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# The Biology of Canadian Weeds. 126. *Amaranthus albus* L., *A. blitoides* S. Watson and *A. blitum* L.

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# The biology of Canadian weeds. 126.
# *Amaranthus albus* L., *A. blitoides* S. Watson and *A. blitum* L.

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Costea, M. and Tardif, F. J. 2003. **The biology of Canadian weeds. 126. *Amaranthus albus* L., *A. blitoides* S. Watson and *A. blitum* L.** Can. J. Plant Sci. **83**: 1039–1066. A review of biological information is provided for three species of the genus *Amaranthus*: *A. albus* L., *A. blitoides* S. Watson and *A. blitum* L. The last species has been revised taxonomically and a new subspecies for Canada is presented—*A. blitum* subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garmendia & Pedrol. *Amaranthus albus* and *A. blitoides* are native to the U.S.A. and introduced to Canada. Both species are annual ruderal and agrestal weeds. During the past 100 yr the two species have spread across most provinces of Canada, but the greatest frequency and abundance have been recorded in Saskatchewan. Originating from Europe, Asia and North Africa, *A. blitum* was initially considered a non-persistent species. The present study shows that *A. blitum* especially, subsp. *emarginatus*, has continued to spread in Québec. The three species are alternate hosts to many insects, nematodes, viruses, bacteria and fungi that affect cultivated plants. In other areas (U.S.A., Europe and Asia), the three species have developed multiple resistance to triazine and acetolactate-synthase-inhibiting herbicides.

**Key words**: *Amaranthus albus*, *Amaranthus blitoides*, *Amaranthus blitum*, weed biology, ecology, taxonomy, herbicide resistance

Costea, M. et Tardif, F. J. 2003. **Biologie des mauvaises herbes au Canada. 126. *Amaranthus albus* L., *A. blitoides* S. Watson et *A. blitum* L.** Can. J. Plant Sci. **83**: 1039–1066. Les auteurs ont passé en revue les données existantes sur la biologie de trois espèces du genre *Amaranthus* : *A albus* L., *A. blitoides* S. Watson et *A. blitum* L. La taxinomie de la troisième a été modifiée et on propose une nouvelles sous-espèce pour le Canada – *A blitum* sous-esp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garmendia & Pedrol. *Amaranthus albus* et *A. blitoides* sont des espèces indigènes des États-Unis introduites au Canada. Ces deux annuelles rudérales et agrestes se sont répandues dans la plupart des provinces canadiennes au cours du dernier siècle, mais elles sont particulièrement courantes et abondantes en Saskatchewan. Originaire d'Europe, d'Asie et d'Afrique du Nord, *A. blitum* a d'abord été considérée comme une espèce non persistante. La présente étude révèle toutefois qu'elle n'a cessé de se propager au Québec, surtout la sous-espèce *emarginatus*. Les trois espèces servent d'hôte de rechange à maints insectes, nématodes, virus, bactéries et cryptogames qui s'attaquent aux cultures. Ailleurs (É.-U., Europe et Asie), elles ont acquis une résistance multiple à la triazine et aux désherbants qui inhibent l'acétolactate-synthase.

**Mots clés**: *Amaranthus albus*, *Amaranthus blitoides*, *Amaranthus blitum*, biologie des mauvaises herbes, écologie, taxinomie, résistance aux herbicides

## 1. Names

I. *Amaranthus albus* L. = *A. graecizans* auct., non L.— **tumble pigweed** (Darbyshire et al. 2000), tumbling amaranth, white pigweed, tumble-weed (Alex 1992), **amarante blanche** (Darbyshire et al. 2000), herbe roulante (Alex 1992; Royer and Dickinson 1999).

II. *Amaranthus blitoides* S. Watson = *A. graecizans* auct., non L.— **prostrate pigweed** (Darbyshire et al. 2000), prostrate amaranth, spreading amaranth (Alex 1992), spreading pigweed, mat amaranth, tumbleweed (Royer and Dickinson 1999), **amarante fausse-blite** (Darbyshire et al. 2000) amarante étalée, amarante basse, amarante charnue (Alex 1992; Royer and Dickinson 1999).

III. *Amaranthus blitum* L.—Livid Amaranth (Britton and Brown 1896), purple amaranth, amarante livide (Lonchamp 2000).
III.1. *Amaranthus blitum* subsp. *blitum*
III.2. *Amaranthus blitum* subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garmendia & Pedrol Amaranthaceae, Amaranth family, Amarantacées, Subgenus Albersia.

The binomial *Amaranthus graecizans*, has been widely misapplied in North America to either *A. albus* or *A. blitoides*. *Amaranthus graecizans* subsp. *graecizans* is a taxon native to Europe, North Africa and Asia. It superficially resembles *A. blitoides* var. *reverchonii* Uline & Bray but it has not been found in North America. For more information see Costea et al. (2001a).

The specific epithet "*albus*" refers to the adult white stems of tumble pigweed. The species names of both prostrate pigweed and livid amaranth derive from the latinised Greek word "blitum" (βλιτου) which means a tasteless vegetable.

## 2. Description and Account of Variation

(a) *Description*—Descriptions are based on herbarium specimens and on plants grown in a growth room (under 16 h photoperiod at 26°C and an 8 h dark period at 15°C; atmospheric humidity 75%). Light was supplied by a mixture of incandescent bulbs and fluorescent tubes to achieve photosynthetically active radiation (PAR) of 450 μmol $m^{-2}$ $s^{-1}$. The seeds were obtained from the USDA germplasm collection. All three species are annual, with a taproot, and reproduce only by seeds.

I. *A. albus*. **Seedlings**—with a short hypocotyl (0.5–2 cm) and variable shaped cotyledons—narrow-ovate to lanceolate, 10–12 × 2.5–3 mm and 6–7 × 3 mm, respectively. The cotyledon petioles are short, 2.5–3 mm long. The epicotyl is sparsely pubescent. The first leaves resemble the mature leaves in shape and are glabrescent (nearly hairless), with 2–4 secondary veins. **Mature plants**—Stem is erect, 5–100 cm long, usually divaricate-branched (bushy), scurfy-villous in the inflorescence region; at maturity whitish, stiff. Dead stems persist over the winter season. Leaves are rhombic-ovate, elliptic to obovate or spathulate (spoon shaped, broad at the tip and narrowed towards the base), pale green; early leaves (formed on the main and secondary axis) are up to 8 cm long; later leaves (formed on higher order branches) are much smaller, sometimes 5–10 mm long. The margins of the leaves are green, often undulated. Inflorescences are dense axillary cymes. Bracteoles are rigid, spinose, 2–3 times as long as the flowers. The 3 tepals are shorter than the fruit, linear-elliptic to lanceolate. Stamens 3. Stigma 3, short, erect. Fruit circumscissile, 1.4–1.8 mm long, wrinkled when dry especially around the dehiscence line. Seeds round, 0.8–1.1 mm in diameter, lenticular. Pollen grains 17–22 μm in diameter, with 20–30 pores, each of 1.5–1.7 μm in diameter.

**Chromosome Number.** Mulligan (1984) reported a chromosome count of 2n = 32 for *A. albus* from Indian Head, Saskatchewan. This is identical to that reported in California (Heiser and Whitaker 1948) and in other regions of the world (see the database of Missouri Botanical Garden—W[3] Tropicos 2003). In contrast, Sharma and Banik (1965) reported 2n = 34 from India.

II. *Amaranthus blitoides* S. Watson—**Seedlings** usually with a longer hypocotyl than *A. albus* (2.5–7 cm). The cotyledons are uniform in shape, lanceolate, 15 × 3 mm, with a longer petiole (up to 7 mm) than *A. albus*. The epicotyl is glabrescent (nearly hairless) and the first leaves are obovate, glabrescent, with 2–4 secondary veins. **Mature plants**—According to Cole and Holch (1941) the roots may reach 50 cm in depth and spread horizontally for 120 cm. Stems are 10–70 cm long, branched, prostrate to decumbent, glabrescent (the hairs are sparse, microscopic, formed from 1–3 cells). The stems shrivel and disappear after the first frost. The entire plant is somewhat fleshy, with oblong-lanceolate (between four and six times as long as wide, with parallel margins) or obovate-spathulate (about three times as long as wide, wider above and spoon shaped) leaves with white-membranous, plane (flattened) margins. The inflorescences are dense axillary cymes. The bracteoles are foliaceous (leaf-like, not spinose as in *A. albus*), shorter than the flowers. Tepals 4–5, unequal, oblong to elliptic. Stamens 3. Stigma 3, recurved. Fruit circumscissile, 2–2.2 mm long, smooth or weakly wrinkled above the dehiscence line, globose to obovoidal, longer than the tepals. Seeds round to broad-elliptic, 1.5–1.7 × 1.4–1.5 mm. Pollen grains 21–25 μm in diameter, with 30–45 pores, each of 2.8–3.3 μm in diameter.

**Chromosome Number.** No chromosome counts are available from North America, but the species was reported to have 2n = 32 in Europe (see the chromosome counts reviewed by Missouri Botanical Garden—W[3] Tropicos 2003).

III. *Amaranthus blitum* L. **Seedlings**—are variable at the subspecies level (see section 2c). **Mature plants**—Stems up to 120 cm, procumbent, ascending to erect, glabrous or with sparse, multicellular, uniseriate hairs. Leaves 2–8 × 1–5 cm, rhombic-ovate (rhombic, about three times as long as wide and widest near the base) short-cuneate (wedge shaped) to truncate at base, emarginate (having a broad notch) to bilobed at apex, somewhat fleshy, green or reddish. Flowers in axillary cymes or with both axillary cymes and a terminal, variable inflorescence: short, dense and thick, to long thin, branched and flexuous. Bracteoles foliaceous or membranous, shorter than the flowers. Tepals 3, equal, 1.5–2 mm long, linear to (rarely) spathulate, shorter than the fruit. Fruit indehiscent, 1.2–2.6 (–3) mm long, ellipsoidal to globose, gradually or abruptly-narrowed toward the stigma region. When fresh, the pericarp is almost smooth, when dried, it is irregularly wrinkled in the zone with the seed, the rest of the fruit being smooth. Seeds round to broad-ovate. Pollen grains 19–23 μm in diameter, with 32–45 pores. The size of the seeds and fruits is variable at the subspecies level (see section 2c).

**Chromosome Number.** Chromosome counts are available only from Europe, Asia and Africa and are identical for both subspecies: 2n = 34 (Hügin 1987; reviewed by Missouri Botanical Garden—W[3] Tropicos 2003).

(b) *Distinguishing Features*—Wetzel et al. (1999) used PCR-based molecular markers (restriction enzyme analysis and amplified ribosomal DNA) to identify young plants of *Amaranthus* species. The three species described in the present account can be easily identified morphologically at the adult stage, and normally cannot be confused with any other *Amaranthus* species recorded in Canada (Costea and Tardif 2003a). The only exception is *Amaranthus californicus* (Moq.) S. Wats., which is very closely related to *A. albus*, but *A. californicus* is restricted to southern Alberta and Saskatchewan, where it is rare (Scoggan 1978; Costea and Tardif 2003a). During the flowering-fruiting stages, *A. albus* is easily recognizable by its erect, whitish, divaricate stems and spiny bracteoles; *A. blitoides* by its prostrate habit, fleshy (usually) obovate-spathulate leaves, its 4–5 tepals and big seeds; *A. blitum* by its emarginate to bilobed leaves, (often) the terminal inflorescence and indehiscent fruits. Mature plants with fruits and seeds can be identified using the following key.

## Identification key to mature plants of *A. albus*, *A. blitoides* and *A. blitum*.

A. Stems rigid, whitish, bushy-branched, persistent over the winter. Bracteoles spinescent, 2–3 times as long as the flowers ...............................................*A. albus*

A. Stems more fleshy, green or reddish, disappear after frost. Bracteoles minute, foliaceous or membranous, shorter than the flowers.................................................B

    B. Leaves obovate-spathulate to oblong-lanceolate. Flowers with 4–5 tepals. Fruit circumscissile .............*A. blitoides*

B. Leaves rhombic-ovate, emarginate or bilobed. Flowers with 3 tepals. Fruit indehiscent ........................*A. blitum*

(c) *Intraspecific Variation*—All *Amaranthus* species exhibit morphological, phenological and biological variation. Much of the phenotypical variation received taxonomic rank in the past (e.g., Uline and Bray 1894; Thellung 1914; Morariu 1952; Priszter 1953). The pattern of branching and size of the plants and leaves are influenced by the availability of light, water and nutrients. Mechanical factors such as clipping or trampling trigger development of secondary branches. Such ecophenes do not deserve taxonomic status, but are important as ecological indicators (Costea and DeMason 2001).

I. *Amaranthus albus*—Approximately 50 varieties, forms and sub-forms were described in the past, especially in Europe (Thellung 1914; Priszter 1953; Morariu 1952). The range of variation includes the size of plants, the pattern of stem branching and its colour (e.g. red stems in f. *rubicundus* Thellung). Other morphological variations include: lamina crisped on the margins, very short bracteoles (1.5–2 mm long), reduction in the number of tepals (1 or 2 tepals can be rudimentary), colour of the fruits (e.g. red fruits), partially dehiscent or indehiscent fruits and smooth fruits (personal observation).

II. *Amaranthus blitoides*—This species is less variable than *A. albus* but it may also show considerable phenotypic plasticity. Variation includes: stems erect or ascendant, lamina shape, the density of branches and leaves, the number of tepals in the perianth (normally 4–5, sometimes 3) and colour of the fruit (e.g. red fruits in f. *rubricapsulatus* Bujorean). With regard to variation of the leaf shape, one variety may not be an ecophene; var. *reverchonii* Uline & Bray (personal observation). It can be distinguished from var. *blitoides* as follows:

A. Leaves obovate-spathulate (ratio length : width is 2:1, mesophyll thick, somewhat fleshy. Lamina apex rounded .....................................................var. *blitoides*

B. Leaves oblong-lanceolate (ratio length: width >2:1), mesophyll thinner. Lamina apex acute ..........var. *reverchonii*

Although var. *reverchonii* is infrequent in Canada, it is common across the United States (Costea, unpublished) and it appears that the two varieties differ ecologically (Ciocarlan 1978).

