Illinois to become the most troublesome weed throughout the state in less than a decade (Steckel and Sprague 2004). *Amaranthus tuberculatus* var. *rudis* has a superior genetic recombination potential compared to monoecious amaranth species (e.g., *A. retroflexus*, *A. powellii*, etc.), and therefore a higher genetic and phenotypic variability. Its propensity for interspecific hybridization and introgression with other *Amaranthus* species could lead to rapid adaptation in new areas. Added to these characteristics are the high growth rate and competitiveness, the ease of long distance pollen and seed dispersal, production of a large number of viable seeds, the persistent seed bank, and an extended emergence pattern.

The expansion of *A. tuberculatus* var. *rudis* into new areas is expected to progress quickly after initial establishment and this should occur more rapidly than with monoecious amarantths. Given the level of the current infestation in southwestern Ontario, complete eradication is probably already difficult to achieve and re-infestation with new plants from the United States is always possible. It might be possible to reduce or manage the impact of this invasive weed if quick action is taken to identify and map the foci of infestations of this weed, determine its population dynamics under our climate and establish proper methods of control and management. Thorough cleaning of combines after harvest before moving equipment to other fields would limit the transport of seeds. Otherwise, it is probably only a matter of time until this species will become as problematic in Canada as it is now in the United States.

#### ACKNOWLEDGEMENTS

Suzanne Warwick and two anonymous reviewers provided suggestions that improved an earlier version of the manuscript. Thanks are due to Rocio van der Laet and Micheal Owen for sharing their unpublished information about seed predation in common water-hemp. Alexandra Smith kindly assisted us with the scanning electron microscope.

**Aellen, P. 1959.** *Amaranthus* L. Pages: 465–516 in G. Hegi, ed. *Illustrierte flora von Mitteleuropa*, Vol. 3, Part. 2. Munich, Germany.

**Anderson, D. D., Roeth, F. W. and Martin, A. R. 1996a.** Occurrence and control of triazine-resistant common waterhemp (*Amaranthus rudis*) in field corn (*Zea mays*). *Weed Technol.* **10**: 570–575.

**Anderson, D. D., Higley, L. G., Martin, A. R. and Roeth, F. W. 1996b.** Competition between triazine-resistant and -susceptible common waterhemp (*Amaranthus rudis*). *Weed Sci.* **44**: 853–859.

**Anonymous 1960.** Index of plant diseases in the United States. US Dept. Agric. Handbook No. 165. Washington, DC. 531 pp.

**Baker, H. G. and Stebbins, G. L. (eds.) 1965.** The genetics of colonizing species. Academic Press, New York, NY. 588 pp.

**Battles, B., Hartzler, B. and Buhler, D. 1998.** Effect of common waterhemp emergence date in soybeans on growth and competitiveness. *Proc. North Centr. Weed Sci. Soc.* **53**: 145–146.

**Bensch, C. N., Horak, M. J. and Peterson, D. 2003.** Interference of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*) in soybean. *Weed Sci.* **51**: 37–43.

**Beyers, J. T., Smeda, R. J. and Johnson, W. G. 2002.** Weed management programs in glufosinate-resistant soybean (*Glycine max*). *Weed Technol.* **16**: 267–273.

**Bradley, P. R., Johnson, W. G., Hart, S. E., Buesinger, M. L. and Massey, R. E. 2000.** Economics of weed management in glufosinate-resistant corn (*Zea mays* L.). *Weed Technol.* **14**: 495–501.

**Buhler, D. D. and Hartzler, R. G. 2001.** Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. *Weed Sci.* **49**: 230–235.

**Buhler, D. D., Kohler, K. A. and Thompson, R. L. 2001.** Weed seed bank dynamics during a five-year crop rotation. *Weed Technol.* **15**: 170–176.

**Burnside, O. C., Wilson, R. G., Weisberg, S. and Hubbard, K. G. 1996.** Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. *Weed Sci.* **44**: 74–86.

