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ARTICLE

The Biology of Canadian Weeds: 155. *Panicum miliaceum* L.

Paul B. Cavers and Marguerite Kane[a]

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Abstract: Proso millet, *Panicum miliaceum* L. (Poaceae), has been a crop in Asia and Europe for 10 000 years and for over 300 years in Canada, where it is grown for grain, rescue crops, birdseed, forage, and recently for swath grazing. Crop-like biotypes have escaped from cultivation throughout Canada, but these infestations were generally temporary. Probably the first persistent, weedy biotype in Canada (Quebec) has large, dormant, dark red seeds. Its eradication has been attempted for many years. In the 1970s, a worse problem, a black-seeded biotype with many weedy attributes, including shattering as seeds ripen and strongly dormant seeds distasteful to many birds, spread across southern Ontario and became labelled as noxious. Concurrently, it was described as the worst weed in the US Corn Belt. In the 1980s, Canadian studies revealed infestations of other weedy biotypes, differing in seed colour and other attributes. *Panicum miliaceum* is an extremely variable species world-wide. Since the late 1990s, weedy proso millet has declined dramatically after the adoption of newer herbicides, particularly glyphosate. This development may lead to increases in cultivated proso millet, especially where climate change favours short-season crops grown under drier conditions.

Key words: weed biology, proso millet, *Panicum miliaceum* L., weed/crop, intraspecific variation, global distribution and history.

Résumé : On cultive le millet, *Panicum miliaceum* L. (poacées), depuis 10 000 ans en Asie et en Europe et depuis plus de trois siècles au Canada pour ses graines, comme provende de secours, pour nourrir les oiseaux, pour son fourrage et, plus récemment, pour la paissance en andain. Des biotypes domestiqués sont redevenus sauvages un peu partout au Canada, mais les infestations restent le plus souvent temporaires. Le premier biotype envahissant persistant du Canada a probablement été observé au Québec. Il se caractérise par de grosses semences rouges dormantes. On s'est efforcé de l'éradiquer pendant de nombreuses années. Dans les années 1970, un biotype à graines noires, possédant de nombreuses caractéristiques d'une mauvaise herbe (notamment l'égrenage prématuré quand les semences parviennent à maturité et des graines à dormance prolongée que peu d'oiseaux aiment), a soulevé un problème plus épineux en se répandant dans le sud de l'Ontario. Ce biotype a été qualifié de nuisible avant de devenir la pire adventice dans la ceinture du maïs des États-Unis. Dans les années 1980, des études canadiennes ont révélé l'existence de peuplements d'autres biotypes envahissants, aux semences de couleur différente et présentant d'autres caractères. *Panicum miliaceum* est une espèce extrêmement variable dans le monde. Depuis la fin des années 1990, les variétés envahissantes ont diminué de façon draconienne avec l'apparition de nouveaux herbicides, particulièrement le glyphosate. Ce développement pourrait déboucher sur une prolifération du millet cultivé, surtout aux endroits où le changement climatique favorise la croissance des plantes à saison courte qui affectionnent une plus grande aridité. [Traduit par la Rédaction]

Mots-clés : biologie des mauvaises herbes, millet, *Panicum miliaceum* L., plante cultivée/envahissante, variation intraspécifique, répartition dans le monde et histoire.

1. Name

Panicum miliaceum L. — proso millet, panic millet (Darbyshire et al. 2000); other common names in Canada include broomcorn millet, common millet, hog millet, millet panic grass, panicum millet and proso (Dore and McNeill 1980). In the United States, hershey or hershey millet (Hinze 1972), Indian millet (Bavec and Bavec 2006), bread millet, browncorn millet, Egyptian millet and Russian millet (Wanous 1990) are also used. Hershey is probably an anglicized version of the German "echter hirze" (millet) or "rispenhirze" (see Mansfeld 1952; Häfliger and Scholz 1980). In China,

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glutinous varieties are known as "Shu" and non-glutinous as "Ji" (Jiaju 1989). In India, it is called pani varagu (Wanous 1990), but several regional names in that country suggest that it was introduced there from China (Harlan 1975), e.g., cheena [in Bengali] (Harlan 1975; Rai 1985), cheena millet (Datta et al. 1978), chena or cheen [in Hindi] (Harlan 1975), cinaka [in Sanskrit] (Harlan 1975) or varikora [in Tamil] (Rengalakshmi 2005). It is termed milho do canario in Portugal (Kaume 2006), miglio in Italy (Meyer 1980), mijo común in Spain (Anonymous 2007) and segetal in the Czech Republic (Holec et al. 2002). In New Zealand, it is called broom corn millet (James et al. 2011).

Fujita (1974) and Häfliger and Scholz (1980) list many other common names used in countries where this widely cultivated grain crop is grown. Historically, this is the "milium" of the Romans and "dokhan" of the Hebrews (Zohary and Hopf 2001).

Wild proso millet is the name given to the black-seeded weedy biotype in the United States (Strand and Behrens 1979). It has been considered as a separate species, but also as a subspecies or variety of *Panicum miliaceum* [see section 2(c)]. The Americans, and some Canadians, have also assigned common names for the crop or crop-like weed biotypes of proso millet, even referring to them collectively as "tame proso millet" (Wilkins and Robertson 1981) [see section 2(c)]. More logically, Anderson (2000*a*) referred to "volunteer proso millet", thereafter termed "proso" in his paper.

Proso is the transliteration of "просо" meaning "millet" in Russian (Lysov 1975) and is the Russian common name for *Panicum miliaceum* (Häfliger and Scholz 1980).

Poaceae (Gramineae). Grass family. Poacées. Bayer Code: PANMI (Darbyshire et al. 2000). It is a member of the sub-family Panicoideae, tribe Paniceae and was described by Dore and McNeill (1980) as Ontario's only alien panic grass.

The generic name (*Panicum*) is derived from the Latin "*panus*" (an ear of millet) and the specific epithet (*miliaceum*) is Latin for millet (Fernald 1950). The generic name has also contributed the botanical term for a particular type of inflorescence — the panicle.

Panicum is one of the largest genera of grasses, estimated to comprise more than 600 species. Zuloaga (1987) proposed dividing the *Panicum* genus in America into six subgenera. Subsequent work has removed some species from *Panicum* and placed them in closely related genera (e.g., *Dicanthelium*) with a consequent reduction in species number in *Panicum* (Freckmann and Lelong 2003). These authors suggest that the number of species in the genus is subject to change.

2. Description and Account of Variation

A reference that lists publications between 1930 and 1963 that contain information pertaining to sections 2 to 13 inclusive is Anonymous (1967).