III. *Amaranthus blitum*—Three subspecies can be recognized on the basis of their morphology and ecology (Costea et al. 2001a). Subsp. *oleraceus* (L.) Costea is cultivated as a vegetable in Europe, Asia and Africa and therefore is not described in the present account. The two other subspecies—subsp. *blitum* and subsp. *emarginatus*—are partially sympatric, but are separated ecologically (Hügin 1987; Costea et al. 2001a). *Amaranthus blitum* subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garmendia & Pedrol is recorded here for the first time in

Canada. Based on the general habit of the plants, two varieties (treated as subspecies by Hügin 1987) can be recognized in *A. blitum* subsp. *emarginatus*: var. *emarginatus* and var. *pseudogracilis* (Thell.) Lambinon.

## Identification key to subspecies and varieties of *Amaranthus blitum*

A. Stems slender, prostrate or ascendant. Cotyledons narrow-elliptic with acute apices, 6–7 × 3–6 mm. The leaves are not fleshy, are long-cuneate (wedge shaped) at base and deeply emarginate (having a broad notch) to bilobed at apex. Inflorescence entirely formed from axillary cymes (terminal part absent or reduced) or mainly terminal, long, thin and flexuous. Fruit 1.2–1.8 mm long. Seeds 0.8–1.1 mm in diameter ....................................................subsp. *emarginatus*

A1. Prostrate plants, leaves (0.75–)1–2 (–3.5) cm long; inflorescence entirely formed from axillary cymes (terminal part absent or reduced) ................var. *emarginatus*

A1. Ascending more vigorous plants with leaves 2–4 (–6) cm long, inflorescence mainly terminal, long, thin, flexuous ...............................................var. *pseudogracilis*

A. Stems usually more vigorous than in subsp. *emarginatus*, procumbent to ascendant. Cotyledons lanceolate, with rounded to truncate apices, 9–18 × 3–6 mm. Leaves fleshy, emarginate but never bilobed. Inflorescence entirely formed from axillary cymes or with a thick, dense terminal part as well. Fruit 1.7–2.6 (–3) mm long, Seeds 1–1.2 mm in diameter ........subsp. *blitum*

(d) *Illustrations*—*Amaranthus albus* is illustrated in Fig. 1; *A. blitoides* in Fig. 2; *A. blitum* subsp. *emarginatus* in Fig. 3. The variation of leaves in *A. albus* and *A. blitoides* is shown in Fig. 4. The seedlings, details of the fruits, tepals and bracteoles are illustrated in Fig. 5. The seeds are presented in Fig. 6. Photographs of the various stages in the development of the plants are also available in: Hanf, 1983 (all 3 species; seedlings, pp: 60; mature plants, pp: 168); Royer and Dickinson, 1999 (*A. blitoides*, pp: 4–5); Uva et al., 1997 (*A. albus* pp: 91, and *A. blitoides* pp: 93; the photograph from page 93, left corner is *A. blitum*); Bubar et al. 2000 (*A. blitoides*, pp: 224); Costea et al. 2001a (Fig. 1—*A. blitum* subsp *blitum* and Fig. 2, 3—*A. blitum* subsp. *emarginatus*). Illustrations of the three species can be seen online at http://www.weedscience.org/photos/Photodisplayall.asp.

## 3. Economic Importance

(a) *Detrimental*—These three species have received much less attention in North American literature than other species of the genus *Amaranthus*. Crop losses associated with *A. albus* or *A. blitoides* were reported in North America for pinto beans (*Phaseolus vulgaris* L.) and potato (*Solanum tuberosum* L.) in New Mexico (Arnold et al. 1993; Murray et al. 1994), and for cotton (*Gossypium hirsutum* L.) in Oklahoma (Rushing et al. 1985). Crop losses produced by these three species in other crops were reported from Greece (Vizantinopoulos and Katranis 1994, 1998) and Israel (Qasem 1992).

Mulligan and Munro (1990) stated that *A. blitoides*, *A. hybridus* L. and *A. retroflexus* L. can cause poisoning in pigs and cattle in Canada. Poisoning of cattle by *A. blitum* and *A.*

**Fig. 1.** *Amaranthus albus*, upper part of plant (herbarium specimen).

**Fig. 2.** *Amaranthus blitoides*, upper part of plant (herbarium specimen).

**Fig. 3.** *Amaranthus blitum* subsp. *emarginatus* (var. *pseudogracilis*), upper part of plant (herbarium specimen).

*hybridus* was also reported by Ferreira et al (1991) in Brazil.

The three *Amaranthus* spp. are also hosts to fungal, viral and bacterial pathogens, insects and nematodes that can cause considerable damage to crops (see section 13).

(b) *Beneficial*
I. *Amaranthus albus* has had little practical use. Habib and Abdul (1988) studied the phytotoxic influence of *A. albus* extracts on dodder (*Cuscuta campestris* Yuncker) parasitiz-

ing alfalfa (*Medicago sativa* L.). They found that the efficacy of the extracts was comparable to treatments with glyphosate and metribuzin. Fritz (2002) used it as a form of artistic expression.

II. *Amaranthus blitoides* has been proposed as an alternative forage species (Costea and Halmajan 1996). Plants also can be consumed as vegetables at the preflowering stage when the protein concentration in the leaves reaches 25.3–32.9%
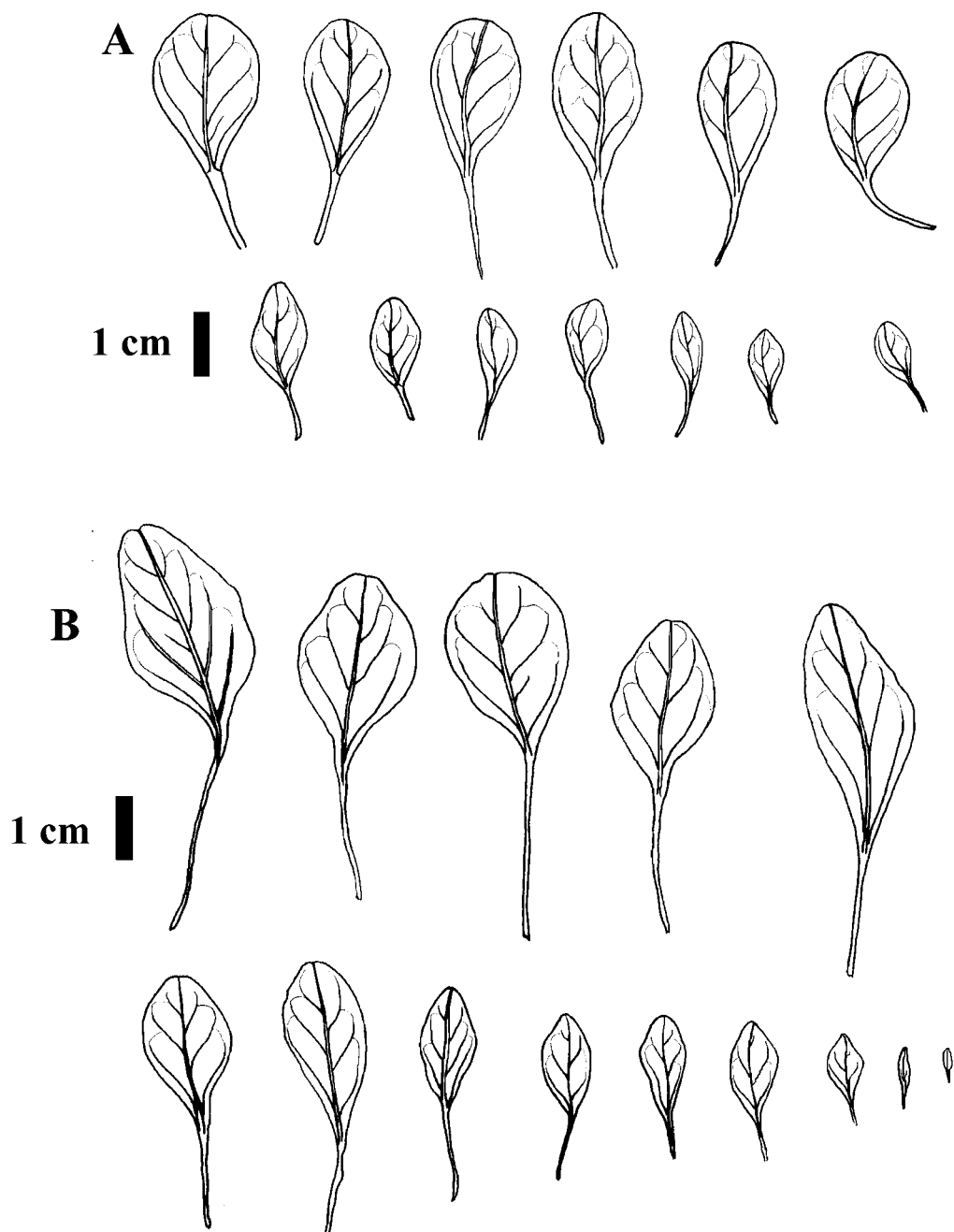
**Fig. 4.** Variation in mature leaves of A. *Amaranthus blitoides* and B. *A. albus*. Leaves in the upper-row for each species are from middle nodes of stems, while lower-row leaves are from higher-order branches.

and the levels of oxalates and nitrates are low (Wesche-Ebeling et al. 1995). The species accumulates As, Pb and Cu and was proposed for phytoremediation of contaminated areas (de Haro et al. 2000).

III. *Amaranthus blitum* has been cultivated as a vegetable in Africa, the Caribbean, China, Greece, India, Italy, Nepal, and the South Pacific Islands (Stallknecht and Schulz-Schaeffer 1993; McIntyre et al. 2001). The species has been

tolerated and allowed to disperse its seeds (semicultivated) in vegetable gardens in Eastern Europe where it is also consumed as a vegetable (Costea 1998). Immigrants from countries where amaranth vegetable use is common, continue to purchase vegetable amaranths in the U.S.A. and they represent a lucrative niche market (Makus 1990; Stallknecht and Schulz-Schaeffer 1993). Oxalate levels are not higher than in other vegetable crops (0.08% in the leaves and 0.15% in the stems) and their content increases
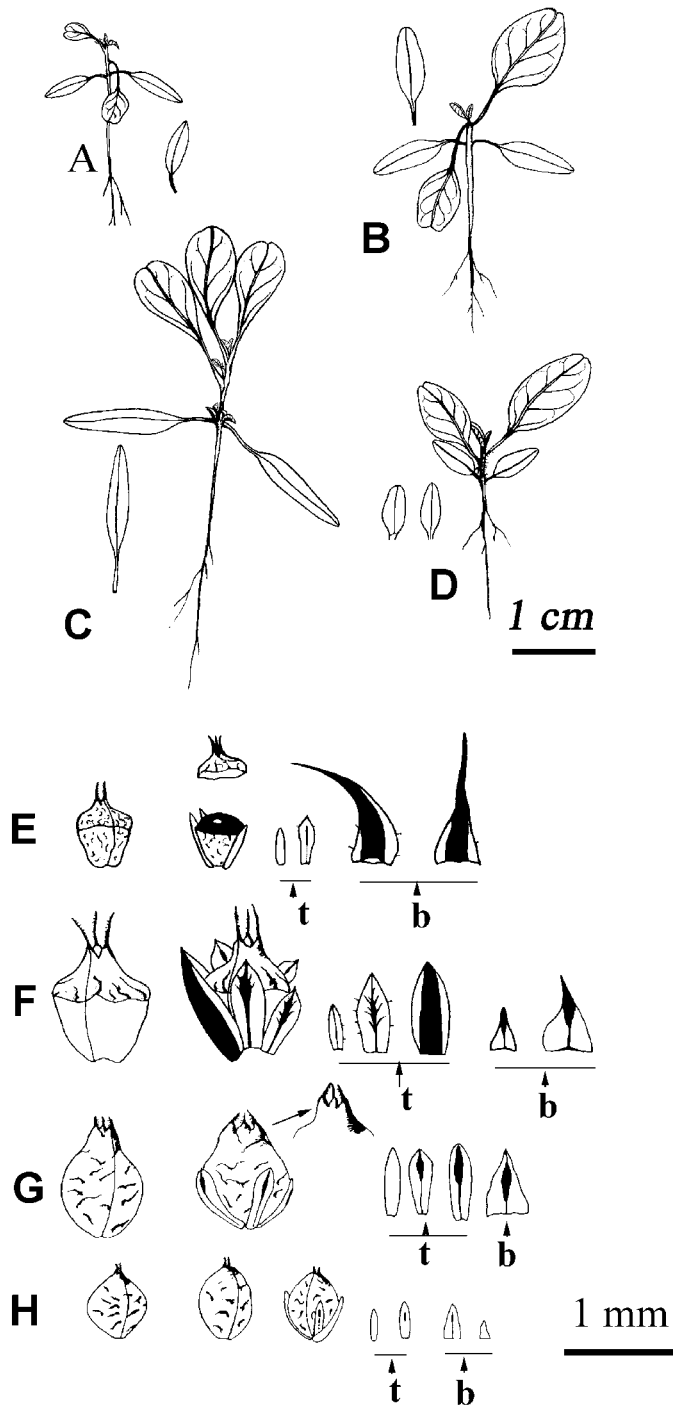
**Fig. 5.** Seedlings of A. *Amaranthus blitum* subsp. *emarginatus*, B. *A. blitum* subsp. *blitum*, C. *A. blitoides*, D. *A. albus*. Scale bar = 1 cm. Fruits, flowers, tepals (t) and bracteoles (b) of E. *A. albus*, F. *A. blitoides*, G. *A. blitum* subsp. *blitum*, H. *A. blitum* subsp. *emarginatus*. Scale bar = 1 mm.

only in plants grown under stress conditions (Der Marderosian et al. 1980). Furthermore, the levels of oxalates can be reduced significantly by steaming or boiling leaves, which does not reduce nutrient levels (Stafford et al. 1976).