**Coetzer, E., Al-Khatib, K. and Peterson, D. E. 2002.** Glufosinate efficacy on *Amaranthus* species in glufosinate-resistant soybean (*Glycine max*). *Weed Technol.* **16**: 326–331.

**Cole, H. E. and Holch, A. E. 1941.** The root habits of certain weeds of southern Nebraska. *Ecology* **22**: 141–147.

**Cordes, J. C. and Johnson, W. G. 2003.** Common waterhemp interference in corn. *Proc. North Centr. Weed Sci. Soc.* **43**: 241 (Abstr.).

**Costea, M. 1996.** The recording of some new adventive taxa for Romania in the Harbor of Constanta. *Rev. Rom. Biol. Veg.* **41**: 91–96.

**Costea, M. 1998.** Monograph of the genus *Amaranthus* L. in Romania. Ph.D. diss., University of Bucharest, College of Biology, Bucharest, Romania. 210 pp.

**Costea, M. and DeMason, D. A. 2001.** Stem morphology and anatomy in *Amaranthus* L. (*Amaranthaceae*): taxonomic significance. *J. Torrey Bot. Soc.* **128**: 254–281.

**Costea, M. and Tardif, F. J. 2003a.** The name of the amaranth: histories of meaning. *Sida* **20**: 1071–1081.

**Costea, M. and Tardif, F. J. 2003b.** Conspectus and notes on the genus *Amaranthus* (*Amaranthaceae*) in Canada. *Rhodora* **105**: 260–281.

**Costea, M. and Tardif, F. J. 2003c.** The biology of Canadian weeds 126. *Amaranthus albus* L., *A. blitoides* S. Watson and *A. blitum* L. *Can. J. Plant Sci.* **83**: 1039–1066.

**Costea, M. and Tardif, F. J. 2003d.** The bracteoles in *Amaranthus* (*Amaranthaceae*): their morphology, structure, function and taxonomic significance. *Sida* **20**: 969–985.

**Costea, M., Sanders, A. and Waines, G. 2001a.** Preliminary results toward a revision of the *Amaranthus hybridus* species complex (*Amaranthaceae*). *Sida* **19**: 931–974.