(a) Species description

Except where noted, the following description of *Panicum miliaceum* has been compiled from Gleason (1963), Cobley and Steele (1976), Dore and McNeill (1980) and from observations by the authors.

In common with other species within the subgenus *Panicum* (*Eupanicum* in some older literature), the blades of the basal and culm leaves are simple and elongate; primary and secondary panicles are similar, their primary branches being simple at the base. All spikelets are fertile.

This C_4 species is a subtropical annual with stout culms arising from a cluster of fibrous roots. The roots spread from 10 to 120 cm laterally and to depths up to 150 cm (Gashkova 2003–2009). Pricop (2003) determined that the number of nodes per culm in genotypes is controlled by "4.4" dominant genes, exhibiting both partial dominance and additivity effects.

Tiller number may range from 1–32. Plants are usually 30–130 cm tall, but may exceed this when proso millet occurs as a weed in tall crops. Flag leaf size is from 29–380 mm long by 6–130 mm wide (Upadhyaya et al. 2008). Leaves are alternate, and leaf sheaths are densely hairy, with overlapping margins enclosing the terete stems. The ligule is a line of dense hairs 2–3 mm long, and the laminae, which may be up to 30 cm long and 2 cm broad, are more or less hairy on both surfaces. Panicles develop in mid to late summer from every stem. These are much branched and vary from diffuse, open, and pyramidal to fairly compact and cylindric. They are usually from 9–20 cm long, but may reach 30 cm (Upadhyaya et al. 2008). Pulvini vary from prominent to less well-developed or absent. The glabrous acute spikelets are borne singly at the ends of branches, or on short pedicels. Each ovoid-ellipsoid spikelet is about 5 mm long and consists of a fertile and a sterile floret enclosed by two outer glumes. The lower glume is usually up to one quarter the length of the spikelet, acute or acuminate and five-nerved.

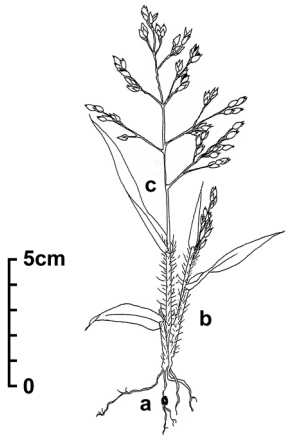
The sterile floret consists of only a lemma and a very small palea. The glumes have no awns. The fertile floret has two lodicules, three stamens and a sessile ovary with two styles with feathery stigmas. The floral biology is discussed in detail in section 8(a).

The fruit of *Panicum miliaceum*, as in all grasses, is a caryopsis. The caryopsis is enclosed by a husk (palea and lemma). This unit (caryopsis plus husk) is often termed a propagule, especially by plant ecologists. The term "seed" is in common use in the literature of this and other grass species to describe the propagule, and this is the term that will normally be used throughout this paper.

Seeds are heavy when mature, 4–6.5 mg, and often cause the panicle to droop. In crop-like weeds, described in Bough et al. (1986), the seeds measure approximately 3.0 mm × 2.0 mm, whereas those of the black-seeded weed are slightly shorter and narrower

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Fig. 1. A small but mature plant of the Black biotype of proso millet (*Panicum miliaceum*), illustrating: (*a*) The persistent husk (palea and lemma) attached to the root system; (*b*) An incipient tiller; (*c*) The diffuse panicle, showing a pulvinus at the base of the lowest panicle branch.



(2.5–2.75 mm long and 1.5–1.75 mm wide). The husk varies in colour from light cream to olive-black and forms an integral part of the seed when it is shed. Husk colour is used to distinguish the biotypes described in section 2(c). The caryopsis itself, when de-husked is cream and almost round. In some biotypes, the seeds shatter easily; in others they remain on the inflorescence when ripe.

Proso millet is a tetraploid, with $2n = 36$ (Chandola 1959*a*; Warwick 1990; Hamoud et al. 1994); $2n = 4x = 36$ (Lágler et al. 2005; Hancock 2012). Bor (1960) reported $2n = 72$ in some Indian races. Lysov (1975) also referred to some tetraploid plants ($2n = 72$) that have bigger panicles and seeds but, surprisingly, lower productivity. Chandola (1959*b*) found that proso millet can produce uni- and multivalents at meiosis and thought it quite likely that tetraploids of *P. miliaceum* originated through autopolyploidy. Hunt et al. (2014) described the $2n = 4x = 36$ chromosomes as small, varying from 2.2 to 6.0 μm in length at metaphase (see also section 6). For further information on the species description, including slight variations from the measurements given here and additional chromosome counts, see Freckmann and Lelong (2003).

(b) Distinguishing features

Many grasses are hard to identify at the very early seedling stage. In proso millet, the husk remains attached to the young seedling following germination. Pulling up a seedling and noticing the attached husk, which is about 2–3 mm long (Fig. 1), would help to distinguish it from very young volunteer corn (*Zea mays* L.) or sorghum (*Sorghum bicolor* (L.) Moench). Either of these species, at that stage, may be of a similar size to proso millet. Proso millet seedlings are also densely hairy, unlike those of corn (Harvey 1979). However, in seedlings of both proso millet and corn the first internode lengthens, enabling germination and emergence from depths of 5 cm or more (Strand et al. 1973). Luellen (1982) described seedlings as resembling volunteer corn in their early stages and fall panicum (*Panicum dichotomiflorum* Michx.) in later stages.

At the early 1–2 leaf stage, proso millet seedlings are about three times larger than those of two species of native panic grasses that may be mistaken for *P. miliaceum*, namely witch grass (*Panicum capillare* L.) and fall panicum.

Witch grass (described in detail by Clements et al. 2004), which, like proso millet, may grow from a few centimetres up to a metre tall, usually has several stems. The laminae of the leaves are densely hairy on both surfaces; the leaf sheath is also hairy. The panicle is large, loose, and diffuse, with numerous fine branches and very small spikelets (about 2.0–2.2 mm long × 1.0 mm broad), which enclose straw-coloured seeds. The culm becomes brittle when the seeds are ripe, and breaks, so that the panicle acts like a tumbleweed, scattering the seeds as it is blown. The seeds, which are the smallest of the three species, are about 1.0–1.5 mm long and about 1/3 as wide. Unlike proso millet, it is diploid, $2n = 18$ (M'ribu and Hilu 1994). Further information on *P. capillare* and slight variations in the measurements provided here may be found in Darbyshire and Cayouette (1995) and Freckmann and Lelong (2003). In a recent paper, Hunt et al. (2014) hypothesized that *P. capillare* or a closely related taxon could have been the maternal ancestor of *P. miliaceum* (see sections 6 and 9).