Nitrate levels diminish in older plants and are influenced by both genotype and environment (Sleugh et al. 2001). The leaves were judged to be equal or superior in taste to spinach
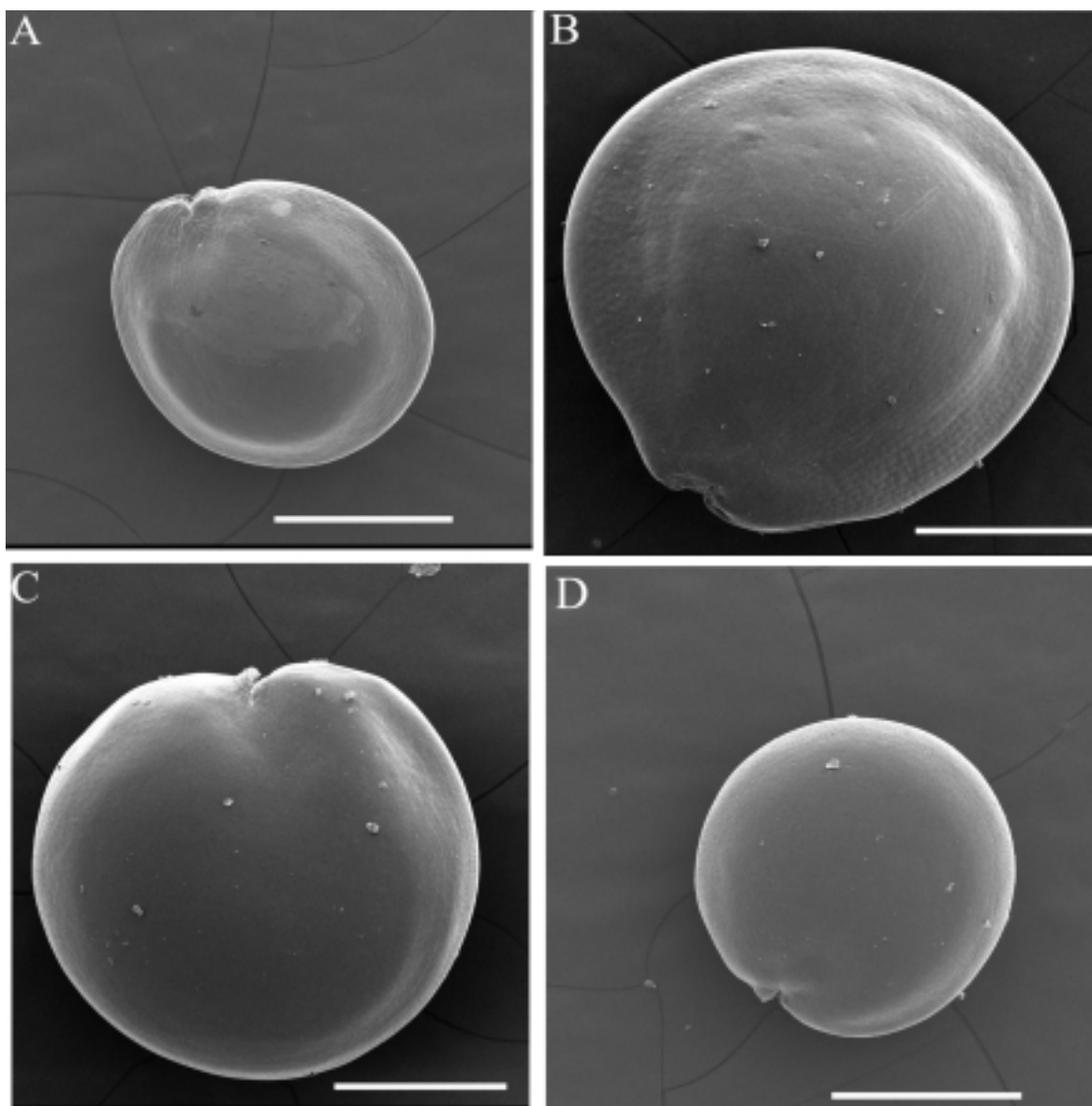
**Fig. 6.** Seeds of A. *Amaranthus albus*, B. *A. blitoides*, C. *A. blitum* subsp. *blitum*, D. A. *blitum* subsp. *emarginatus*. Scale bar = 0.5 mm.

(*Spinacia oleracea* L.) (Abbott and Campbell 1982) and their content of calcium, iron, and phosphorus is considerably higher (Igbokwe et al. 1988; Makus 1990). They are an excellent source of dietary fibre and contain high amounts of protein (22 to 27%, rich in arginine, tryptophan, isoleucine and leucine), vitamins (vitamin C: 130–150 mg 100 g$^{-1}$, vitamin B: 33.7–45 mg 100 g$^{-1}$), minerals (Ca 3.74%, Fe 0.5 mg 100 g$^{-1}$, K 3.84%, Mg 0.77%, P 0.44%, S 593 ppm, Al 592 ppm, Zn 282 ppm, Cu 65 ppm and antioxidants (Makus and Davis 1984; Teutonico and Knorr 1985; Walters et al. 1988; Khader and Rama 1998; Anonymous 2001a). *Amaranthus* spp. can yield 12 400 kg ha$^{-1}$ dry weight of forage, which is highly digestible (Sleugh et al. 2001). The betacyanin pigments of *A. blitum* and other

*Amaranthus* spp. can be used as commercial food colouring, as an alternative for the pigments from red beet (*Beta vulgaris* L.) (Cai et al. 1998b; Cai and Corke 2000). Additionally, the seeds of *A. blitum* are highly nutritious, with a high protein content (19%) composed of easily digestible albumins and globulins (over 50% of total protein), alkali-soluble glutelins (28%) and alcohol-soluble prolamins (12%) (Zheleznov et al. 1997).

*Amaranthus blitum* plants also have medicinal uses. Fluid extracts or a decoction can be used in ulcerated conditions of the throat and mouth, and due to its astringency, it is recommended for diarrhea and dysentery (Grieve 1978). The juice of *A. blitum* was found to inhibit mutagenesis induced by benzo[a]pyrene, 2-amino-fluorene and 3-amino-1,4 dimethyl-5H-pyridol in *Salmonella typhimurium* (Seung et al. 1997).

(c) *Legislation*—In Canada, *A. albus* is listed as a noxious weed only in Manitoba (Anonymous 2001c). In the U.S.A., *A. blitoides* is listed as a "secondary noxious weed" in Minnesota (Anonymous 2001d).

## 4. Geographical Distribution

The current distributions of the three species are based on herbarium specimens from ACAD, ALTA, BH, BRS, DAO, HAM, LRR, 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 from Holmgren et al. 2003). *Amaranthus albus* occurs in all the Canadian provinces, except the coldest ones: Yukon Territory, Northwestern Territories, Nunavut, Newfoundland and Labrador (Fig. 7). *Amaranthus blitoides* occurs in the same provinces as *A. albus*, except Nova Scotia, Prince Edward Island and New Brunswick (Fig. 8). *Amaranthus blitum* subsp. *emarginatus* is naturalized in Québec and there are a few recent collections from the Greater Vancouver Region (UBC) (Fig. 9). Subspecies *blitum* is represented by one old collection from Nova Scotia (1895, MTMG) and some recent collections from Muck Station, Ontario (OAC).

Originally native to the plains of Central North America (Gleason and Cronquist 1991), *A. albus* spread both south and southeast towards dry deserts and canyons, and north towards the more humid and cooler regions of North America. The precise native area of *A. blitoides* is difficult to delimit. Most authors considered it a native of the Western United States (e.g., Britton and Brown 1896; Gleason and Cronquist 1991). *Amaranthus blitum* subsp. *blitum* is native to the Mediterranean region, Eurasia and North Africa and subsp. *emarginatus* to the tropics (Hügin 1987; Costea et al. 2001a). All three species have a wide geographical distribution; *A. albus* is cosmopolitan and *A. blitoides* and *A. blitum* are sub-cosmopolitan.

## 5. Habitat

(a) *Climatic Requirements*—There are no precise data available on the climatic limitations of the three species. *Amaranthus albus* is found in the widest range of climates. Based on herbarium data, it can be found in ruderal vegetal communities up to 1000 m elevation in typical temperate conditions and at even higher elevations (2000–2200 m) in high deserts from SW North America. *Amaranthus blitoides* appears to have similar climatic requirements to *A. albus*. The third species, *A. blitum*, has a narrower range and its higher temperature, water and fertility requirements may be limiting its spread (see section 5b). The minimum temperature required for germination and growth is 12 to 15°C for all three species (see section 8c). Additionally, *A. blitoides* and *A. albus* can tolerate high temperatures (Costea, unpublished). Populations of both species grow on disturbed sands or dunes in many parts of the world. For example, in the Danube Delta, plants are not affected by summer temperatures reaching 70°C at sand level (Costea, unpublished). The ecological preferences for temperature, water and light are summarized below (Barralis 1983; Costea 1998).

I. *A. albus*—thermophyte to sub-thermophyte, xerophyte, heliophyte.

II. *A. blitoides*—thermophyte, xerophyte, heliophyte (var. *blitoides*) or tolerant of shade (var. *reverchonii*). Ciocarlan (1978) in a weed survey of SE Romania observed that populations of var. *blitoides* were preferentially growing at the margins of the crops (e.g. corn). Plants of var. *reverchonii* occurred at high frequency and relative abundance under a canopy of corn plants, suggesting that the two varieties are ecologically separated by their different light requirements.

III. *A. blitum*—thermophyte, mesophyte, heliophyte. Due to its tropical origin, *A. blitum* subsp. *emarginatus* requires warmer temperatures than subsp. *blitum* (Costea et al. 2001a).

(b) *Substratum*—The only available data comparing distribution of these species to soil type are those from the weed surveys undertaken in Saskatchewan (Thomas and Wise 1983c, 1987, 1989). The highest frequencies and relative abundances of *A. albus* and *A. blitoides* were recorded on the Great Groups of Brown Chernozem and Dark Brown Chernozem, medium texture. Such soils have developed under conditions of the lowest available moisture in the prairie region (Anonymous 1998). However, based on our experience, *A. albus* and *A. blitoides* occur over a much wider edaphic spectrum. Both species had higher frequencies, densities and relative abundance on medium and coarse textured soils compared to heavier soils. This concurs with observations recorded on herbarium labels; both species growing on sandy soils, fixed sand dunes and alluvial sands. *Amaranthus albus* and *A. blitoides* can tolerate a range of pH, varying from 4.5 to 8.5, but preferences are for pH values closer to 7 (Costea, unpublished). The nitrogen requirement was evaluated on a scale from 1 (content in the soil very low) to 6 (very high content of nitrogen). Ratings of N4 and N5 characterize nitrophilous plants (Costea 1998). *Amaranthus albus*: N2–3 (–4), *A. blitoides* N4, *A. blitum*, N 4(–5) for subsp. *blitum* and N3–4 for subsp. *emarginatus*.

The subspecies of *A. blitum* have different edaphic preferences. *Amaranthus blitum* subsp. *blitum* can grow on a wide variety of soil types, preferring those that are well-drained and rich in nutrients, such as those used for many field vegetables (Costea 1998). *Amaranthus blitum* subsp. *emarginatus* prefers humid, nitrophilous alluvial sands (Hügin 1986; Costea et al. 2001a). Bachmann and Kinzel (1992) in Austria studied physiological and ecological aspects of the interactions between plant roots and rhizosphere soil using *A. blitum* among five other plant species, and four soil types. *Amaranthus blitum* decreased the sugar and amino acid contents of the rhizosphere in all four soil types. Ponce and Salas (1993), in a greenhouse experiment, studied nutrient uptake by various crops and their associated weeds. Among the weeds, *A. blitoides*, *A. retroflexus* and *Chenopodium album* L. showed the highest macronutrient uptake. Each species had an increased uptake of a particular nutrient: *A. blitoides* of Na, *A. retroflexus* of P and Mn and *Chenopodium album* of Mn.
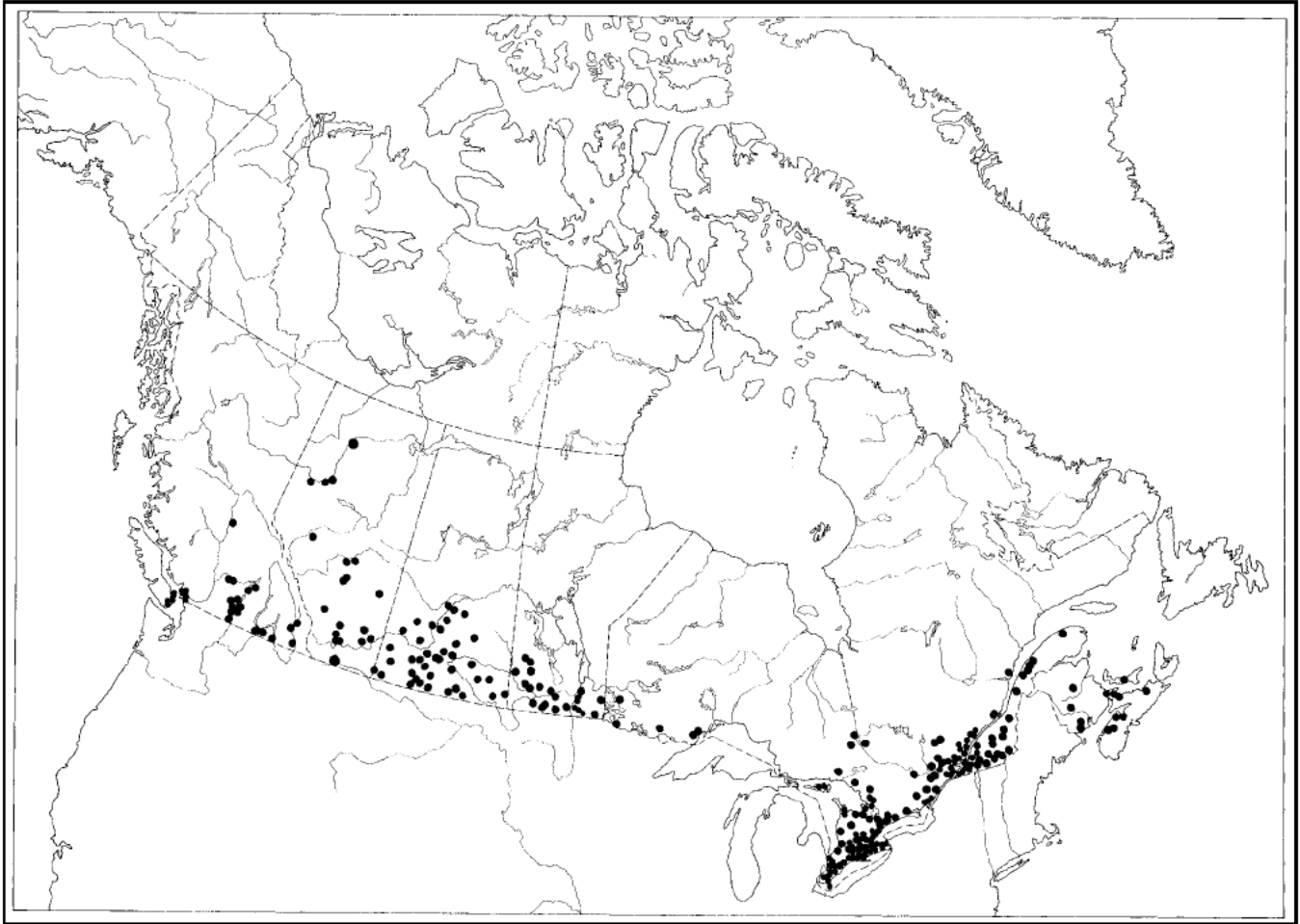
**Fig. 7.** Distribution of *Amaranthus albus* in Canada.