- Costea, M., Waines, G. and Sanders, A. 2001b. Notes on some little known *Amaranthus* taxa (*Amaranthaceae*) in the United States. *Sida* **19**: 975–992.
- Costea, M., Waines, G. and Sanders, A. 2001c. Structure of the pericarp in some *Amaranthus* L. (*Amaranthaceae*) species and its taxonomic significance. *Aliso* **20**: 51–60.
- Costea, M., Weaver, S. E. and Tardif, F. J. 2004. Biology of Canadian weeds 130. *Amaranthus retroflexus* L., *A. powellii* S. Watson and *A. hybridus* L. *Can. J. Plant Sci.* **84**: 631–668.
- Darbyshire, S. J. 2003. Inventory of Canadian agricultural weeds. Agriculture and Agri-Food Canada, Research Branch, Ottawa, ON. 396 pp. [Online] Available: [http://res2.agr.ca/ecorc/weeds/herbes/title-titre\\_e.htm](http://res2.agr.ca/ecorc/weeds/herbes/title-titre_e.htm) [August 2004].
- Douglas, G. W., Straley, G. B., Meidinger, D. and Pojar, J. 1998. Illustrated flora of British Columbia. Vol. 1. Gymnosperms and Dicotyledons (*Aceraceae* through *Asteraceae*). British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests, Victoria, BC. 436 pp.
- Dirks, J. T., Johnson, W. G., Smeda, R. J., Wiebold, W. J. and Massey, R. E. 2000a. Reduced rates of sulfentrazone plus chlorimuron and glyphosate in no-till, narrow-row, glyphosate-resistant *Glycine max*. *Weed Sci.* **48**: 618–627.
- Dirks, J. T., Johnson, W. G., Smeda, R. J., Wiebold, W. J. and Massey, R. E. 2000b. Use of pre-plant sulfentrazone in no-till, narrow-row, glyphosate-resistant *Glycine max*. *Weed Sci.* **48**: 628–639.
- Evans, S. P., Knezevic, S. Z., Lindquist, J. L. and Shapiro, C. A. 2003. Influence of nitrogen and duration of weed interference on corn growth and development. *Weed Sci.* **51**: 546–556.
- Falk, J. S., Shoup, D. E., Al-Khatib, K. and Peterson, D. E. 2004. Survey of common waterhemp resistance to proto- and ALS-inhibiting herbicides in northeast Kansas. *Weed Science Society of America Annual Meeting*, 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 51 (Abstr.).
- Felix, J. and Owen, M. D. K. 1999. Weed population dynamics in land removed from conservation reserve program. *Weed Sci.* **47**: 511–517.
- Foes, M. J., Liu, L., Tranel, P. J., Wax, L. M. and Stoller, E. W. 1998. A biotype of common waterhemp (*Amaranthus rudis*) resistant to triazine and ALS herbicides. *Weed Sci.* **46**: 514–520.
- Franssen, A. S., Skinner, D. Z., Al-Khatib, K., Horak, M. J. and Kulakow, P. A. 2001a. Interspecific hybridization and gene flow of ALS resistance in *Amaranthus* species. *Weed Sci.* **49**: 598–606.
- Franssen, A. S., Skinner, D. Z., Al-Khatib, K. and Horak, M. J. 2001b. Pollen morphological differences in *Amaranthus* species and interspecific hybrids. *Weed Sci.* **49**: 732–737.
- Galatowitsch, S. M. and van der Valk, A. G. 1996. The vegetation of restored and natural prairie wetlands. *Ecol. Appl.* **6**: 102–112.
- Grant, W. F. 1959. Cytogenetic studies in *Amaranthus*. I. Cytological aspects of sex determination in dioecious species. *Can. J. Bot.* **37**: 413–417.
- Greene, H. C. 1945. Notes on Wisconsin parasitic fungi. VII. *Am. Midl. Naturalist* **34**: 258–270.
- Gregory, P. H. 1973. *The microbiology of the atmosphere*. 2nd ed. John Wiley & Sons, New York, NY. 377 pp.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J. E., Trehane, P., Turland, N. J. and Hawksworth, D. L. 2001. International code of botanical nomenclature (St Louis Code). [Online] Available: <http://www.bgbm.org/IAPT/Nomenclature/Code/SaintLouis/0000St.Luistitle.htm> [2004 Aug.]
- Guo, P. and Al-Khatib, K. 2003. Temperature effects on germination and growth of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*). *Weed Sci.* **51**: 869–875.