The stems of fall panicum are slightly flattened, unlike the cylindrical stems of the other two species. These stems also bend slightly at each node to give a zig-zag appearance. A fall panicum plant may produce several stems; the central ones are nearly erect, but the outer ones may spread and also may root at the nodes. Unlike witch grass and proso millet, the leaves of this species have smooth shiny laminae. Although the leaf sheaths of early-formed leaves may be slightly hairy, later ones are hairless. The inflorescence, although branched and open, is not as fine as the witch grass inflorescence and is slightly flattened dorsi-ventrally. See Dore and McNeill (1980) and Alex (1992) for detailed descriptions of fall panicum. Seeds (2.0 mm long × 0.75 mm broad) are larger than those of witch grass and greenish brown. The chromosome number is $2n = 54$ (Hamoud et al. 1994). Further information on *P. dichotomiflorum* may be found in Freckmann and Lelong (2003).

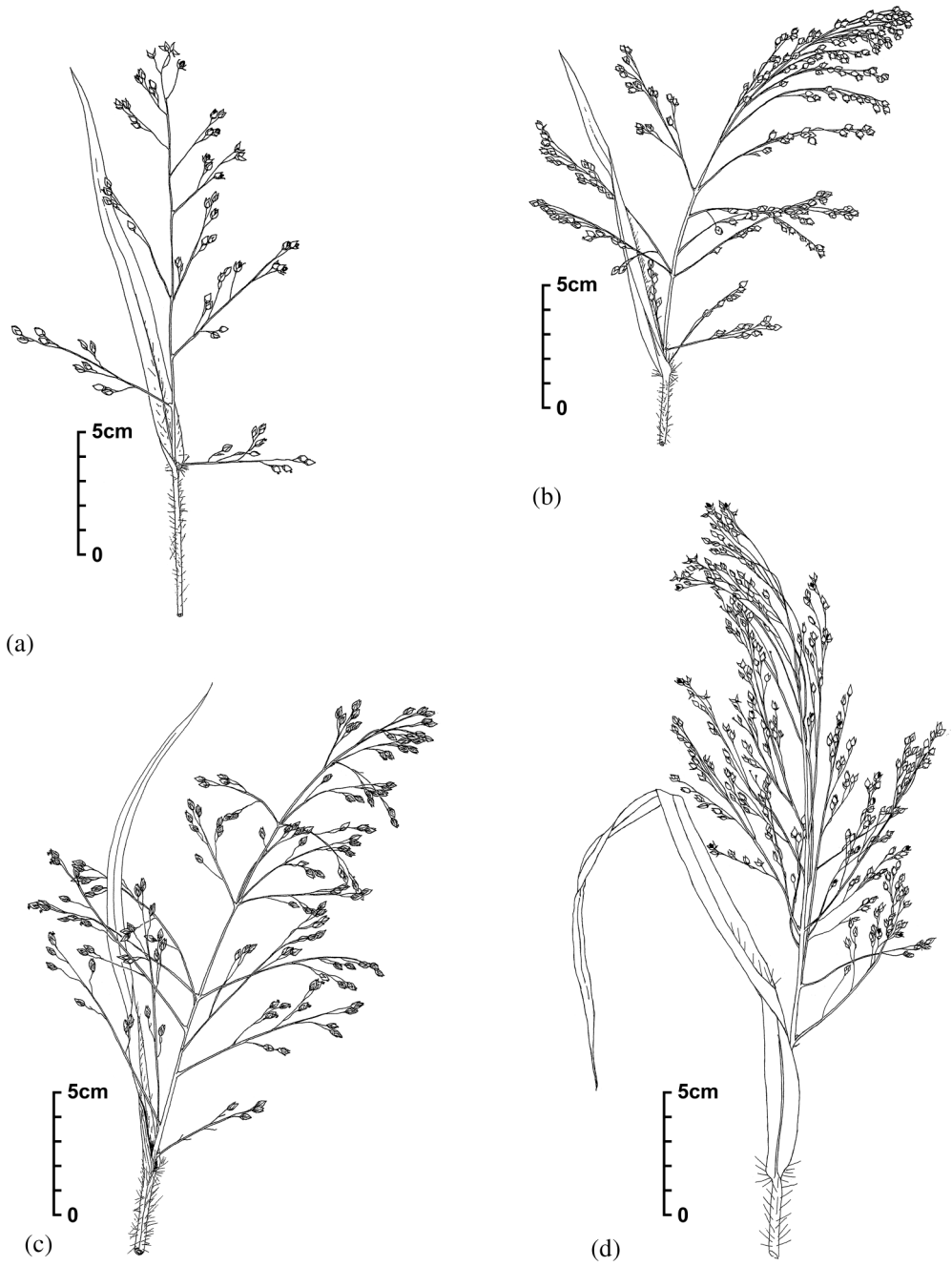
(c) Intraspecific variation

The species encompasses both a wide range of crop types and several weedy biotypes (Bough et al. 1986).

Morphologically, the species is highly variable. This has resulted in many intraspecific classifications of *P. miliaceum*. Variation within *P. miliaceum* occurs with respect to plant size, amount of tillering, colouring and

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Fig. 2. Representative inflorescences of weedy proso millet (*Panicum miliaceum*) biotypes: (*a*) Black, (*b*) Golden, (*c*) Crown, (*d*) Dark red.



laxness of the panicle, time of flowering and seed maturity, size and colour of the seed, amount of shattering, palatability to birds, and seed dormancy (Cavers 1985). Several biotypes of *P. miliaceum* occur as weeds in Canada. Bough et al. (1986) used these features to describe seven weedy biotypes of this species infesting fields in Manitoba, Ontario and Quebec. They based the names they ascribed to five of these biotypes on seed colour: White, Golden, Orange-red, Black and Dark red. A biotype that closely resembles a named crop variety (cv.) Crown [see section 3(c)] with grey-green seeds with light stripes, they named Crown. A unique type, which is tall, with a large drooping inflorescence and golden seeds, and is only found in one Ontario county, they named Elgin, after this county. These names are used to identify the Canadian biotypes of *P. miliaceum* throughout the remainder of this paper. See Fig. 2 for drawings of the inflorescences of the Black, Golden, Crown and Dark red biotypes. In Quebec, Bouchard et al. (1999) listed six biotypes based on seed colour

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Table 1. Proposed subdivisions of *Panicum miliaceum* based primarily on morphological variation, 1885 until the present.