(c) *Communities in which the Species Occur—Amaranthus albus* and *A. blitoides* occur in a wide variety of habitats in Canada, both ruderal (disturbed ground, along roadsides and railways, waste land, rubbish tips, fallow fields) and agrestal (spring cereals and other grains, winter wheat, canola, mustard, rape, sunflower, flax, cotton, vegetable crops, orchards, tree nurseries and vineyards). *Amaranthus blitum* subsp. *blitum* grows mostly as a ruderal. *Amaranthus blitum* subsp *emarginatus* var. *emarginatus* is a pioneer of periodically flooded sandy mud on shores and riverbanks. Variety *pseudogracilis* occurs in the same communities as *A. blitum* subsp. *blitum* or sometimes together with var. *emarginatus* (Costea et al. 2001a).

The Canadian weed survey conducted between 1922 and 1944 and based on 4686 survey lists, of settled regions, provided the first data on the occurrence and frequency of *A. albus* and *A. blitoides* in Canada (Table 1) (Groh and Frankton 1949). Frequency was calculated as the number of lists in which a particular species was recorded in every hundred survey lists. The two species are usually ruderals, not mentioned in many weed surveys from Alberta and British Columbia (Thomas and Wise 1983b; Thomas and

Wise 1985; Thomas et al. 1986), New Brunswick (Thomas et al. 1994), Nova Scotia (McCully et al. 1991), Prince Edward Island (Thomas and Ivany 1990) and most of the weed surveys from Québec (Doyon et al. 1986; Doyon et al. 1987a, c; Lemieux et al. 1988a, b, c). In Québec, *A. albus* and *A. blitoides* were included among species with less than 10% presence in L'Assomption and Richelieu (Doyon et al. 1987b, d). Furthermore, the two species were not classified among the top 15 (Alex 1964; Richards 1979) or top 39 weed species in Ontario (Frick et al. 1990; Frick and Thomas 1992). Information regarding the frequency and relative abundance of *A. albus* and *A. blitoides* in various crops is summarized in Tables 2 and 3. Taking into account that in an earlier survey of cultivated land in the Prairie Provinces (Alex 1966) the two species were not ranked among the 45 top species, we concluded that an increase in frequency and relative abundance has occurred in the last 35 yr in some situations (Tables 2 and 3).

Dale and Thomas (1987) described weed communities of cereal and oilseed crops in Saskatchewan using data from surveys of more than 400 fields. Cluster analysis of the entire data set grouped *A. blitoides* on the same dendrogram
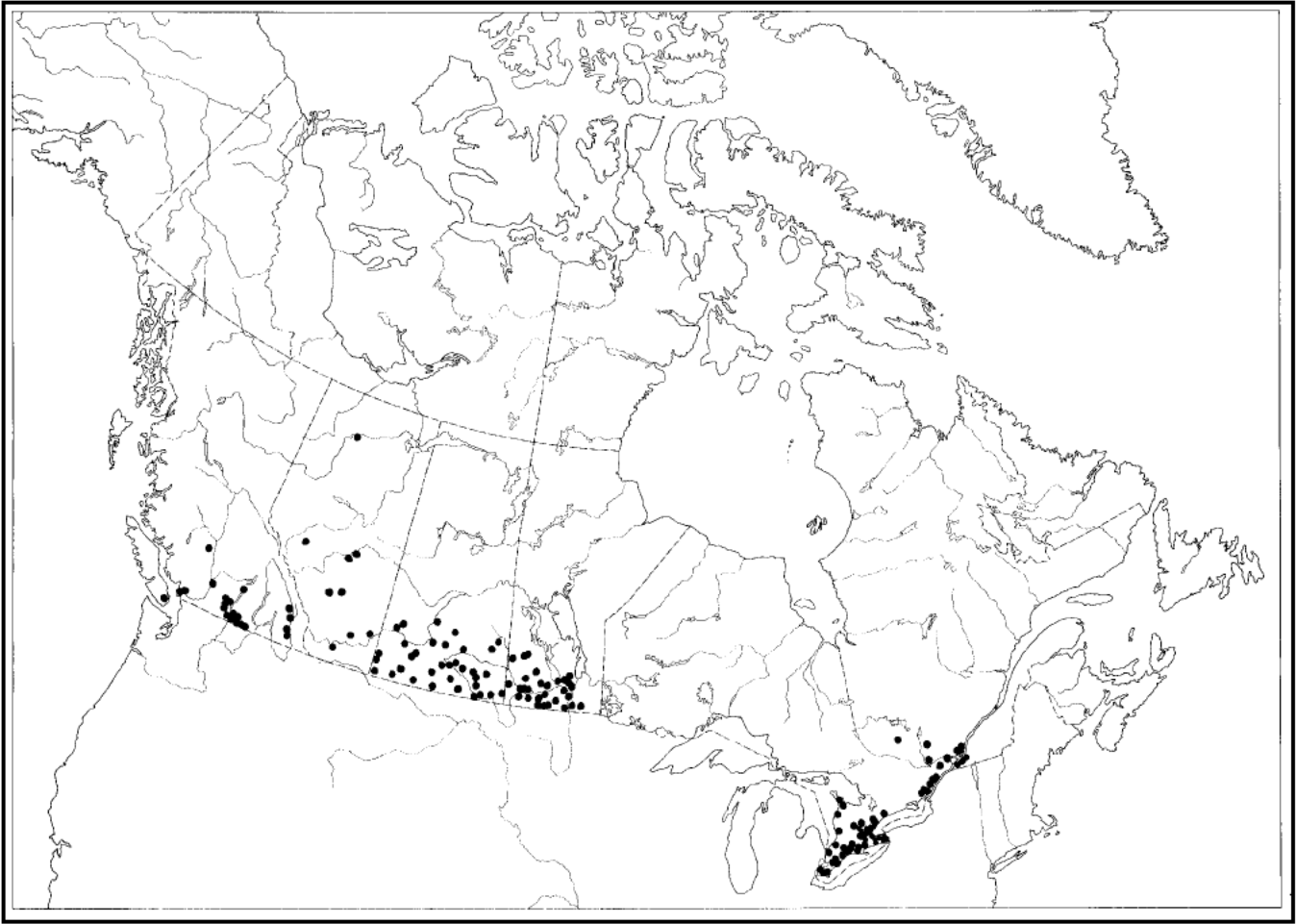
**Fig. 8.** Distribution of *Amaranthus blitoides* in Canada.

branch with (listed in decreasing order of similarity measures): *Euphorbia serpyllifolia* Pers., *Kochia scoparia*, *Lepidium densiflorum* Schrad., *Artemisia biennis* Willd., *Hordeum jubatum* L., *Polygonum aviculare* L. and *Echinochloa crus-galli* (L.) Beauv. Derksen et al. (1993, 1995) studied the impact of tillage systems and herbicide application on weed communities from Saskatchewan. The results showed stability of the weed community diversity or even an increase in the number of species after herbicides were applied. *Amaranthus blitoides* was one of the few species completely eliminated under zero and minimum tillage, or drastically reduced under conventional tillage and PRE and POST herbicide application. Frick et al. (1990) conducted a weed survey in corn, soybean and wheat fields managed with different systems in southwest Ontario. *Amaranthus blitoides* was not encountered in any survey. *Amaranthus albus* scored the highest values for frequency (F), density (D), rank (R) and abundance (A) under no-till systems (F = 1.5%, D = 6.7 plants m$^{-2}$, R = 48 and A = 0.4). In fields under conservation tillage systems the values were lower (F = 0.9, R = 55, D = 0.2 and A = 0.2).

In Europe, the highest incidence of *A. albus* and *A. blitoides* is in row and vegetable crops, vineyards and orchards (Hanf 1983; Qasem 1992; Saavedra and Pastor 1996; Dorado et al. 1999; Vizantinopoulos and Katranis 1994, 1998). Some of the highest frequencies of *A. blitoides* in Canada have been reported from tomato and corn crops in Ontario (Alex 1964). *Amaranthus blitum* was mentioned in only one weed survey so far in Canada—from L'Assomption, Quèbec (Doyon et al 1987d), where it was included among species with less than 10% presence. Taking into consideration its ecological preferences, we estimate that it might become an agrestal weed only in Southern Ontario and Québec, in vegetable crops and vineyards.

*Amaranthus albus* was recorded as a dominant weed in non-irrigated fields in Yugoslavia (Momirovic et al. 1998), Turkey (Pohl et al. 1998) and Spain (Carretero 1995).

## 6. History
In 1917, *A. albus* and *A. retroflexus* were the only weedy amaranths mentioned from Alberta (Smith 1917), and in 1940 the two-above mentioned species, together with *A. blitoides* were the only three *Amaranthus* species known as weeds from Ontario (Howitt and MacLeod 1940). Rousseau (1968), studying the distribution of *A. albus*, *A. blitoides* and *A. blitum* among 220 adventive species in Québec, suggest-
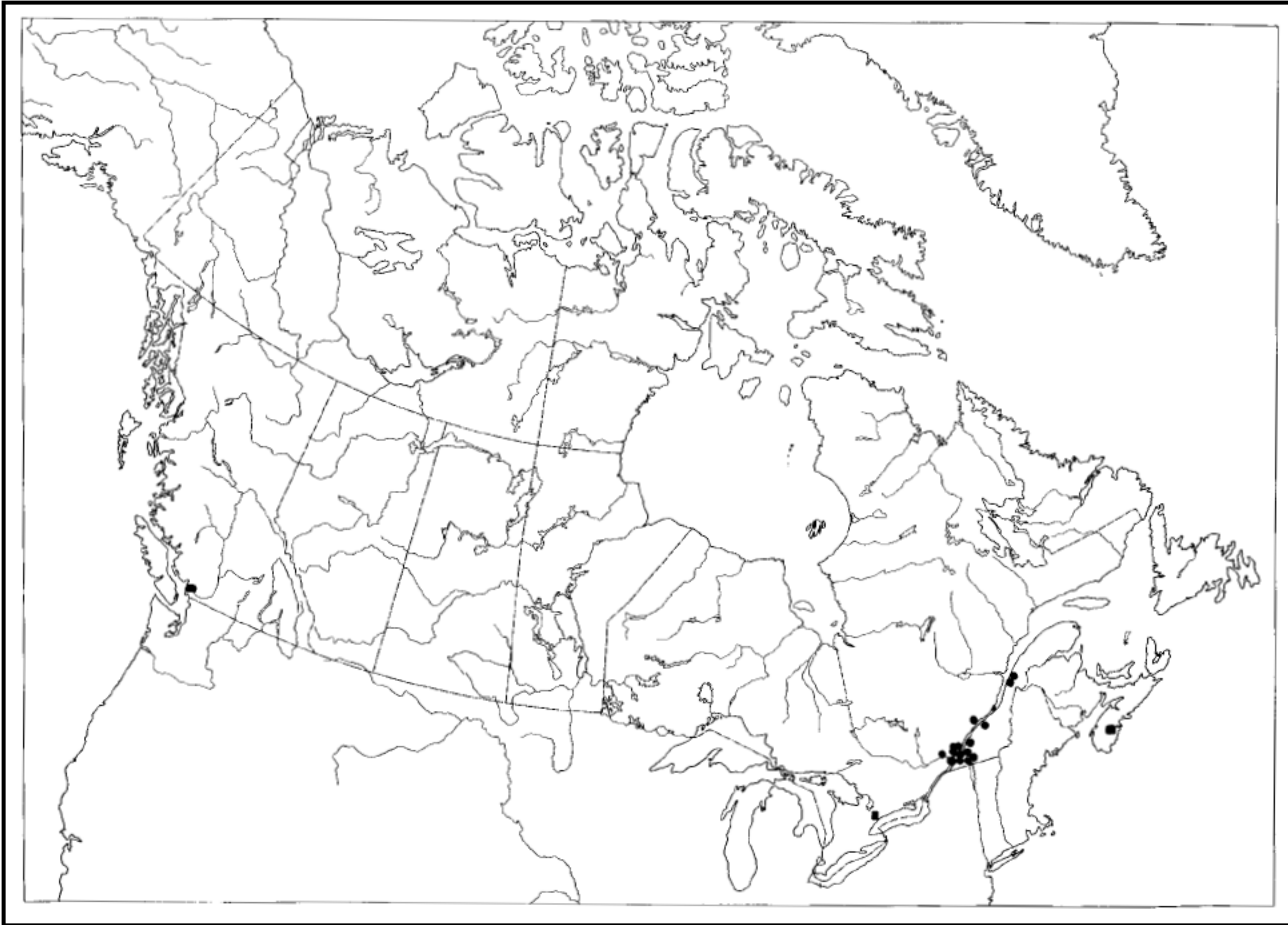
**Fig. 9**. Distribution of *Amaranthus blitum* in Canada. Dots represent *A. blitum* subsp. *emarginatus* and squares (Nova Scotia and Ontario only) *A. blitum* subsp. *blitum*.

ed that the 3 species were probably not persistent in that province. This prediction has not been confirmed. Based on data from herbarium collections, the three species have continued to spread in Québec.