- Hager, A. G. 1998. Waterhemp – a contemporary riddle for corn and soybean producers. *Illinois Fertilizer Conference Proceedings*. 1998 Jan. 26–28. [Online] Available: <http://frec.cropsci.uiuc.edu/1998/index.htm> [2004 Aug.]
- Hager, A. G., Wax, L. M., Simmons, F. W. and Stoller, E. W. 1997. Waterhemp management in agronomic crops: *Univ. Ill. Bull.* No. 855. 12 pp.
- Hager, A. G., Wax, L. M., Bollero, G. A. and Simmons, F. W. 2002a. Common waterhemp (*Amaranthus rudis* Sauer) management with soil-applied herbicides in soybean (*Glycine max* (L.) Merr.). *Crop Prot.* **21**: 277–283.
- Hager, A. G., Wax, L. M., Stoller, E. W. and Bollero, G. A. 2002b. Common waterhemp (*Amaranthus rudis*) interference in soybean. *Weed Sci.* **50**: 607–610.
- Hager, A. G., Wax, L. M., Bollero, G. A. and Stoller, E. W. 2003. Influence of diphenylether herbicide application rate and timing on common waterhemp (*Amaranthus rudis*) control in soybean (*Glycine max*). *Weed Technol.* **17**: 14–20.
- Hartzler, R. G., Buhler, D. D. and Stoltenberg, D. E. 1999. Emergence characteristics of four annual weed species. *Weed Sci.* **47**: 578–584.
- Hartzler, R. G., Battles, B. A. and Nordby, D. 2004. Effect of common waterhemp (*Amaranthus rudis*) emergence date on growth and fecundity in soybean. *Weed Sci.* **52**: 242–245.
- Heap, I. 2004. International survey of herbicide resistant weeds. [Online] Available: <http://www.weedscience.com> [2004 Aug.].
- Hellwig, K. B., Johnson, W. G. and Massey, R. E. 2003. Weed management and economic returns in no-tillage herbicide-resistant corn (*Zea mays*). *Weed Technol.* **17**: 239–248.
- Hinz, J. R. R. and Owen, M. D. K. 1997. Acetolactate synthase resistance in a common waterhemp (*Amaranthus rudis*) population. *Weed Technol.* **11**: 13–18.
- Holmgren, P. K., Holmgren, N. H. and Barnett, L. C. 1990. *Index Herbariorum*. Part I: The herbaria of the world. 8th ed. New York Botanical Garden, Bronx, NY. 693 pp.
- Horak, M. J. and Loughin, T. M. 2000. Growth analysis of four *Amaranthus* species. *Weed Sci.* **48**: 347–355.
- Horak, M. J. and Peterson, D. E. 1995. Biotypes of Palmer amaranth (*Amaranthus palmeri*) and common waterhemp (*Amaranthus rudis*) are resistant to imazethapyr and thifensulfuron. *Weed Technol.* **9**: 192–195.
- Hoss, N. E., Al-Khatib, K., Peterson, D. E. and Loughin, T. M. 2003. Efficacy of glyphosate, glufosinate, and imazethapyr on selected weed species. *Weed Sci.* **51**: 110–117.
- Invaders Database System. 2003. Agricultural Research Service U.S.D.A. [Online] Available: <http://invader.dbs.umd.edu>. [2004 Aug.].
- Jeschke, M. R., Tranel, P. J. and Rayburn, A. L. 2003. DNA content analysis of smooth pigweed (*Amaranthus hybridus*) and tall waterhemp (*A. tuberculatus*): implications for hybrid detection. *Weed Sci.* **51**: 1–3.
- Joel, D. M. and Liston, A. 1986. New adventive weeds in Israel. *Israel J. Bot.* **35**: 215–223.
- Johnson, W. G., Bradley, P. R., Hart, S. E., Buesinger, M. L. and Massey, R. E. 2000. Efficacy and economics of weed management in glyphosate-resistant corn (*Zea mays*). *Weed Technol.* **14**: 57–65.
- Jones, S. M., Smeda, R. J., Smith, G. S. and Johnson, W. G. 1998. The effect of waterhemp competition on soybean yield: *Proc. North Centr. Weed Sci. Soc.* **53**: 146 (Abst.).
- Jurik, T. W. and Zhang ShuYu. 1999. Tractor wheel traffic effects on weed emergence in central Iowa. *Weed Technol.* **13**: 741–746.
- Krausz, R. F., Kapusta, G. and Mathews, J. L. 1998. Sulfentrazone for weed control in soybean (*Glycine max*). *Weed Technol.* **12**: 684–689.