Author(s)	Proposed subdivision of *P. miliaceum*
Lysov (1968, 1975)	Included descriptions of many named varieties of *P. miliaceum* from 1885 onwards from several named authors, including Arnold and Shibaev (1929).
Alefeld and Körnike (1929) (cited in Lysov 1975)	Grouped 38 of these named varieties into three 'variety groups' *effusum; contractum; compactum*.
Popov (1924, 1929) (cited in Lysov 1975)	Used 800 worldwide samples and added two more 'variety groups'; *patentissimum* and *ovatum* to make five in all.
Lysov (1975)	Renamed Popov's five 'variety groups' as subspecies and called 'variety group' *effusum* subsp. *miliaceum*, a synonym for *P.miliaceum* subsp. *effusum* Arn. (see Arnold and Shibaev 1929). These were summarized in a dichotomous key, based on panicle differences. Seed colour was considered too variable and inconsistent for use in the key.
Mansfeld (1952)	Called the three 'variety groups' of Alefeld and Körnike (1929) 'convarieties'.
Cochrane (1984)	Divided the species into two subspecies: subsp. *ruderale*; subsp. *miliaceum*.
Scholz and Mikoláš (1991)	Added a third subspecies, subsp. *agricolum*, subsp. nov. to those of Cochrane (1984) and described all three subspecies as functioning as weeds or ruderals in Europe.
de Wet (1989)	Considered the Lysov (1975) subspecies to be without taxonomic validity, but recognized them as races.
Gashkova (2003–2009)	Recognized the five Lysov subspecies and gave them common names: 'branchy millet' (subsp. *miliaceum* — the type for the species), 'spreading millet' (subsp. *patentissimum*), 'oval millet' (subsp. *ovatum*), 'contracted millet' (subsp. *contractum*) and 'compacted millet' (subsp. *compactum*).
ICRISAT (Anonymous 2010)	Retained the names used by Lysov, but subdivided the species into five races (Miliaceum, Patentissimum, Ovatum, Contractum and Compactum).
Kaume (2006)	Recognized two subspecies: subsp. *ruderale* Kitag. and subsp. *miliaceum*.

[names used by Bough et al. (1986) in brackets]; white, yellow (Golden), olive-green (Crown), orange (Orange-red), red-brown (Dark red) and dark green (Black). Dark green is the most invasive weed in that province.

Some of these biotypes have been shown to be more aggressive as weeds than others. All of them, except Black, have characteristics and attributes that suggest relationships to crop varieties. A subspecific taxon with blackish seeds was named *P. miliaceum* var. *ruderale* Kitag. var. *nov.* in the flora of Manchuria and Boreal China by Kitagawa (1937). In this taxon, the Black biotype of Bough et al. (1986), the seeds shatter when ripe. It is the most widely-spread weedy biotype in Ontario and in many of the northern states of the USA.

Westra and Callan (1990) evaluated fifteen seed accessions characterized as weedy from the United States and Canada; all but two had seeds that shattered. The two were a 'crown' type from Minnesota and a 'black' type from Colorado, with a dense drooping panicle that grew taller than plants of all the other accessions and produced double the dry weight. Had the seeds shattered in this accession, its weediness would have been formidable!

(i) Intraspecific relationships using morphological characteristics

The morphological variability within *Panicum miliaceum* has led to many attempts to subdivide this species. Much of this work was carried out in the former USSR in the early 20th century. Most divisions were based on panicle morphology, including the presence or absence of pulvini. Seed/fertile floret colour and shattering of the panicle were other characteristics often used. This literature is summarized in Table 1.

In addition to these subspecies and varieties, many named variants of the species are grown as commercial crops in North America, China, India, Russia and parts of Eastern Europe. In Udaipur, India, Baghel and Maloo (2002) measured 12 characters for each of 34 crop varieties and strains of proso millet grown in two different locations, one with a much higher annual rainfall than the other. Statistical analysis showed highly significant differences among the genotypes for all characters studied, including seed yield. Reddy et al. (2007) tabulated the variability in several morphological and phenological characteristics within 842 accessions of the species from 27 countries grown in a common garden at the gene bank at ICRISAT, Patancheru, Andhra Pradesh, India. All five of Lysov's (1975) races (see Table 1) were represented.

All of the extensive research presented points to great morphological variability within the species (singular or plural depending on the placement of the Black biotype). Genetic analyses incorporating more recent molecular approaches are providing further insights into these intraspecific relationships.

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(ii) Classification based on genetic studies of seed traits

As noted in Table 1, Lysov (1975) considered caryopsis colour to be variable and inconsistent. Ayyangar and Rao (1938), Yashovskii (1974), Il'in et al. (1978) and others have attempted to elucidate the genetic control of caryopsis colour in crop varieties. They found the number of genes involved to be small, about four. Krasavin and Ul'yanova (1989) suggested that the weedy subsp. *ruderale* (Kitag.) Tsvelev could most easily be distinguished from the cultivated subsp. *miliaceum* by seed colour; the weedy plants have "dirty yellow" seeds, unlike those of the cultivated plants, which have light to bright yellow seeds. They stated that the two subspecies easily hybridize and that the F_1 hybrids have dirty yellow seeds. In the F_2, seed colour segregates in a monohybrid ratio. Later, Krasavin (1991) suggested that cultivated and weedy forms may be distinguished by testing the exposed caryopsis (husk removed) with a solution of 5% iodine in alcohol. In his work, weedy forms turned dark brown after 5–7 min, whereas cultivated forms remained either unchanged or turned light pink. More recently, Graybosch and Baltensperger (2009) studied the waxy (amylose-free) endosperm trait [see section 3(a)] in some USDA accessions. Only six of the 650 accessions had this trait, of which five derived from mainland China. This trait was found to be under the control of duplicate recessive alleles at two loci.

(iii) Intraspecific relationships using molecular techniques

Mansfeld (1952), Zhukovsky (1964) and Lysov (1975) regarded *Panicum* plants with olive–black grains and open panicles as a separate species, *P. spontaneum* Lyssov ex Zhuk. (see also Table 1). Based on electrophoretic studies, Oestry and de Wet (1981) considered plants with this description to be only a subspecies of *P. miliaceum* (i.e., subsp. *ruderale*).

In another electrophoretic study, using seedlings from 110 world-wide collections of proso millet in which 11 enzyme systems were examined, Warwick (1987) detected only very low levels of isozyme variation. This is in contrast to the striking phenotypic and life-history differences among populations of the species. All black-seeded weedy strains of the species, from both Europe and North America, contained the most common multilocus genotype out of the eight possibilities in this study. In a later paper, Warwick (1990) examined five northwardly colonising North American weed species, including proso millet. In all cases, there were low levels of allozyme variation. She suggested that the limited allozyme variability present in new introductions, particularly in predominantly selfing species, may be a reflection of founder effects.