I. *A. albus*—*A. albus* is one of the "tumbleweed" species, archetype and part of the North American culture, a metaphor for drifting, loneliness and desolation. "It is as much a visual trademark of Western romance as the moonlit silhouette of a coyote" (Harrigan 2001). According to Rousseau (1968), Holmes collected it in 1821 from Montreal where it was growing along railway tracks. Macoun in 1886, in the "Catalogue of Canadian Plants" noted about *A. albus*: "[...] naturalized on waste heaps near towns and extensively spreading along railways throughout the country, being found in North-west and British Columbia whenever railway construction is going on". He also collected the weed from Hastings Co., Ontario in 1870 (MTMG).

II. *A. blitoides*—The seeds of *A. blitoides* were part of the diet of the Zuni People of New Mexico "who believed that the original seeds of it had been brought up from the underworld at the time of the race's emergence into the light of the day" (Saunders 1934). *Amaranthus blitoides* seeds were mixed and ground with corn and salt; the flour shaped into balls and the pats afterwards steamed (Saunders 1934). It has been known in Ontario since at least 1860 (Groh and Frankton 1949). Other early records based on herbarium material include those from Ontario: London 1879 (MTMG); Ottawa 1879 (MTMG) and 1890 (UWO). Macoun (1886) suggested that it had been introduced by the railway.

III. *A. blitum*—Theophrastus (ca. 371–287 BC) in ancient Greece was the first who described and mentioned "blite" as a cultivated vegetable. The plant had "not a single straight root, but a number of roots which start directly from top" (VII. III. 1–3) and it was sown in summer ("in the month Monychion", VII, I. 2–3) (Theophrastus 1916). This species was also referred to as a potherb by Discorides (II. 143; see Gunther 1959). Pliny the Elder (ca. 23–79 A.D.) mentioned some of the cultural aspects (XIX. 35. 118 and 36. 119–122) and medicinal properties (XX. 59. 245) (Pliny the Elder 1951). Approximately 15 centuries later, in 1542 Fuchs noted: [...]" if once has been grown in cultivated soil, it replaces itself for many sea-

**Table 1. Frequency (%) of *Amaranthus albus* and *A. blitoides* in different longitudinal areas of Canada between 1922 and 1944 (Groh and Frankton 1949). – = species not encountered. BC = British Columbia, AL = Alberta, SK = Saskatchewan, MN = Manitoba, ON = Ontario, QC = Québec; w = western, e = eastern, nw = northwestern**

| | Area of Canada | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 131–116°W BC & w AL | 115–108°W e AL & w SK | 107–100°W SK & w MN | 99–92°W e MN & w ON | 91–84°W Superior ON | 83–76°W Central ON & nw QC | 75–68°W e ON & Central QC | 67–60°W Maritimes & Gaspé |
| Number of surveys | 713 | 364 | 427 | 192 | 117 | 947 | 921 | 1005 |
| *A. albus* | 4.0 | 11.4 | 18.7 | 15.6 | 4.2 | 9.5 | 5.3 | 1.9 |
| *A. blitoides* | 0.5 | 7.9 | 9.0 | 8.3 | 0.8 | 5.6 | 1.5 | – |

sons by scattering seeds, so that you could scarcely get rid of it if you wished" (Fuchs 1999). Apparently, cultivation of *A. blitum* in the Mediterranean region began to decline in the 18th century after the introduction of spinach (Costea et al. 2001a).

The precise date when *A. blitum* was introduced to North America is not known. According to Britton and Brown (1896) and Fernald (1950), "*A. lividus*" growing from eastern Massachusetts to southern New York, United States, had a tropical origin. However, a specimen collected from Central Park, New York City in 1861 was identified as *A. blitum* subsp. *blitum* by Costea et al (2001a), and therefore had been introduced from Europe or North Africa. The earliest Canadian specimen that we saw belongs also to *A. blitum* subsp. *blitum* and it was collected from Tatamagouche, Nova Scotia in 1895 (MTMG). The first records of the tropical *A. blitum* subsp. *emarginatus* in North America are more recent, dating from the 1930s. In Canada, the earliest specimen that we saw was collected in 1938, in Saint-Vincent de Paul, Québec (DAO).

## 7. Growth and Development

(a) *Morphology*—The three *Amaranthus* species have all the attributes required by ecologically successful annual weeds: rapid growth, early reproduction and continuous seed production (Cousens and Mortimer 1995). Cheplick (2001), studying the relationships between vegetative (VA) and reproductive allocation (RA) that occur in *A. albus* in relation to soil nutrients, found that unfertilized plants had significantly higher RA than fertilized plants. Root and leaf masses were negatively correlated with RA. If sufficient resources were available, VA was temporarily allowed, but only to support new allocations towards flowering and seed maturation. The result is an indeterminate vegetative growth pattern, accompanied by continuous initiation of flowers and maturation of seeds. Unfavorable conditions and senescence stop the process. In *A. albus*, the size of leaves is maximal in young plants and constantly decreases in older plants, on the secondary and higher order branches. Cavers and Steel (1984) observed a similar pattern of variation in the size and weight of the seeds in *A. blitoides*, and seven other species. The first seeds produced were the largest, and progressively smaller seeds developed as the plants aged. This observation can be explained for *A. blitoides* through the allocation of the same (or diminished) amount of resources to a constantly increasing number of fertilized flowers, due to the devel-

opment pattern of the dichazial cymose units in the inflorescences [see section 8 (a)].

Horak and Loughin (2000) conducted a 2-yr field study comparing the growth rates of *A. albus*, *A. retroflexus, A. rudis* Sauer and *A. palmeri* S. Watson. Of the four species, *A. albus* had the slowest rate of height increase (0.08–0.09 cm per growing degree day), the smallest values for plant volume (8 152–983 230 cm$^3$), the lowest dry weight (163–524 g) and smallest specific leaf area (127–190 cm$^2$ g$^{-1}$).

The size of plants is correlated with architectural traits such as branch number and branch length, which together determine fitness, expressed as the number of seeds produced by the plant (Cheplick 2002). Branch number and length are the main determinants of overall plant size, with more seeds being produced on longer branches (Cheplick 2002). The number of primary branches in *A. albus* was found to be similar to that in *A. palmeri* and *A. powellii* S. Watson (Horak and Loughin 2000), with all three species having a high potential for seed production. *Amaranthus blitoides* normally starts branching early, from the axillary buds of cotyledons (Costea and DeMason 2001). The stem of *A. albus* continuously ramify divaricately, with the plants finally reaching a semispherical shape that aids in seed dispersal. The prostrate stems of *A. blitoides* branch many times and form compact mats with diameters of up to 1 (1.5) m. *Amaranthus blitum* may have a prostrate, ascendant or erect habit depending on infraspecific variability and the environmental conditions.

*Anatomical data*—The most interesting anatomical feature of *Amaranthus* spp. is the mechanism of secondary growth in the roots and the base of the stems (reviewed by Costea and DeMason 2001). Secondary growth is characterized by the development of successive, concentric and centrifugally developing cambial zones, which generate a complex structure consisting of hundreds of collateral bundles included in a ground-tissue. The growth activity of the first cambium in stems in *A. blitoides* and *A. blitum* is much more limited compared to that of *A. albus*, which explains why the stems of the latter species are more lignified and persistent over the winter.

The leaves and bracteoles of the three species have C$_4$ anatomy (Toma et al 1994; Costea 1998; Costea and Tardif 2003b). In the leaves, the tertiary bundles are surrounded by a bundle sheath formed by a layer of tightly packed, thick-walled cells containing many large chloroplasts (Kranz-wreath). The mesophyll is dorsiventral, but the general pattern is obscured by the radial organization of both palisade and spongy parenchyma cells around the tertiary veins. The

**Table 2. Frequency, density and relative abundance of *Amaranthus albus* from weed surveys across Canada. Relative abundance is a combination of the frequency, field uniformity (all fields) and mean field density (all fields) (see any of the cited weed surveys for more information). Most surveys were conducted in the summer after herbicide treatment. x, data not available; –, species not recorded in the survey**

| Province | Crop(s) | Year | Frequency (%) | Relative density (no m$^{-2}$) | Relative density rank | Relative abundance | Source |
|---|---|---|---|---|---|---|---|
| Alberta | Spring wheat | 1997 | 0 5 | 0.6 | 61 | 0.1 | Thomas et al. (1998) |
| | Barley | 1997 | 0 5 | 0.8 | 62 | 0.1 | Thomas et al. (1998) |
| | Canola | 1997 | 0.6 | 0.2 | 76 | 0.1 | Thomas et al. (1998) |
| Saskatchewan | Wheat, barley, oats, flax, rape, rye | 1976 | x | x | 54 | x | Thomas (1977) |
| | Wheat, barley, oats, flax, rape, rye | 1977 | x | x | 54 | <0.1 | Thomas (1977) |
| | Wheat, barley, oats, flax, rape, rye | 1978 | 2.3 | 5.6 | 40 | 0.2 | Thomas (1978a) |
| | Wheat, barley, oats, flax, rape, rye | 1979 | x | x | 101 | <0.1 | Thomas (1979) |
| | Spring wheat/durum | 1976–1979 | 1.1 | 1.2 | 48 | 0.2 | Thomas and Wise (1983c) |
| | Spring wheat/durum | 1986 | 4.8 | 2.6 | 23 | 2.2 | Thomas and Wise (1987) |
| | Winter wheat | 1985 | 0.4 | 0.4 | | <0. 0.1 | Thomas and Wise (1986b) |
| | Winter wheat | 1985–1988 | 0.5 | 0.4 | 75 | 0.1 | Thomas and Wise (1989) |
| | Barley | 1976–1979 | 0.2 | 104.0 | 46 | 0.3 | Thomas and Wise (1983c) |
| | Barley | 1986 | 0.8 | 1.6 | 54 | 0.3 | Thomas and Wise (1987) |
| | Oats | 1976–1979 | 0.9 | 3.7 | 54 | 0.2 | Thomas and Wise (1983c) |
| | Oats | 1987 | 4.2 | 1.8 | 29 | 1.2 | Thomas and Wise (1987) |
| | Spring wheat/durum, barley oat | 1995 | 2.0 | 2.5 | 38 | 0.8 | Thomas and al. (1996) |
| | Lentil | 1985 | 1.2 | 0.8 | 35 | | Douglas and Thomas (1986) |
| | Lentil, field pea | 1995 | 1.1 | 0.2 | 67 | 0.2 | Thomas and al. (1996) |
| | Canola, flax, mustard | 1995 | 0.7 | 0.2 | 65 | 0.2 | Thomas and al. (1996) |
| | Sunflower | 1985 | 6.0 | 0.3 | 25 | | Thomas and Wise (1986a) |
| Manitoba | Wheat, barley, oats, flax, rape | 1978 | – | – | – | <0.1 | Thomas (1978a) |
| | Barley | 1997 | 3.6 | 0.2 | 58 | 0.7 | Thomas et al. (1998) |
| Ontario | Tomato | 1960–1961 | 22 | x | 20 | x | Alex (1964) |
| | Corn | 1960–1961 | 18 | x | 20 | x | Alex (1964) |
| | Corn, soybean, winter wheat | 1988–1989 | 0.8 | <0.1 | 56 | 0.2 | Frick and Thomas (1990) |

dense vascularization ensures a fast and efficient loading of sugars in the phloem and a greater capacity for translocation. The stomata are located in each epidermis and are surrounded by 3–8 cells that do not differ in size and shape from other epidermal cells (anomocytic type). The average density of stomata in mature leaves is: *A. albus*—116 stomata mm$^{-2}$ in the lower epidermis and 92 stomata mm$^{-2}$ in the upper epidermis; *A. blitoides*—90 stomata mm$^{-2}$ in the lower epidermis and 63 stomata mm$^{-2}$ in the upper epidermis; *A. blitum*—130 stomata mm$^{-2}$ in the lower epidermis and 106 stomata mm$^{-2}$ in the upper epidermis (Costea 1998).

*Embryological data* have only been published for other *Amaranthus* spp. (e.g., Salakhova et al. 1995; Coimbra and Salema 1999). The ovule is campylotropous (oriented transversely and with a curved embryo sac), protected by two thin (two-cell layered) integuments. The embryo sac is of the "Polygonum" type. The endosperm is nuclear. The embryo is curved around the seed margin. The food reserve materials (starch and proteins) are not deposited in the thin endosperm layer located outside the embryo, but in the perisperm that develops from the nucellus and is enclosed by the embryo (Koval 1954; Klopfer and Robel 1989). After fertilization, the epidermal cells of the outer integument start to accumulate tannin and their walls are thickened following a specific pattern, forming projections called "stalactites" in the cells of the seed coat (Klopfer and Robel 1989; Tikhomirov and Fedorova 1997). The inner cell layer of the inner integument is crushed during seed development. The result of these developmental changes is a thin and struc-turally simple exotestal seed coat, but at the same time impermeable and resistant to mechanical and chemical agents. The mature pericarp (fruit) also has a very simple structure, two-layered in *A. blitoides*, three-layered in *A. albus* and three- to four-layered in *A. blitum* (Costea et al. 2001b). Large intercellular spaces filled with air are formed between the epidermis-mesocarp and the endocarp in the fruits of *A. blitum*, giving them good buoyancy. Furthermore, due to the intercellular spaces, the pericarp of indehiscent fruits could play a significant role in imbibition (Costea et al. 2001b).

(b) *Perennation*— The three species are annuals and over-winter as seeds on or below the surface of the soil. Some seeds of *A. albus* may overwinter on the mother plant if this is not uprooted or if its stems do not break (see section 8b).

(c) *Physiological data*—*Amaranthus* spp. have $C_4$ photosynthesis, with all the characteristics derived from it. The literature devoted to photosynthesis in *Amaranthus* spp. is quite extensive (e.g. reviewed by Weaver and McWillimas 1980, Nielsen and Anderson 1994; Ziska and Bunce 1999), but studies referring to the three species examined in the present paper are scarce. The aspartate aminotransferase enzyme that participates as an electron shuttle and intercellular transport of metabolites during $C_4$ photosynthesis was detected by ultra-cytochemistry in the cristae of mesophyll and bundle sheath mitochondria of *A. blitum* (Fomina et al. 1981). Soluble Ca was found to inhibit pyrophosphatase activity in crude plant extracts of *A. blitum* (Gavalas and Manetas 1980).