- Krausz, R. F. and Young, B. G. 2003.** Sulfentrazone enhances weed control of glyphosate in glyphosate-resistant soybean (*Glycine max*). *Weed Technol.* **17**: 249–255.
- Kyaw Tha Paw, U. and Hotton, C. 1989.** Optimum pollen and female receptor size for anemophily. *Am. J. Bot.* **76**: 445–453.
- Lemen, C. 1980.** Allocation of reproductive effort to the male and female strategies in wind-pollinated plants. *Oecologia* **45**: 156–159.
- Leon, R. G. and Owen, M. D. K. 2003.** Regulation of weed seed dormancy through light and temperature interactions. *Weed Sci.* **51**: 752–758.
- Leon, R. G., Knapp, A. D. and Owen, M. D. K. 2004.** Effect of temperature on the germination of common waterhemp (*Amaranthus tuberculatus*), giant foxtail (*Setaria faberi*), and velvetleaf (*Abutilon theophrasti*). *Weed Sci.* **52**: 67–73.
- Lewis, H. W., Vinay, P. and Zenger, E. V. 1983.** Airborne and allergenic pollen of North America. The Johns Hopkins University Press. Baltimore and London, 254 pp.
- Li, J., Smeda, R. J., and Wait, J. D. 2004a.** Population differences in waterhemp treated with glyphosate and lactofen. *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 15 (Abstr.).
- Li, J., Smeda, R. J., Nelson, K. A. and Dayan, F. E. 2004b.** Physiological basis for resistance to diphenyl ether herbicides in common waterhemp (*Amaranthus rudis*). *Weed Sci.* **52**: 333–338.
- Lovell, S. T., Wax, L. M., Horak, M. J. and Peterson, D. E. 1996.** Imidazolinone and sulfonylurea resistance in a biotype of common waterhemp (*Amaranthus rudis*). *Weed Sci.* **44**: 789–794.
- Mayo, C. M., Horak, M. J., Peterson, D. E. and Boyer, J. E. 1995.** Differential control of four *Amaranthus* species by six postemergence herbicides in soybean (*Glycine max*). *Weed Technol.* **9**: 141–147.
- Menalled, F. D., Liebman, M. and Buhler, D. 2004.** Impact of composted swine manure and tillage on common waterhemp (*Amaranthus rudis*) competition with soybean. *Weed Sci.* **52**: 605–613.
- Moquin-Tandon, C. H. B. A. 1849.** The genus *Acnida*. Pages 277–278 in A. P. DeCandolle, ed. *Prodromus systematis naturalis regni vegetabilis* 13(2), Paris, France.
- Mosyakin, L. S. and Robertson, R. K. 1996.** New infrageneric taxa and combinations in *Amaranthus* (Amaranthaceae). *Ann. Bot. Fenn.* **33**: 275–281.
- Murray, M. J. 1940.** The genetics of sex determination in the family *Amaranthaceae*. *Genetics* **25**: 409–431.
- Niekamp, J. W. and Johnson, W. G. 2001.** Weed management with sulfentrazone and flumioxazin in no-tillage soybean (*Glycine max*). *Crop Prot.* **20**: 215–220.
- Nolte, S. A. and Young, B. G. 2002a.** Efficacy and economic return on investment for conventional and herbicide-resistant corn (*Zea mays*). *Weed Technol.* **16**: 371–378.
- Nolte, S. A. and Young, B. G. 2002b.** Efficacy and economic return on investment for conventional and herbicide-resistant soybean (*Glycine max*). *Weed Technol.* **16**: 388–395.
- Nordby, D. E. and Hartzler, R. G. 2004.** Influence of corn on common waterhemp (*Amaranthus rudis*) growth and fecundity. *Weed Sci.* **52**: 255–259.
- Patzoldt, W. L., Tranel, P. J. and Hager, A. G. 2002.** Variable herbicide responses among Illinois waterhemp (*Amaranthus rudis* and *A. tuberculatus*) populations. *Crop Prot.* **21**: 707–712.
- Patzoldt, W. L., Dixon, B. S. and Tranel, P. J. 2003.** Triazine resistance in *Amaranthus tuberculatus* (Moq.) Sauer that is not site-of-action mediated. *Pest Management Sci.* **59**: 1134–1142.
- Patzoldt, W. L., Hager, A. G. and Tranel, P. J. 2004.** Evaluation of glyphosate responses in tall waterhemp (*Amaranthus tuberculatus*) using a quantitative genetics approach. *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 66 (Abstr.).