Although the isozyme and protein electrophoresis patterns may indicate low genetic differentiation among proso millet biotypes, Colosi and Schaal (1997) wondered if the allozyme systems normally selected for study accurately reflected the genetic diversity of colonizing plants. In their paper, Colosi and Schaal employed DNA molecular techniques on 398 individuals representing a range of proso millet biotypes (weeds, crop-like weeds, crops and hybrids) to examine relationships among them. They used Random Amplified Polymorphic DNA (RAPD) markers to assess genetic relationships within the species. The premise of the technique is that several RAPD primers taken together provide a genetic signature of an individual and genetic relatedness of two individuals may be inferred from the degree of similarity of these signatures. Their work revealed that five RAPD markers consistently differentiated wild-proso millet from crops and crop-like weeds. They reported more variability among wild-proso millet samples than expected for a plant that had only been described as present in North America from about 1970 (Harvey 1979), which might suggest multiple introductions rather than a single entry. Their work also indicated possible hybridization between wild and crop biotypes (see section 9). Colosi and Schaal (1997) illustrated the genetic distance of the 97 genotypes identified in their study of 398 individuals, in the form of a phenogram. In this, the wild proso millets separated into two groups. Crop and most crop-like weeds formed another group as did cv. Crown and Crown-like weeds. An additional group was also distinguished. It was comprised of two genotypes that were morphologically intermediate between crop and wild-proso millet. The authors suggested that these two genotypes may have been hybrids. Three Elgin [for description of this biotype see section 2(c), paragraph 2] plants were grouped together. Other than the group of possible hybrids, these Elgin individuals appeared to be genetically closest to wild-proso millet, even though morphologically and phenologically they were the most dissimilar.

M'Ribu and Hilu (1994), in a study of four *Panicum* species, were also of the opinion that the use of RAPD markers was more effective than previous methods for studying genetic diversity and defining gene pools. In their work, they used 13 accessions of proso millet cultivars from several parts of the world. These grouped according to geographical region of origin.

Hu et al. (2008) employed polymerase chain reaction (PCR) analysis, using six primers, to investigate genetic diversity among 32 Chinese accessions of *P. miliaceum* and six Indian landraces. The results revealed extensive polymorphism among the accessions. A cluster dendrogram produced by similarity coefficient analysis revealed geographical groupings consistent with those of the M'Ribu and Hilu (1994) study, but not with the results of Karam et al. (2004) described below. Hu et al. (2008) mentioned "hard" (which millet breeders call non-glutinous) and "soft" (glutinous) grain characteristics among the samples. Glutinous varieties have a waxy endosperm (Kaume 2006). This is not a distinction used widely in the literature, but is useful for interpreting

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how the various millet forms would be used and eaten [see section 3(b)].

Karam et al. (2004) used the Amplified Fragment Length Polymorphism (AFLP) technique on three domestic and nine wild biotypes of proso millet. Subsequent cluster analysis resulted in two distinct groups without any geographical association. Six weedy types with some cultivated characteristics clustered with the domesticated plants and three plants with typical wild-type traits formed another group.

From all of these studies, we conclude firstly that weedy types of proso millet in North America are highly variable and no doubt have several origins, and secondly that intraspecific relationships have not been determined completely.

(d) Illustrations

Drawings are presented of a small, but mature plant of the Black biotype of proso millet (Fig. 1) and representative inflorescences of weedy proso millet biotypes; (*a*) Black, (*b*) Golden, (*c*) Crown, (*d*) Dark red (Fig. 2). Additional drawings and photographs of weedy biotypes of *Panicum miliaceum* can be found in Bough et al. (1986), Bough and Cavers (1987) and Bouchard et al. (1999).

3. Economic Importance

(a) Detrimental

Black-seeded proso millet was first recognized as a serious weed threat in parts of the mid-west United States in the early 1970s (Harvey 1979; Hurst 1981). By 1981 it had spread to contaminate at least 400 000 ha in a belt from south eastern North Dakota across Minnesota, Wisconsin and northern Iowa to Illinois (Anonymous 1981). In fact, Doersch and Harvey (1980) reported that it infested over 400 000 ha in Wisconsin alone by 1980. Luellen (1982) added Idaho, Colorado and Nebraska to the States in which the weed was becoming a problem. In Nebraska, Wilson and Westra (1991) reported a drop in irrigated corn (*Zea mays*) yields of between 13% and 22% when this weed was present at a density of 10 plants m^{-2}. Wilson (1993*a*) evaluated irrigated dry bean (*Phaseolus vulgaris* L.) yields in Nebraska when proso millet was present at the same density and found that the yield dropped by 12%–31%. So et al. (2009*a*, 2009*b*) ran a study of the role of proso millet as a weed in fields of 25 sweet-corn cultivars and found that the presence of the weed had minimal effects on crop height and leaf uprightness, but that ear number (reduced by 11% to 98%) and mass (reduced by 24% to 82%) were greatly affected. In general, early-maturing sweet-corn hybrids were less competitive with the weed.

Black proso millet was introduced to Huron County in southern Ontario in the mid to late 1970s (O'Toole 1982; J.F. Alex, personal communication; see section 6). It was dispersed to different farms on farm equipment used for ploughing, cultivating, and spraying on arable land [see section 8(b)]. Within five years it had become a problem weed, particularly in corn (*Zea mays*), soybeans (*Glycine max* L.) and other row crops including white beans (*P. vulgaris*), potatoes (*Solanum tuberosum* L.) and tomatoes (*Lycopersicon esculentum* L.) [O'Toole 1982; J.F. Alex, personal communications]. In a summary of "weed alert" information collected across southern Ontario in the 1980s, proso millet (mostly the Black biotype) was reported from field corn at 127 farms, soybeans at 16 farms, field beans (*P. vulgaris*) at 13 farms and barley (*Hordeum vulgare* L.), winter wheat (*Triticum aestivum* L. subsp. *aestivum*), oats (*Avena sativa* L.) and sunflower (*Helianthus annuus* L.) at two to six farms each (J.F. Alex and R.D. McLaren, personal communications). At that time, it was described as a weed of row crops in Ontario and Manitoba (Wilkins and Robertson 1981), but after an intensive examination of all recorded proso millet infestations in the corn-growing areas of Manitoba in 1984, we determined that all infestations labelled as "wild" proso millet (the Black biotype) were actually Crown, the most important cultivated biotype (P. Cavers and M. Kane, unpublished data). By 1981 some farmers in Manitoba were abandoning the growing of corn year after year in the same field (Wilkins and Robertson 1981). After we (P. Cavers and M. Kane) identified the weed in these fields as the Crown biotype they were able to practice crop rotation and better cleaning of farm machinery, which reduced the seed banks of proso millet to very low levels within one year (see section 12). In contrast, Black proso millet soon became a major problem in parts of southern Ontario and Quebec. It posed its biggest threat in corn, since there was at that time no consistently effective herbicide for use in this crop. In Ontario in the 1980s, we visited farms in which crop suppression by the Black biotype in corn was so great that, financially, the field was not worth harvesting.