**Table 3. Frequency, density and relative abundance of *Amaranthus blitoides* from weed surveys across Canada. Most surveys were conducted in the summer after herbicide treatment. x, data not available; –, species not recorded in the survey**

| Province | Crop(s) | Year | Frequency (%) | Relative density (no m$^{-2}$) | Relative density rank | Relative abundance | Source |
|---|---|---|---|---|---|---|---|
| British Columbia | Barley | 1978–1980 | 0.7 | 5.8 | 56 | 0.2 | Thomas and Wise 1983a |
| Alberta | Spring wheat | 1997 | 0 9 | 0.3 | 50 | 0.2 | Thomas et al. (1998) |
| Saskatchewan | Wheat, barley, oats. flax, rape, rye | 1976–1977 | 6.3 | 7.9 | 26 | 0.4, 1.5 | Thomas (1977) |
| | Wheat, barley, oats. flax, rape, rye | 1978 | 5.2 | 1.4 | 31 | 1.2 | Thomas (1978a) |
| | Wheat, barley, oats. flax, rape, rye | 1979 | 4.1 | 1.4 | 30 | 1.1 | Thomas (1979) |
| | Spring wheat/durum | 1976–1979 | 5.5 | 2.1 | 24 | 1.4 | Thomas and Wise (1983c) |
| | Spring wheat/durum | 1986 | 10.0 | 2.1 | 12 | 3.8 | Thomas and Wise (1987) |
| | Winter wheat | 1985 | 1.4 | 0.8 | 61 | 0.3 | Thomas and Wise (1986b) |
| | Winter wheat | 1985–1988 | 1.9 | 0.5 | 44 | 0.6 | Thomas and Wise (1989) |
| | Barley | 1976–1979 | 2.2 | 1.3 | 42 | 0.4 | Thomas and Wise (1983c) |
| | Barley | 1986 | 3.4 | 11.3 | 28 | 1.5 | Thomas and Wise (1987) |
| | Oats | 1976–1979 | 1.3 | 0.3 | 59 | 0.2 | Thomas and Wise (1983c) |
| | Oats | 1986 | 4.2 | 4.4 | 28 | 1.6 | Thomas and Wise (1987) |
| | Spring wheat/durum, barley oat | 1995 | 3.0 | 1.3 | 36 | 0.8 | Thomas and al. (1996) |
| | Lentil | 1985 | 6.0 | 0.7 | 17 | 1.6 | Douglas and Thomas (1986) |
| | Lentil, field pea | 1995 | 1.1 | 1.0 | 59 | 0.3 | Thomas and al. (1996) |
| | Lax | 1976–1979 | 10.7 | 0 9 | 21 | 2.6 | Thomas and Wise (1983c) |
| | Flax | 1986 | 11.1 | 0.8 | 19 | 3.6 | Thomas and Wise (1987) |
| | Rape | 1976–1979 | 0.6 | 1.1 | 58 | 0.1 | Thomas and Wise (1983c) |
| | Mustard | 1985 | 5.6 | 3.0 | 28 | 1.2 | Douglas and Thomas (1986) |
| | Canola, flax, mustard | 1995 | 3.1 | 1.4 | 37 | 0.8 | Thomas and al. (1996) |
| | Sunflower | 1985 | 6.0 | 1.5 | 22 | 1.9 | Thomas and Wise (1986a) |
| Manitoba | Wheat, barley, oats, flax, rape | 1978 | 3.6 | 2.9 | 32 | 0.9 | Thomas (1978b) |
| | Wheat, barley, oats, flax, canola | 1986 | 1.0 | 1.3 | 54 | 0.3 | Thomas and Wise (1988) |
| | Barley | 1997 | 1.4 | 0.2 | 51 | 0.7 | Thomas et al. (1998) |
| | Canola | 1997 | 0.9 | 1.2 | 54 | 0.2 | Thomas et al. (1998) |
| | Annual crops | 1978, 1979 | | | | | |
| | | 1981 | 1.8 | < 0.1 | 40 | 0.5 | Thomas (1991) |

Based on our observations, populations of these three species growing in temperate regions have a facultative short-day flowering response. Stoller and Myers (1989) studied the responses to reduced irradiance in *A. albus*, common lamb-squarters (*Chenopodium album*), eastern black nightshade (*Solanum ptycanthum* Dun.) velvetleaf (*Abutilon theophrasti* Medik.) and soybean [*Glycine max* (L.) Merr.]. Net photosynthesis of *A. albus* at 50 µE m$^{-2}$ s$^{-1}$ PPFD was surpassed by the other species, and it was concluded that this species was better adapted to intense light environments where it could use its superior photosynthetic capacity.

The cultivated biotypes of *A. blitum* were used to assess physiological and biochemical responses of plants to heavy metals, salt, cold and heat stress. Bhattacharjee (1997–1998) determined that heavy metals caused a decline in ethylene evolution in germinating seedlings and a considerable decrease in the activities of free radical scavengers such as peroxidase, catalase and superoxide dismutase. High salinity levels caused membrane deterioration by membrane lipid peroxidation and a decrease in ethylene formation by the primary leaves (Bhattacharjee and Mukherjee 1996). An interdependence between the concentration of Ca$^{2+}$ and the accumulation of proline was observed in seedlings subjected to short-term heat and cold (Bhattacharjee and Mukherjee 1995a). Cold treatments in the early imbibitional phase at 4°C for 12h decreased germination and inhibited growth of seedlings. A decline of ethylene formation and a loss of membrane integrity were observed in chilled seedlings. The concentration of photosynthetic pigments and the activity of protease were reduced.

Proline content did not change significantly in different treatments (Bhattacharjee and Mukherjee 1995b). *Amaranthus blitum* was also used in studies of fatty acid biosynthesis: acyl lipid synthesis by chloroplasts isolated from chilling-sensitive plants (Roughan 1986); the influence of endogenous acyl-acyl carrier protein concentrations (e.g., Roughan and Matsuo 1992); the role of acetate concentrations in leaves (Roughan 1995) and the evidence for organization of enzymes of fatty acids in chloroplasts into a multienzyme assembly that channels acetate into long-chain fatty acids (Roughan and Ohlrogge 1996).

*Amaranthus* spp. pigments are betacyanins called amaranthine, the 5-O-[2-O-(β-D-glycopyranosyluronic acid) β-D-glucopyranoside] of betanidine (Cai et al. 1998a). A peculiarity of *Amaranthus* spp. betacyanins is their association with proteins (Cai et al. 1998a). The average protein content of dried pigment of *A. blitum* was 24.2%.

(d) *Phenology*—Germination of *A. albus* and *A. blitoides* occurs in Southern Ontario from the middle of May to the beginning of June. The first seeds of *A. blitum* germinate at the end of June or beginning of July. Based on information collected from herbarium specimens, flowering of *A. albus* and *A. blitoides* in Southern Ontario begins at the end of June or beginning of July, and of *A. blitum* at the end of July or early August, continuing until senescence is induced by the first fall frost (Stevens 1924). Seeds appeared to be mature 20–30 d after flowering. Shedding of seeds (*A. albus* and *A. blitoides*) and of the seeds enclosed in fruits (*A. bli-*

*tum*) extends throughout the rest of the growing season, due to the indeterminate growth pattern of inflorescences and the continuous formation of new flowers.

In Canada, *A. blitum* could have more than one generation per year only if germination of the second generation occurs at the end of August and if the growing season lasts until the end of October or November. The temperature requirements for germination and growth of *A. albus* and *A. blitoides* are lower than that for *A. blitum* and this makes it possible for them to have two generations per year. However, further studies are necessary to determine if seeds are capable of germinating as soon they are produced, as are those of *A. blitum* (see section 8c).

Prather and Kearney (1995) in California used accumulated degree-days to predict emergence and phenological development of *A. blitoides*, *A. retroflexus* and three other annual weeds. *Amaranthus blitoides* seedlings emerged fastest, at 400 degree days, followed by *A. retroflexus* at 700 degree days. The prostrate plants of *A. blitoides* grew faster than plants of *Solanum nigrum* L., an erect species.

(e) *Mycorrhiza* – *Amaranthus* spp. have been regarded as non-mychorrizal species (reviewed by Jordan et al. 2000). However, Arriola et al. (1997) reported successful inoculation with *Glomus intraradicens* Schenck & Smith, followed by arbuscular mycorrhizal root colonization in *Amaranthus caudatus* L. and *A. tricolor* L. Furthermore, vesicular-arbuscular mycorrhiza formation has been observed in *A. blitoides* growing as a weed in citrus orchards in Japan (Ishii et al. 1998). Nodule-like structures containing colonies of microorganisms that may be involved in nitrogen fixation were reported on both the roots and the stems of *A. blitum* (Sampath and Mishra 1971).

## 8. Reproduction

(a) *Floral biology*—The flowers in *Amaranthus* spp. develop in small and contracted dichazial cymes, the first flower within each cyme being male and the subsequent flowers being female (Murray 1940). Due to the dichazial pattern of branching of the cyme axis, the number of female flowers within the inflorescence units increases in a geometric progression. New cymes develop acropetally along with stem growth and the male flowers from the upper cymes can fertilize female flowers from lower cymes (personal observation). The cymes arise from leaf axils in *A. albus* and *A. blitoides*. They are also borne in a racemose or spiciform terminal synflorescence in *A. blitum*. The flowers are small, green and unattractive. The three species have self-compatible breeding systems and are predominately self-pollinated by wind and gravitation (personal observation). There is no information available on the outcrossing rate for these three *Amaranthus* species. The stigmas (2 or 3) of *Amaranthus* spp. belong to the "dry" type, with the receptive part provided with 2–4 rows of uni- or bicellular hairs (Costea et al., 2001b). The pollen grain is small, with a diameter of 18–28 µm (Costea et al. 2001a; Franssen et al. 2001). Generally, it has more than 18 sunken pores (apertures) uniformly distributed (pantoporate), and it is covered with granules or spinules, which ensure adherence to the stigma hairs.

(b) *Seed Production and Dispersal*—Both dehiscent (in *A. albus* and *A. blitoides*) and indehiscent (in *A. blitum*) fruits originate from the same type of syncarpous gynoecium. It consists of two or three carpels, is not divided into compartments and contains only one ovule (Costea et al. 2001b). According to our observations of plants under greenhouse conditions, the development of seeds after fertilization required 20 to 30 d in all species, which is consistent with the observations reported for cultivated amaranths (Gaspar et al. 2001).

A plant of *A. albus* can produce approximately 92 000 fertile + 58 000 sterile seeds (Hügin 1986); 129 000 seeds (Stevens 1932) or 400 000 seeds (Priszter 1953). A plant of *A. blitoides* can produce 14 600 seeds (Stevens 1932). Dispersal of seeds is accomplished in the same way as in other *Amaranthus* spp. (Weaver and McWilliams 1980): by wind, by birds, by other animals after ingestion and excretion, as well as through farm machinery. The distance the wind can carry seeds is limited to only a few m (1–3) around the mother plant (personal observation). Mammals ingest the seeds with the rest of the plants. Riegel (1942) in Kansas found that some seeds from pellets of cottontails (*Sylvilagus* spp.) and jack-rabbits (*Lepus californicus melanotis* Mearns) were able to germinate. Furthermore, Seoane et al (1998) studying the endozoochorous dispersal of *A. albus* by sheep, found that the losses through chewing and/or digestion varied from 11 to 50%. The seeds appeared in the dung after a maximum of 10 d following ingestion, with a peak appearance 2 d after ingestion (Seoane et al. 1998). The seeds of *Amaranthus* spp. are consumed and spread by many bird species (ornithochory) (Oberholser 1925). Water is another agent of dispersal although it has received less attention in *Amaranthus* spp. The seeds and fruits (in *A. blitum*) float easily and can be dispersed by rain drops or streamlets produced on the soil by rain, surface irrigation, water courses, etc. Wilson (1980) in a field study in western Nebraska, found that seeds of *A. retroflexus* and *A. blitoides* were among the most common encountered in surface irrigation canals, accounting for 37% of all seeds collected in 1977. *Amaranthus* spp. seeds were able to survive the high temperatures generated during composting (Geisel and Unruh 2001) and thus could be dispersed at sites where compost is used. Additionally, stems of *A. albus* can be uprooted (Britton and Brown 1896) or they break off at ground level; and then the entire plant can be carried long distances by the wind (Clark and Fletcher 1906; Uva et al. 1997; Liebman et al. 2001). According to our observations, the dried stems break off in the collet region (the transition zone between the root and stem). The seeds are released gradually while the plant is blown by the wind (Muzik 1970).

(c) *Seed Banks, Seed Viability and Germination*—There are no data available on the longevity of seeds of these three species. However, taking into account their morphological and physiological similarity to seeds of other *Amaranthus* spp., it can be speculated that the seed banks of the three species are relatively persistent (see literature reviewed by Weaver and McWilliams 1980; Burnside et al 1996).

Dorado et al. (1999) described the weed seed bank response to crop rotation and tillage in semiarid agroecosystems from Spain. *Amaranthus albus*, and to a lesser extent *A. blitoides*, dominated the seed bank, together having a relative abundance of 39.8%. The results revealed large differences in the weed seed bank as a consequence of different tillage systems and crop rotations. Under a no-tillage system, *Amaranthus* spp. exhibited an increase in the number of seeds in the seed bank (18 264 *A. albus* seeds m$^{-2}$; 106 *A. blitoides* seeds m$^{-2}$) compared to a conventional tillage system (641 *A. albus* seeds m$^{-2}$; 32 *A. blitoides* seeds m$^{-2}$). With regard to crop rotations, the number of seeds in the seed bank was greater in barley-vetch (*A. albus* 19 855 seeds m$^{-2}$; *A. blitoides* 45 seeds m$^{-2}$), followed by barley-sunflower rotation (*A. albus* 9805 seeds m$^{-2}$; *A. blitoides* 146 seeds m$^{-2}$) and barley monoculture (*A. albus* 7467 seeds m$^{-2}$; *A. blitoides* 6 seeds m$^{-2}$). Bàrberi et al. (1998) described the changes in the seed bank under different tillage systems after 5 yr of continuous maize cropping. Although the weed seed bank was largest under the organic system (100 761 seeds m$^{-2}$), *A. blitoides* had the highest values under the conventional system (0.7% of total seeds in the 10–20 cm soil layer and 0.4% in the 20–30 cm layer). Interestingly, the percentage of seeds in the 0–10 cm soil layer was zero. In the organic system, with reduced inputs and strip cultivation, the relative density of *A. blitoides* seeds in the seed bank was 0.1 or < 0.1%. In Bulgaria, Dechkov (1985) reported 5 230 seeds m$^{-2}$ of *A. blitoides* var. *reverchonii* in a survey of soil samples (0–25 cm soil depth) within an area of 24 863 ha.