- Peterson, D. E. 1999.** The impact of herbicide-resistant weeds on Kansas agriculture. *Weed Technol.* **13**: 632–635.
- Pfeifer, T. L., Cho, I., Gibson, D. J., Young, B. G. and Wood, A. J. 2001.** Utility of trigonelline as a biochemical marker for interspecific competition between soybean and weed common waterhemp. *Biol. Plant.* **44**: 619–622.
- Pratt, D. B. and Clark, L. G. 2001.** *Amaranthus rudis* and *A. tuberculatus*—one species or two? *J. Torrey Bot. Soc.* **128**: 282–296.
- Preston, D. A. 1945.** Host index of Oklahoma plant diseases. *Oklahoma Agric. Coll. Agric. Exp. Sta. Techn. Bull. T 21*: 1–168.
- Preston, D. A. and Dostall, L. 1955.** *Minnesota Plant Diseases*. USDA, Plant Diseases Epidemiology and Identification Section, Special Publication **8**: 1–184.
- Quinn, J. A., Bram, M. R. and Taylor, T. E. 2000.** Female resource allocation in response to pollen availability in plants from freshwater and salt marsh populations of *Amaranthus cannabinus*. *J. Torrey Bot. Soc.* **127**: 83–86.
- Riddell, J. L. 1835.** Synopsis of the flora of the western states. *W. J. Med. Phys. Sci.* **41**: 367.
- Roehl, S. R., Bredehoeft, M. and Fischer, J. 2001.** Efficacy and economic viability of current and potential weed control options at Southern Minnesota Beet Sugar Cooperative. *Proc. 31st Biennial Meeting of the Am. Soc. Sugar Beet Technologists*, pp. 72–74.
- Sauer, J. D. 1955.** Revision of the dioecious amaranths. *Madroño* **13**: 5–46.
- Sauer, J. D. 1972.** The dioecious amaranths: a new species name and major range extensions. *Madroño* **21**: 426–434.
- Sellers, B. A., Smeda, R. J., Johnson, W. G., Kendig, J. A. and Ellersieck, M. R. 2003.** Comparative growth of six *Amaranthus* species in Missouri. *Weed Sci.* **51**: 329–333.
- Shoup, D. E., Al-Khatib, K. and Peterson, D. E. 2003.** Common waterhemp (*Amaranthus rudis*) resistance to protoporphyrinogen oxidase-inhibiting herbicides. *Weed Sci.* **51**: 145–150.
- Smith, D. A. and Hallett, S. G. 2004a.** Epidemiology of the candidate bioherbicide *Microsphaeropsis amaranthi* infecting waterhemp, *Amaranthus tuberculatus*. *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 74. (Abstr.).
- Smith, D. A. and Hallett, S. G. 2004b.** Interactions between *Microsphaeropsis amaranthi* and glyphosate for the control of waterhemp, *Amaranthus tuberculatus*. *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 73. (Abstr.).
- Sprague, C. L., Stoller, E. W. and Wax, L. M. 1997a.** Response of an acetolactate synthase (ALS)-resistant biotype of *Amaranthus rudis* to selected ALS-inhibiting and alternative herbicides. *Weed Res.* **37**: 93–101.
- Sprague, C. L., Stoller, E. W., Wax, L. M. and Horak, M. J. 1997b.** Palmer amaranth (*Amaranthus palmeri*) and common waterhemp (*Amaranthus rudis*) resistance to selected ALS-inhibiting herbicides. *Weed Sci.* **45**: 192–197.
- Steckel, L. E. and Sprague, C. L. 2004.** Common waterhemp (*Amaranthus rudis*) interference in corn. *Weed Sci.* **52**: 359–364.
- Steckel, L. E., Sprague, C. L. and Hager, A. G. 2002.** Common waterhemp (*Amaranthus rudis*) control in corn (*Zea mays*) with single preemergence and sequential applications of residual herbicides. *Weed Technol.* **16**: 755–761.
- Steckel, L. E., Sprague, C. L., Stoller, E. W. and Wax, L. M. 2004.** Temperature effects on germination of nine *Amaranthus* species. *Weed Sci.* **52**: 217–221.
- Steckel, L. E., Sprague, C. L., Hager, A. G., Simmons, F. W. and Bollero, G. A. 2003.** Effects of shading on common waterhemp (*Amaranthus rudis*) growth and development. *Weed Sci.* **51**: 898–903.