Biologically, proso millet plants are sufficiently closely related to corn, and the culms are robust enough to serve as hosts for the earlier instars of corn borer larvae (see section 13). Thus, the presence of proso millet in a corn field can contribute to the build-up of a corn borer population (Alex et al. 1980). Proso millet is also one of at least eight plant species whose ingestion can cause hepatogenous photosensitization in ruminants, mostly because these plants contain steroidal saponins [Miles et al. 1993; see also section 7(c)]. Weedy proso millet is a host of several other diseases and animal pests that attack proso millet crops and other crop species (see section 13).

During the past twenty years there has been a great reduction in the severity of infestations of the Black biotype in Ontario, after growers switched to the growing of glyphosate-tolerant corn and soybeans (see section 4), and similar reductions have been noted across North America. For example the acetolactate synthase enzyme (ALS)-herbicide era in the 1990s, followed by the glyphosate-tolerant crop era, starting in 1996 and

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continuing to the present, has greatly reduced the presence and thus the severity of weedy *Panicum miliaceum* in Minnesota and the US Corn Belt (J.L. Gunsolus, personal communication). In Wisconsin, wild-proso millet is well established and widespread but not common like other weed species (M. Renz, personal communication). There have been concomitant reductions in populations of crop-like weed populations in southern Ontario (personal observations by the authors; C.J. Swanton, personal communication; J.J. O'Toole, personal communication).

In Europe, weedy proso millet biotypes may be weeds in crop millet (A. Terpó, personal communication). At lower densities, proso millet may reduce crop yield (Czimber et al. 1977) in Hungary. This is a greater problem for farmers growing corn for grain than for those using corn for silage. Nevertheless, by the early 1980s *Panicum miliaceum* subsp. *ruderale* was increasingly infesting fields of *Zea mays* in Austria (Scholz 1983). In an experiment conducted in northeast Italy, Berti and Zanin (1994) studied the effects of multi-species weed infestations in soybeans. Using three weed species (*Xanthium strumarium* L. subsp. *italicum* (Moretti) D. Löve, *Polygonum persicaria* L. and *Panicum miliaceum*) in three density ratios, it was found that the yield loss caused by one *Panicum* plant m^{-2} was 3.8% compared with a 40% loss caused by one *Xanthium* plant m^{-2}. At a higher density (32 plants m^{-2}), losses caused by *Panicum* were 73% of those caused by *Xanthium*.

In Hungary, Lehoczky et al. (2006) showed that the presence of weedy proso millet, like many weeds of row crops such as corn, can reduce the soil water content caused by their own water use, thus diminishing water availability to the crop. This, in turn, inhibits corn growth. The authors concluded that weed competition for water is most damaging to the crop under drought conditions.

In New Zealand, the recent introduction of the Black biotype has caused significant reductions in crop yields, particularly in sweet corn. This weed also interferes with harvesting by clogging machinery (James et al. 2011).

(b) Beneficial

Proso millet was introduced to Canada in the 17th century for grain cropping and had limited use as a forage crop in the early 1900s (Dekker et al. 1981). It has been grown for seed in southern Ontario and Manitoba, primarily for use in feeding hogs and birds (Dekker et al. 1981; Manitoba Agriculture, personal communication; see section 13). The general information accompanying the registration of Crown proso millet in 1937 was as follows: "This variety has been widely grown, particularly in Ontario and Manitoba. In all experimental tests, it has given high yields of well matured grain and in many instances has proven superior in yield to the other proso millets in the same maturity group. Yields comparable to oats, and in some cases to barley, have been obtained in many cases. This variety may be seeded as late as the last of June in some areas with fair expectation of a substantial grain yield. The stubble left after Crown millet is harvested is usually clean and in this respect it compares favourably with buckwheat" (M. Forhan, personal communication, CFIA). Crown has been grown for seed production for many years. In many situations, its most important role was that of a rescue crop because of its short growing season (B. Todd, personal communication, Manitoba Agriculture).

Crops of proso millet with golden, orange, and white seeds have been grown for birdseed in Oxford and nearby counties in Southern Ontario (Dekker et al. 1981; personal observations by the authors) for the last 50 years. The nutritive content of the plants and seeds makes even the weedy biotypes acceptable for silage according to some Canadian farmers with whom the authors have spoken [see also section 13(a)]. In Ontario, the ability of the species to grow in warm sandy soil makes the crop a feasible alternative to tobacco (*Nicotiana tabacum* L.), but care would have to be taken to select non-persistent varieties (C. Swanton, personal communication). In the Canadian prairies, research with proso millet has continued and Crown is still the most commonly grown variety (Johns 2015). On the Prairies, Crown is usually grown for seed, but its rapid maturity also makes it an excellent emergency forage crop (Johns 2015).

Proso millet has long been grown as a crop in warm arid areas of Europe and Asia (Anderson and Martin 1949). Bavec and Bavec (2006) found that in Slovenia, seeds of landrace cultivars are often sown, for example Kornberško proso and Belo strniščno proso. They stated that proso millet accounts for 14% of all millet production in Asia. In 2000, China produced 1.6 million tons out of a global production of five million tons, a majority of which was used for human consumption (Zeller 2000). Senft (1978) considered that growing the crop would increase seed production in the Central High Plains of the United States and provide a dependable protein source for developing countries. As a crop, proso millet is renowned for its quick growth and low water requirement (Cobley and Steele 1976; Agdag et al. 2001) although, as Upadhyaya et al. (2008) mentioned, the high water-use efficiency probably is due to its short growing season rather than its drought resistance. However, Gashkova (2003–2009) noted that it can support temporary deep-tissue dehydration without a great reduction in yield. This annual grass has been grown extensively in warm dry areas of the world, under which conditions it can produce a greater yield than other cereal crops, accumulating more reproductive dry matter when compared with wheat, corn and sorghum (Upadhyaya et al. 2008).

Hunt et al. (2014) reported increased interest in the use and improvement of proso millet. Its relatively short maturation time and other attributes make it a desirable crop given the world-wide need for sustainable rain-fed agriculture as fresh water becomes increasingly scarce.