Purwanto and Poerba (1990) in Indonesia studied the effects of drying, temperature and storage time on the longevity of seeds of *A. blitum*, cultivated as a vegetable. After 3 mo of storage at 28°C, the seeds showed a decline in viability (from 92–95% to 79–90%) and moisture content (from 17.2–19.1 to 14.4–15.8%) and an increased ion leakage. The effects gradually increased, and after 1 yr, less than 50% of the seeds were viable.

In all three species, germination occurs after imbibition, when the radicle penetrates the micropyle and emerges from the seed. The hypocotyl then elongates, pushing the seed out of the soil. During movement through the soil the cotyledons and the epicotyl are protected by the seed coat. The seeds must be near the surface of the soil, at 0.5–4 cm depth for emergence. *Amaranthus blitoides* seedlings were able to emerge from deeper in the soil than *A. albus* (Giannopolitis 1981). Similar results were reported for other amaranths (reviewed by Weaver and McWilliams 1980), and are probably the consequence of the limited nutritional resources of the perisperm. Additionally, the nature of the soil surface influences seedling emergence. Emergence of *A. blitum* seedlings (cultivated as a vegetable) was delayed and considerably reduced in the case of crust formation and muddy soils (Gaspar et al. 2001).

I. *Amaranthus albus*. The base temperature for germination of *A. albus* was estimated to be 15.7°C. (Steinmaus et al. 2000). The fastest germination —2 d until emergence—was obtained at 20 to 26.6°C and 37.7°C (Santelmann and Evetts 1971). Seed dormancy is controlled by phytochrome (Taylorson

1970; Chadoeuf-Hannel and Taylorson 1985a, b). Germination is promoted by single or repeated short exposures to white or red light, and temperature influences sensitivity to light. Chadoeuf-Hannel and Taylorson (1985a) reported that dark imbibition at 35 to 40°C, followed by 5 minutes of irradiation with red light markedly increased germination. In order to examine the relationship between light and temperature, the authors suppressed germination with a pre-treatment of continuous incandescent light and a terminal far-red irradiation. Red irradiation of inhibited seeds increased germination only in seeds held at high imbibition temperatures (32–39°C). Chadoeuf-Hannel and Taylorson (1985a) observed that when pre-treated seeds were transferred to a lower temperature (20°C) a reversal of the enhanced photosensitivity occurred. Similarly, the high germination potential was re-established by repeating a high temperature treatment. The light-temperature interdependency could be an adaptation that prevents the germination of seeds briefly exposed to light during tillage, but buried at depths where successful seedling emergence is unlikely (Gallagher and Cardina 1998). Membrane lipids are involved in the transition between the dormant and non-dormant states in seeds. Changes in polar lipids were observed within four hours after dormancy had been overcome by a treatment with far-red light. The percentage of saturated lipid increased in seeds in which dormancy was overcome, while it decreased in dormant seeds (Chadoeuf-Hannel and Taylorson 1987). Germination of dormant seeds of *A. albus* is promoted by NaNO$_3$, thiourea, hydroxylamine salts, catechol and pyrogallol, accompanied by irreversible inhibition of catalase (Hendricks and Taylorson 1975). Treatment with concentrated sulfuric acid for two minutes increased germination to 60% while untreated seeds had 41% germination (Santelmann and Evetts 1971). Schonbeck and Egley (1981) observed enhanced germination in *A. albus*, *A. retroflexus* and *A. spinosus* when seeds were treated with ethylene. Increased germination was also observed when seeds of *A. albus* and *A. retroflexus* were treated with sodium azide (Hurtt and Taylorson 1980). Germination of *A. albus* seeds was inhibited by two non-ionic surfactants (Tween 20 and Tween 80 at 0.05–0.2%) at 20 or 30°C (Hurtt and Hodgson 1987).

II. *Amaranthus blitoides* germinated well at 25, 30, 35°C and the germination percentage was greater at higher temperatures (Martin 1943). Germination of *A. blitoides* is also under phytochrome control. Kadman-Zahavi (1955) reported that intermittent white or red light stimulated germination, while continuous incandescent illumination inhibited it. Partially or entirely removing the seed coat stimulated germination (Martin 1943). Santelmann and Evetts (1971) reported that *A. blitoides* had a lower percentage germination than five other *Amaranthus* species (*A. retroflexus*, *A. hybridus*, *A. albus*, *A. spinosus* and *A. palmeri*). The highest germination, 37%, was observed after the seeds had been treated with concentrated sulfuric acid for four minutes.

III. *A. blitum* showed increased germination after 2 yr of burial in paddy fields and a decreased percentage of germination after the third year in an experiment conducted in Japan (Suzuki 1999). Teitz et al. (1990) studied the germi-

nation response of *A. blitum* to temperature and light, seed maturity [expressed as number of days after sowing (DAS)], scarification and the influence of growth regulators (gibberellic acid and ethephon). The optimum temperature for germination was 35°C. The seeds germinated better in light regardless of DAS; percent germination was 84% and 49% for 65 DAS and 85 DAS, respectively. Germination was inhibited at 40°C. Treatment with 50% sulphuric acid for 2.5 minutes reduced the germination differences between 65 DAS and 85 DAS, but percent germination at 85 DAS was consistently lower than at 65 DAS seeds (61% and 72% respectively). Gibberellic acid ($GA_3$) at 1 mM improved germination of seeds in the dark to 73% for the 65 DAS seeds and to 45% for the 85 DAS seed lot. Both seed lots showed similar trends in response to ethephon, although germination in the dark was lower than in the GA treatment (22% for 65 DAS and 9% for 85 DAS). It was concluded that the seeds of *A. blitum* have a light and seed-coat-imposed dormancy. Costea (1998), using seeds from Eastern European populations of subsp. *blitum* and subsp. *emarginatus*, obtained similar results. The first seeds produced by the plants (end of June for *A. blitum* subsp. *blitum* and middle of July for *A. blitum* subsp. *emarginatus*) germinated better than the seeds produced before senescence (late November for both taxa). Treatment with 1 mg $L^{-1}$ gibberellic acid ($GA_3$) increased the percentage of seeds germinating in the dark and of the seeds collected in late autumn by 54 and 17%, respectively.

Bhattacharjee and Mukherjee (1998) investigated the effect of high temperature treatment on the germination of cultivated *A. blitum*. Transfer of seeds during the early imbibitional phase, from 25 to 45°C, resulted in impairment of germination by leakage of UV-absorbing substances (alpha-$NH_2$) and carbohydrates, a decrease in ethylene formation and an increase in membrane damage. The authors suggested that greater membrane damage resulted from membrane-lipid peroxidation in germinating seeds (Bhattacharjee and Mukherjee 1998).

Germination of *A. blitum* subsp. *blitum* and subsp. *emarginatus* was not affected by leaving the pericarp intact. In fact, it was suggested that the pericarp could play a significant role in imbibition, due to the presence of extensive intercellular spaces that absorb and retain water (Costea et al. 2001b). Under high atmospheric humidity in the growth room, newly produced seeds of some *A. blitum* accessions germinated in the fruits, on the mother plants. According to our knowledge, this is the first case of vivipary reported for *Amaranthus* spp.

(d) *Vegetative Reproduction*—There has been no evidence of vegetative reproduction. However, cuttings of *A. blitum* root easily (Larkom 1991). We have also observed formation of adventive root primordia on the stems of the weedy subspecies of *A. blitum* under growth–room conditions.

## 9. Hybrids

*Amaranthus blitoides* may hybridize with *A. albus* (= *A.* × *budensis*) (Priszter 1958) and *A. blitum* may hybridize with *A. viridis* L. (Coons 1981). The hybrid between *A. albus* and *A. blitoides* is intermediate between the parents. It differs from *A. albus* through the shorter bracts and larger fruits and seeds, and from *A. blitoides* by the ascendant or erect stems, the longer bracts and smaller fruits and seeds (Priszter 1958; Morariu 1952). Hybridization in amaranths in temperate regions occurs infrequently and the F1 plants have reduced fertility, but there is no data published so far regarding outcrossing rates for the three species.

## 10. Population Dynamics

Similar to other amaranths (Weaver and McWilliams 1980), the three species can germinate and emerge throughout the growing season if moisture and temperature conditions are adequate (Manabe and Itoh 1990; Costea 1998). A study of the seedling emergence pattern of a weed community in a semi-arid site in Colorado showed two major peaks (Anderson 1994). *Amaranthus blitoides*, green foxtail [*Setaria viridis* (L.) Beauv.] and proso millet (*Panicum miliaceum* L.) predominated in the second peak, between May 30 and June 13. Tillage increased the number of emerging seedlings, but did not affect the overall weed community emergence pattern.

Taking into consideration their photosynthetic characteristics, the three species have good competitive abilities at high light intensities and temperatures. At reduced irradiance, *A. albus* was inferior to *Solanum ptycanthum* (Stoller and Myers 1989). Likewise, when growing under the canopy of a crop such as soybean, *A. albus* was not as troublesome as other *Amaranthus* species (*A. retroflexus* and *A. hybridus*) (Chandler et al. 1984).

Qasem (1994, 1995) investigated the alellopathic effects of *A. blitoides*, *A. retroflexus* and *A. viridis* on wheat (*Triticum durum* Desf.) and barley (*Hordeum vulgare* L.) under laboratory and field conditions. Laboratory experiments showed that fresh shoot and root extracts of the three species reduced germination, and growth of wheat seedlings (coleoptile length, root length and root dry weight). Under field conditions, incorporation of *A. blitoides* residues in soil reduced height, grain and straw yield of wheat and barley (Qasem 1994, 1995).

Alfalfa (*Medicago sativa*) residues mixed into vermiculite at concentrations of more than 10% resulted in 80% inhibition of germination and growth of *A. blitum* and several other weed species (Jeon et al. 1995). A phytotoxic compound, diethil pthalate, isolated from buckwheat (*Fagopyrum esculentum* Moench), inhibited germination of *A. blitum* at 250 ppm (Eom et al. 1999). Cut leaves of *Imperata cylindrica* (L.) Palisot, mixed with soil at 1.6–3.2 g 100 $g^{-1}$ soil in a greenhouse experiment, significantly reduced the growth of *A. blitum* and chickweed (*Stellaria media* (L.) Vill.) (Tominaga and Watanabe 1997). Arteether, a derivative of artemisin from wormwood (*Artemisia annua* L.) retarded seed germination and seedling growth of *A. blitum* and several other weed and crop species (e.g. Bagchi et al. 1998). A new compound, cycloxamide, isolated from a strain of *Streptomyces* spp. found in upland soils of Korea, showed herbicidal activity on several weeds, *A. blitum* included, even at 10 ppm concentration (Choi et al. 1992).

## 11. Response to Herbicides and Other Chemicals

*Amaranthus* species are susceptible to most soil-applied and foliar (postemergence) herbicides recommended for the

control of dicot annual weeds in a range of crops (e.g. Derksen et al. 1995; Dusky and Stall 1996; Sweat et al. 1998; Anonymous 2002). Residual control is often desirable, because multiple flushes of emergence usually occur throughout the season. Selective foliar-applied herbicides generally are effective up to the four to six leaf stage. *Amaranthus* species also can be controlled readily by nonselective herbicides, such as glyphosate, glufosinate, and paraquat (Krausz et al. 1996; Jordan et al. 1997).

Vencill et al. (1990) studied the patterns of clomazone translocation and metabolism in *A. blitum*, *A. hybridus* and *A. retroflexus*. They reported greater absorption of $^{14}$C clomazone in the roots of the sensitive *A. blitum* and *A. retroflexus* than in a tolerant biotype of *A. retroflexus*. Most of the absorbed clomazone was traslocated acropetally to the leaves via the xylem. The absorption and translocation of pyridate, its effect on photosynthetic activity and its metabolism were studied in *A. blitoides*, rigid ryegrass (*Lolium rigidum* Gaudin) and chickpea (*Cicer arietinum* L.) (Gimenez-Espinosa and De Prado 1998). The absorption of pyridate in *A. blitoides* was slower than in chickpea plants, but much faster than in *L. rigidum*. The study of translocation of pyridate showed that most of this herbicide (60–90%) remained in treated leaves.