- Steinau, A. N., Skinner, D. Z. and Steinau, M. 2003. Mechanism of extreme genetic recombination in weedy *Amaranthus* hybrids. *Weed Sci.* **51**: 696–701.
- Stevens, O. A. 1932. The number and weight of seeds produced by the weeds. *Am. J. Bot.* **19**: 784–794.
- Sweat, J. K., Horak, M. J., Peterson, D. E., Lloyd, R. W. and Boyer, J. E. 1998. Herbicide efficacy on four *Amaranthus* species in soybean (*Glycine max*). *Weed Technol.* **12**: 315–321.
- Thellung, A. 1914. *Amaranthus* L. Pages 225–356 in P. Ascherson and P. Graebner, eds. *Synopsis der Mitteleuropaischen flora*. Vol. 5. Leipzig.
- Tranel, P. J. and Wright, T. R. 2002. Resistance of weeds to ALS-inhibiting herbicides: what have we learned? *Weed Sci.* **50**: 700–712.
- Tranel, P. J., Wassom, J. J., Jeschke, M. R. and Rayburn, A. L. 2002. Transmission of herbicide resistance from a monoecious to a dioecious weedy *Amaranthus* species. *Theor. Appl. Genet.* **105**: 674–679.
- Tranel, P. J., Trucco, F., Tatum, T. C. and Rayburn, L. A. 2004. Molecular, cytogenetic and morphological analysis of smooth pigweed (*Amaranthus hybridus*) × waterhemp (*Amaranthus tuberculatus*) BC<sub>1</sub> progeny. *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 229. (Abstr.)
- Trucco, F., Tranel, P. J., Jeschke, M. R. and Rayburn, L. A. 2004. Field hybridization frequencies between monoecious smooth pigweed (*Amaranthus hybridus*) and dioecious waterhemp (*Amaranthus tuberculatus*). *Weed Science Society of America Annual Meeting*. 2004 Feb. 07–11. Kansas City, MO. Vol. 44, p. 229. (Abstr.)
- Uline, E. B. and Bray, W. L. 1895. Synopsis of North American Amaranthaceae. II. *Bot. Gaz.* **20**: 155–161.
- Umbanhowar, C. E., Jr. 1992. Abundance, vegetation, and environment of four patch types in a northern mixed prairie. *Can. J. Bot.* **70**: 277–284.
- USDA, NRCS. 2004. The PLANTS Database. Version 3.5. National Plant Data Center, Baton Rouge, LA. [Online] Available: <http://plants.usda.gov> (2004 Aug.).
- Wetzel, D. K., Horak, M. J. and Skinner, D. Z. 1999a. Use of PCR-based molecular markers to identify weedy *Amaranthus* species. *Weed Sci.* **47**: 518–523.
- Wetzel, D. K., Horak, M. J., Skinner, D. Z. and Kulakow, P. A. 1999b. Transfer of herbicide resistance traits from *Amaranthus palmeri* to *A. rudis*. *Weed Sci.* **47**: 538–543.
- Wilson W. G. 1908. Studies in North American Peronosporales—IV. Host index. *Bull. Torrey Bot. Club.* **11**: 543–554.
- Weed Science Society of America. 2004. Common/Latin weed names. [Online] Available: <http://www.wssa.net/weednames/common.asp> [2004 Aug.].
- Young, B. G., Young, J. M., Gonzini, L. C., Hart, S. E., Wax, L. M. and Kapusta, G. 2001. Weed management in narrow- and wide-row glyphosate-resistant soybean (*Glycine max*). *Weed Technol.* **15**: 112–121.