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A newer plan in the Central Great Plains of the United States is to substitute a short-season spring-planted crop (such as proso millet) for summer fallow in situations where soil moisture is sufficient at planting time (Felter et al. 2006). Such a plan may be of particular value when production of other crops is limited by lack of growing-season precipitation. Anderson (2004) also recommended proso millet as a suitable warm-season crop in dryland rotations in the Central Great Plains of the United States. The best sequence was a four-year rotation of four different crops, two warm-season and two cool-season. If the same crop was grown for two years in a row, the benefit of a rotation design was reduced considerably (Anderson 2004).

In the United States, as in Canada, proso millet is grown for poultry and hog feed (hence "hog millet"). In tests with laying hens in North Dakota, five different grains were fed without added fat. Corn, wheat and proso millet supported better rates and efficiencies of egg production than rations containing oats or barley (Sell 1977). Hens fed on proso millet were said by Gashkova (2003–2009) to lay more eggs with harder shells.

Hybrids among Eurasian cultivars of *Panicum miliaceum* have vigour that increases yield several fold (de Wet 1992). Researchers in Romania are producing hybrids from the best local varieties in a renewed program to increase yield (Pricop 2003).

Proso millet is considered to be a short-day crop [Baltensperger 1996; Bavec and Bavec 2006; but see section 5(a)], and the short growing season of 60–70 days (Senft 1978) and low water requirement make it a good catch crop, or a second crop in areas of the world where monsoons may come late. If hail destroys an emergent crop, the short growing season allows time for replanting (Shanahan et al. 2000). It is also suggested as a crop to substitute for a summer fallow in the Central Great Plains of the United States if soil water is sufficient, to reduce soil degradation (Felter et al. (2006). The use of a no-till system increased grain yield and water use efficiency (Anderson 1990). Anderson (1994*b*) suggested that, in the Central Great Plains of the United States, it could be planted in early June as a summer annual crop in a no-till system following winter wheat.

Bavec and Bavec (2006) noted that proso millet ripens unevenly. They suggested two-phase harvesting [see also sections 8(b) and 13(a)(i)].

Since 1998, proso millet production has been concentrated in three States of the Central Great Plains: Colorado, Nebraska and South Dakota (Lyon et al. 2008). Total American production ranged from just under 2 million to nearly 10 million cwt. yr^{-1} from 1999 to 2006 (Lyon et al. 2008). Nearly all of the proso millet grown in the major production areas of the United States is "white"-seeded (Lyon et al. 2008).

In North America, the warm dry conditions of North and South Dakota and Colorado are suitable for proso millet seed production, as are parts of central Canada (see above). The species is also grown in many other semi-arid areas of the world (see section 4). In the dryland Loess Plateau of China, the practice of including *P. miliaceum* in some crop rotations improved water use efficiency and increased the duration of coverage, thus reducing soil erosion (Huang et al. 2003).

As a crop, *P. miliaceum* is widely used for food in Russia, Eastern Europe and many countries in Asia. Léder (2004) compared the nutrients of this seed with those of other cereals. In comparison to wheat, per 100 g it has 1 g less protein (10.6 g), twice the fat (4.0 g), similar carbohydrates (70 vs. 71 g), far less calcium (8 mg vs. 30), comparable iron (2.9 mg vs. 3.5), similar thiamine content, more than twice as much riboflavin (0.279 mg) and slightly less niacin (4.54 vs. 5.05 mg). Amounts of protein and trace elements other than calcium are higher than in a comparable weight of corn.

The cereal can be cooked as gruel or porridge. Anderson and Martin (1949) described it as being widely grown in the southern half of "Soviet Russia" and a staple food throughout that country, where it was consumed mostly as a thick porridge called "kasha". In Asia and elsewhere, the flour may be used to make unleavened bread (Rachie 1975; Lorenz 1980; Bavec and Bavec 2006). In the United States, Hinze (1972) suggested that proso millet flour could be used to replace wheat flour in certain baked products. Lorenz (1980) noted that a blend of 15% proso millet flour with wheat flour produced acceptable risen bread.

For culinary purposes, two types of proso millet seed are recognized [see section 2(c)(iii)]: "hard" or non-glutinous and "soft"/glutinous/amylase-free/"waxy"/"sticky". Starch of the "sticky" type is composed solely of amylopectin [Gashkova 2003–2009; Graybosch and Baltensperger 2009; see section 2(c)]. Sakamoto (1987) and Weber and Fuller (2008) noted that in parts of East and Southeast Asia there is a preference for "sticky" (glutinous) cereal. This has led to artificial selection for varieties that become sticky when cooked. Tanaka (1912) reported that the type of starch in glutinous varieties of proso millet stains red with iodine rather than dark purple, in common with the starch in glutinous rice.

The seeds can also be used as a source of starch or for alcohol production — wine or beer (Rachie 1975). Baby foods may be made from proso millet (Bavec and Bavec 2006). Delost-Lewis et al. (1992) demonstrated that proso millet may be puffed successfully and that the puffed seeds showed potential for food. In India, malted or puffed proso millet seeds have been used to develop convenience mixes for five types of baby food (Sarita et al. 2001). Malted grains may be used as a raw material for gluten-free foods, for which there is increasing demand in some countries (Zarnkow et al. 2007). Graybosch and Baltensperger (2009) also noted that proso millet products may be used in diets for those

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with coeliac disease. Kaume (2006) specified non-glutinous cultivars for this purpose.

An unusual use of glutinous types of broomcorn (proso) millet is as the basis of a substrate on which to grow a fungus pathogenic to some insects: planthoppers, leafhoppers and aphids (Feng and Liang 2003). It is also used in mushroom production (Baltensperger 1996). In China, the straw of proso millet is used as a pulp in papermaking (Steyermark 1963). In Australia, proso millet is sown as a soil stabilizer (S. Navie, personal communication).

(c) Legislation

Under the Weed Seeds Order, 2005 of the Canada Seeds Act and Regulations (Anonymous 2009), panic grass seeds (*Panicum* spp.) are listed as class 4, secondary noxious weed seeds, and also under class 5, noxious weed seeds. The Ontario Weed Control Act lists proso millet (*Panicum miliaceum*, Black biotype) as one of 23 noxious weeds in the province (Anonymous 1988*a*).

At the time that we began our studies of proso millet in the 1980s, 'Crown' was the only licenced crop variety of proso millet in Canada (Cavers and Bough 1985). It was registered on 18 May 1937 in Schedule III of the Seeds Regulations of Canada, registration number (licencing number) 0283, but this registration was cancelled on 1 Aug. 1993. This information regarding the registration of Crown proso millet was supplied by Mark Forhan, Variety Registration Office, Canadian Food Inspection Agency, Ottawa, ON.