*Herbicide Resistance*—No herbicide-resistant biotypes have been reported in Canada for any of the three species examined so far. An atrazine- and simazine-resistant biotype of *A. albus* was reported in Spain in 1984, where it infested 40–200 ha in 11–50 sites (Heap 2002). *Amaranthus blitoides* was reported to have developed resistance to photosystem II inhibitors (atrazine and simazine) in Israel in 1983 (Sibony and Rubin 1996; Rubin 1997; Heap 2002) and in Spain in 1986 (De Prado et al. 1993; Heap 2002). Results indicated that resistance to atrazine and simazine in both *A. albus* and *A. blitoides* was caused by an altered target site, similar to other atrazine resistant weeds (De Prado et al. 1993). Resistance is due to a point mutation in the chloroplast psbA gene, resulting in the substitution of Gly for Ser at residue 264 in *A. blitoides* (Sibony and Rubin 2001). In Israel, the triazine-resistant *A. blitoides* biotype infests between 405 and 4046 ha of cropland and roadsides in 501–1000 different sites (Heap 2002). A combination of flumioxazin + triazines at 2.5 g a.i. ha$^{-1}$ + 0.062 kg a.i. ha$^{-1}$ efficiently controlled triazine-resistant biotypes of *A. blitoides* and *A. hybridus* (Yacoby et al. 1996). In Spain, triazine-resistant *A. blitoides* infests 40–202 ha of orchards in 11 to 50 different sites. Sibony and Rubin (2001) in Israel reported that two biotypes of *A. blitoides* examined on a whole-plant basis using in vitro assays, revealed multiple-resistance to sulfonylureas, imidazolinones, triazolopyrimidines, pyrimidinylthiobenzoates and triazines. A single nuclear encoded gene, dominantly expressed, was responsible for conferring resistance to the ALS inhibitors. Two different point mutations were observed after sequencing the ALS gene: $Cyt_{337}Thy$ in domain A, which determined a substitution $Pro_{188}$ Ser, and $Gua_{1721}Thy$ in domain B, which resulted in a $Trp_{569}Leu$ substitution. Based on whole-plant dose responses, the resistance to sulfometuron-methyl conferred by the mutation in domain B was greater than the resistance conferred by the mutation in domain A. Additionally, the 2 bio-

types exhibited a point mutation in the chloroplastic psbA gene, $Ser_{264}Gly$ substitution in the D1 protein, which conferred resistance to atrazine. The same mutation in the psbA gene was noticed in a triazine-resistant biotype collected from another location in Israel (Sibony and Rubin 2001). Populations of dodder (*Cuscuta campestris* Yunker) resistant to ALS inhibitors were detected parasitizing resistant plants of *A. blitoides* (Sibony et al. 1995).

Herbicide-resistant biotypes of *A. blitum* have been reported from North America, Europe and Asia. In New Jersey, approximately 25 ha are infested with imazethapyr- or imazaquin (ALS inhibitors)-resistant *A. blitum* (Manley et al. 1996; Heap 2002). The molecular basis of resistance in *A. blitum* biotypes is currently unknown. Atrazine-resistant populations of *A. blitum* were found in maize monocultures in Ticino and Valais, Switzerland and in France (Heap 2002). In Malaysia, paraquat (bipyridiliums)-resistant *A. blitum* was discovered in potato and sweet peas (*Lathyrus odoratus* L.) (Itoh et al. 1992).

## 12. Response to other Human Manipulations

Anderson (2000) studied different cultural systems in attempts to reduce or eliminate herbicide application in proso millet (*Panicum miliaceum*) in semiarid Great Plains conditions (Akron, Colorado). *Amaranthus albus* comprised about 30% of the weed community, which also included *A. retroflexus*. *Amaranthus* spp. data were combined together due to the difficulty of identifying seedlings. In general, minimum tillage (sweep plow once or twice) increased *Amaranthus* spp. density sevenfold compared to the no-till system. Within the minimum-till system, a higher density of crop seeding, nitrogen fertilizer applied in bands and a delayed planting of proso millet reduced *Amaranthus* spp. density, biomass and seed production by 80% compared to other methods. With the no-till system, only a delayed planting of proso millet caused a significant reduction of *Amaranthus* spp. biomass and seed production. There is no information available regarding the responses of these species to fertilizing, solarization, burning and other human manipulations.

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

*Herbivory*
(a) *Mammals*—See 8(b).
(b) *Birds and/other Vertebrates*—See 8(b).
(c) *Insects*—El Aydam and Bürki (1997) provided a comprehensive review of insects associated with *Amaranthus* spp., worldwide. Some 241 insect species were recorded from 21 *Amaranthus* spp. However, only a few insect species were associated with the *Amaranthus* spp. examined in the present account. Predation studies (pre- and post-dispersal) are available only for other *Amaranthus* species (*A. retroflexus* and *A. powellii*) and this information is reviewed in an updated version of Weaver and McWilliams (1980) (Costea et al. in preparation).

*Diptera*—*Amaranthus blitoides* is a host of *Tetanops myopaeformis* Roder, one of the most important insect pests of sugarbeets in North America (Blickenstaff et al. 1977;

Campbell et al. 1998), and of *Asphondylia amaranthi* Felt. (Barnes 1948).

*Homoptera*—Umeda (1996), citing unpublished data of Natwick and Bell, mentioned that *A. albus* is a host for the silverleaf whitefly (*Bemisia argentifolii* Bellows & Perring), on which the insects occurred at low densities. In Egypt and Iran, *A. blitum* was associated with *Bemisia tabaci* Gennadius, the tobacco whitefly, also referred to as the silverleaf or sweet potato whitefly (reviewed by Bendixen et al. 1981) and *Aphis gossypii* Glover (cotton and/or melon aphid, Kolaib et al. 1986).

*Lepidoptera*—*Amaranthus albus* is a host of caterpillars of *Pholisora catullus* Fabricius in the Chihuahuan Desert, El Paso (Texas) and Ciudad Juarez (Mexico) (Lieb 2001). *Amaranthus blitum* was recorded to be a host of Hawaiian beet webworm, (*Hymenia recurvalis* Fabricius), in Australia, Pakistan and India (Bendixen et al. 1981; Miyahara 1993).

*Orthoptera*—*Amaranthus blitum* is an alternate host of the rice grasshopper, (*Hieroglyphus banian* Fabricius) in India (Vyas et al. 1984).

*Thysanoptera*—*A. blitum* ("*A. oleraceus*") is a host of *Haplothrips longisetosus* Anathakrishnan in India (Waterhouse 1994 cited by El Aydam and Bürki 1997).

(d) *Nematodes*—Gaskin (1958) reported *A. albus* and *A. blitoides* as hosts for *Meloidogyne incognita* (Kofoit and White) Chitwood in Indiana. Faulkner and McElroy (1964) found *M. hapla* Chitwood on "*A. graecizans*" from Washington. Hafez and Seyedbagheri (1999) in Idaho and Eastern Oregon reported both *A. albus* and *A. blitoides* as hosts for the sugar beet cyst nematode (*Heterodera schachtii* Schmidt), one of the major pests of sugar beet production in the world. *Amaranthus blitum* in Hungary was found to be infected with *Meloidogyne incognita* and *M. arenaria* (Neal) Chitwood (Amin and Budai 1994) but was considered a "moderate" host for *Meloidogyne* ssp. in Pakistan by Anwar et al. (1992). *Pratylenchus coffeae* Goodey was found on *A. blitum* in Central America (Edwards and Wehunt 1973).

*Diseases*

(a) *Fungi—North American Records*: *Albugo bliti* (Biv.-Bern.) Lev. on "*A. graecizans*" from "North America" (Wilson 1908), Minnesota (Preston and Dosdall 1955), North Dakota (Brenckle 1917) and on *A. blitoides* from North Dakota (Brenckle 1917); *Cercospora brachiata* Ellis & Everh. on *A. albus* from the U.S.A. (Farr et al 1989) and *A. blitoides* from Delaware (Sumstine 1949; Greene 1955); *Colletotrichum coccodes* (Wallr.) Hughes on *A. blitum* from the U.S.A. (Raid and Pennypacker 1987); *Phoma amaranthicola* Brunaud on "*A. graecizans*" from Oregon (Shaw 1973); *Puccinia aristidae* Tracy on *A. blitoides* and *A. albus* from the U.S.A. (Anonymous 1970; Farr et al. 1989); *Phymatotrichopsis omnivora* (Duggar) Hennebert on "*A. graecizans*" from Texas (Anonymous 1970; Farr et al. 1989); *Pythium* ssp. on "*A. graecizans*" from British Columbia (Ginns 1986); *Pythium intermedium* De Bary and *P. irregulare* Buisman on "*A. graecizans*" from Ontario and British Columbia (Ginns 1986);

*Puccinia aristidae* Tracy on *A. blitoides* from Colorado (Anonymous 1970); *Rhizoctonia solani* Kühn on *A. blitoides* and *A. albus* from Illinois, Texas and Washington (Anonymous 1970; Farr et al. 1989); *Thanatephorus cucumeris* (A.B. Frank) Donk on "*A. graecizans*" from Washington (Shaw 1973); *Verticillium dahliae* Kleb. on "*A. graecizans*" from British Columbia (Ginns 1986).

*Fungi—World-wide Records*: *Albugo bliti* (Biv.-Bern.) Lev. on *A. albus* from Bulgaria and Russia, on *A. blitum* from Bulgaria, China, Greece and Nepal (Anonymous 2001b); *Alternaria amaranthii* (Peck) Van Hook on *A. blitum* from China (Anonymous 2001b); *Oidium* spp. on *A. blitum* from Pakistan (Anonymous 2001b); *Peronospora amaranthi* Gäum on *A. blitum* from Switzerland (Constantinescu 1991); *Thielaviopsis basicola* (Berkeley & Broome) Ferraris on *A. blitum* (Klimova 1979). Additional fungi parasitizing *Amaranthus* spp. in Europe are recorded in Brandenburger (1985).

Infection by *Albugo bliti* (Biv.) Kuntze on the leaves of *A. blitum* caused a decrease in turgor, total chlorophyll and total proteins, but increased total carbohydrates, polyphenols and titrable acidity (Sakhare and Thite 1986).

*Biocontrol with fungi*—Mintz et al. (1992) conducted growth chamber and field tests to evaluate the pathogenity of *Aposphaeria amaranthi* Ell. & Barth. Seedlings of *A. albus* in the growth chamber were killed within 2 d of inoculation with $1 \times 10^6$ conidia per milliliter and an 8 h dew period at 28°C. Dew temperatures from 20 to 28°C positively influenced disease development. In field tests, 99% of seedlings were killed when sprayed "to run off" with *Aposphaeria amaranthi* at $1 \times 10^6$ conidia per milliliter.

Roskopf et al. (2000a) described a new fungal species, *Phomopsis amaranthicola*, isolated in Florida from stem and leaf lesions of weedy amaranths. This fungus was found to be pathogenic on 22 *Amaranthus* spp., causing stem and leaf blight. After penetration of the leaf cuticle, the fungus grew within the intercellular spaces of the mesophyll, causing a growing necrotic area, and after 8 d, abscission of the leaves occurred (Wyss and Charudattan 1999). Field results indicated that *Phomopsis amaranthicola* was an effective biocontrol agent for *A. blitum*, *A. hybridus* (including a triazine-resistant population), *A. viridis* and *A. spinosus* (Roskopf et al. 2000b). The best level of control was obtained when the fungus was applied at $6 \times 10^7$ conidia per ml in conidial suspensions. A high percentage of plant mortality (up to 100%) was recorded two, four and six weeks after inoculation. The advantage of this biocontrol agent is that pathogenity is restricted to *Amaranthus* spp., and that the fungus produces a secondary inoculum in the field. Wyss and Charudattan (2000) studied the interactions between this fungus and various pesticides. Of the 22 pesticides evaluated, three herbicides, diuron, sethoxydim and imazethapyr, at the highest labeled rate (LR), were highly toxic to *Phomopsis amaranthicola* but glyphosate and trifluralin at 0.25 LR and imazethapyr at 0.75 LR were compatible. In general, the pesticides did not affect spore germination, but did inhibit mycelial growth. It was concluded that it was possible to integrate the use of *P. amaranthicola* with that of reduced rates of compatible pesticides.

(b) *Bacteria*—Black rot of crucifers (*Xanthomonas campestris* pv. *Campestris*) in Jordan, was found on the leaves (showing no symptoms of infection) of *A. blitoides* (Mahyar and Khlif 1999). *Amaranthus blitum* in Greece is a host of the bacterial leaf blight (*Pseudomonas viridiflava* (Burkholder) Dowson) of melon, tomato, eggplant and pith necrosis of chrysanthemum plants (Goumans and Chatzaki 1998).

(c) *Viruses*—The virus nomenclature follows Brunt et al. (2002). Horváth (1991) published a comprehensive world-wide review of viruses associated with *Amaranthus* spp. The 63 *Amaranthus* species investigated were found to be susceptible to 121 viruses. Zitter (2002) provided a checklist of weeds and crops as natural hosts for viruses in the Northeastern U.S.A.
*North American Records*—*Amaranthus albus* is a host of the alfalfa mosaic alfamovirus (AMV) (Kaiser and Hannan 1983; Zitter 2002); beet yellows closterovirus (BYV) (Thornberry 1966); potato potyvirus Y (PVY) and strawberry latent ringspot nepovirus (SLRSV) (Zitter 2002). *Amaranthus blitoides* is a host of alfalfa mosaic alfamovirus, cucumber mosaic cucumovirus (CMV) and potato potyvirus Y (Zitter 2002). "*Amaranthus graecizans*" has been reported as a host of tomato spotted wilt tospovirus (TSWV) (Anonymus 1970), beet curly top geminivirus (BCTV) and beet yellows closterovirus (BYV) (Thornberry 1966). World-wide viruses associated with of *A. albus* and *A. blitoides* can be found in Horváth (1991).

There is no information about *A. blitum* as a host for viruses in North America, but the species is a susceptible host of amaranthus mosaic potyvirus (AMV) in India and Central Asia (Brunt et al. 2002) and of tobacco mosaic tobamovirus (TMV) (Cho et al. 2000). The species is additionally a host of alfalfa mosaic alfamovirus, cucumber mosaic cucumovirus, tobacco mosaic tobamovirus (Horváth 1991), potato potexvirus X (PVX) (Nagaich and Upreti 1965) and tomato spotted wilt tospovirus (TSWV) (Jorda et al 1995). "*Amaranthus ascendens*" (= *A. blitum* subsp. *blitum*) was a reported host for the alfalfa mosaic alfamovirus, cucumber mosaic cucumovirus, potato carlavirus M (PVM), potato potexvirus X, potato potyvirus Y, tobaco mosaic tobamovirus and turnip mosaic potyvirus (TuMV) (Horváth 1991). "*Amaranthus emarginatus*" (= *A. blitum* subsp. *emarginatus*) was reported as a susceptible host for alfalfa mosaic alfamovirus, cucumber mosaic cucumovirus, potato potexvirus X and tobacco mosaic tobamo virus (Horváth 1991). The tospovirus in *A. blitum* was confined to the cortical zone of stems; the chloroplasts showed peripheral vesicles and virions occurred as clusters (Garg. et al. 1999).

## ACKNOWLEDGEMENTS

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