Proso millet is listed as noxious in three American States, including Minnesota (OMAFRA 2014).

4. Geographical Distribution

As a crop, proso millet has been grown primarily in Ontario and Manitoba [see section 3(b)].

Weedy proso millet has been reported from every province in Canada, usually as plants growing near bird feeders in urban settings, but also in crops produced for feed or feed supplements by individual farmers (George Jones, personal communication, University of Guelph). Several Canadian herbarium records, particularly for specimens with golden seeds, describe the plants as growing near bird feeders, but the progeny of the proso millet varieties used in birdseed mixtures are not generally those causing the most aggressive and widespread infestations. In contrast, the Black biotype became a troublesome weed in Southern Ontario in the 1970s and 1980s [see section 3(a)].

The distribution of *P. miliaceum* as a weed in Canada is shown in Figs. 3, 4, 5 and 6. These maps are based on information from herbarium specimens from DAO, UWO, CAN, TRT, UBC, OAC, QUE, QFA and SFS (now closed, northern material is at QFA, the remainder at MT); collections made by the authors from Ontario; Weed Alert data from Ontario (J.F. Alex and R.D. McLaren, University of Guelph); data collected by the authors from Manitoba with the help of staff of the Manitoba Department of Agriculture; and Quebec data, collected with the assistance of scientists at the Agriculture and Agri-Food Canada Station at Saint-Jean-sur-Richelieu. R. Néron (personal communication, Feb. 2013, June 2014), reported that, although personally he has collected no further herbarium specimens in Quebec since 1985, he has noticed several more colonies of the weedy biotype with 'dark green' seeds (which we assume to be 'Black'), and that it has become more common in the Montérégie area of Quebec — the south west corner of the province, south of Montreal. Néron et al. (1982) had previously reported local infestations of *P. miliaceum*, particularly the biotype with dark red seeds, in southern Quebec. In the Canadian weed survey series (e.g., Thomas et al. 1998; Leeson et al. 2002, 2005), proso millet is listed as a minor weed in numerous fields across the Prairie Provinces, but these surveys do not state which biotype(s) of proso millet were involved and whether the plants originated from volunteer crops or from weed populations. This is unfortunate since volunteers from a wide variety of other crop species are identified as such in this series. However, we believe that many of these infestations did arise from crop volunteers since crops of several crop biotypes including Crown, orange-red, white and golden have been grown in Manitoba (P. Cavers and M. Kane, unpublished data; B. Todd, personal communication, Manitoba Agriculture), and at least two biotypes have been grown in Saskatchewan (Lardner et al. 2011; P. Cavers, personal observation). In addition, these surveys were not done in corn fields in Manitoba, where proso millet has been most important as a weed of arable fields in the Prairie Provinces [see section 3(a)].

Wild proso millet (black-seeded) has been reported as infrequent in British Columbia, occurring in corn fields in the Kamloops, Salmon Arm, Enderby and Abbotsford areas and along field edges and roadsides in the Okanagan, Thompson, Lower Mainland and Peace River agricultural areas (Anonymous 2015). However, this may not be Black proso millet, in at least some places, since the publication also states that this weed is "grown for human consumption, chicken feed or birdseed" (Anonymous 2015). During the past ten years, we have visited numerous sites in Ontario that formerly had heavy infestations of the Black biotype. We found that there has been a great reduction in such infestations and that in many of these sites it was difficult to find any plants of *Panicum miliaceum*. This assessment has been confirmed by C. Swanton, P. Sikkema and D. Robinson at the University of Guelph (personal communications), and they pointed out that growers can now control this weed with the advent of glyphosate-tolerant corn and soybeans (see section 11). There has been a concomitant decrease in small populations of other biotypes in Ontario (personal observations by the authors and information from J. O'Toole and the weed scientists listed above).

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Fig. 3. The southern latitudes of Canada showing, by means of shading, the three main areas in which weedy proso millet (*Panicum miliaceum*) occurs.

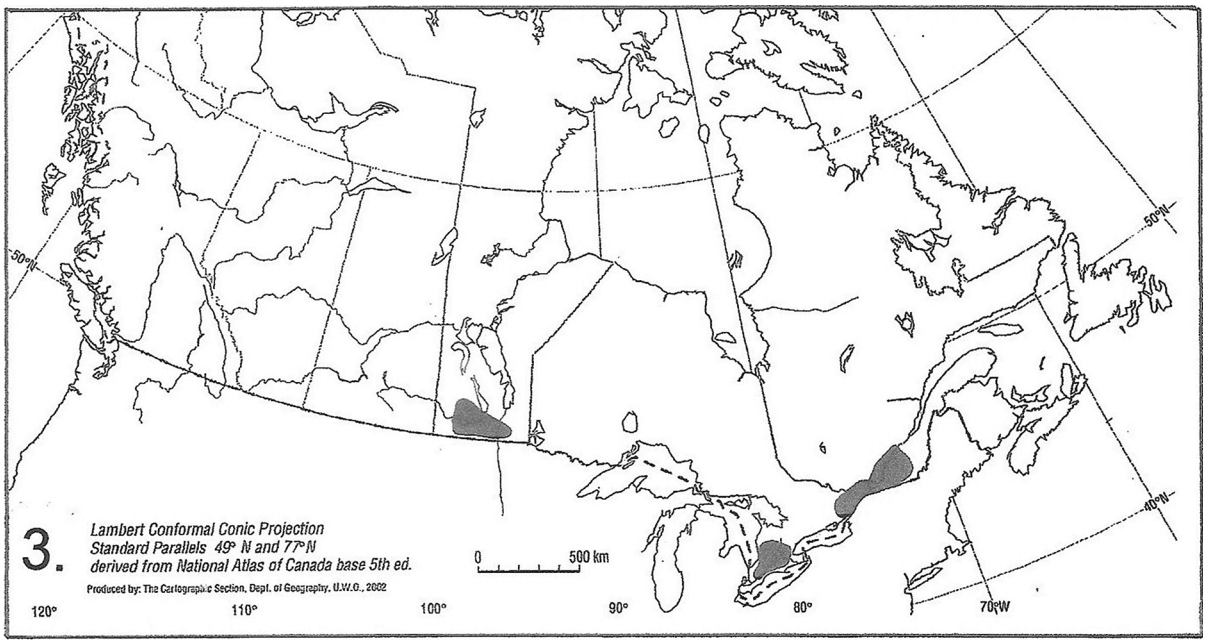
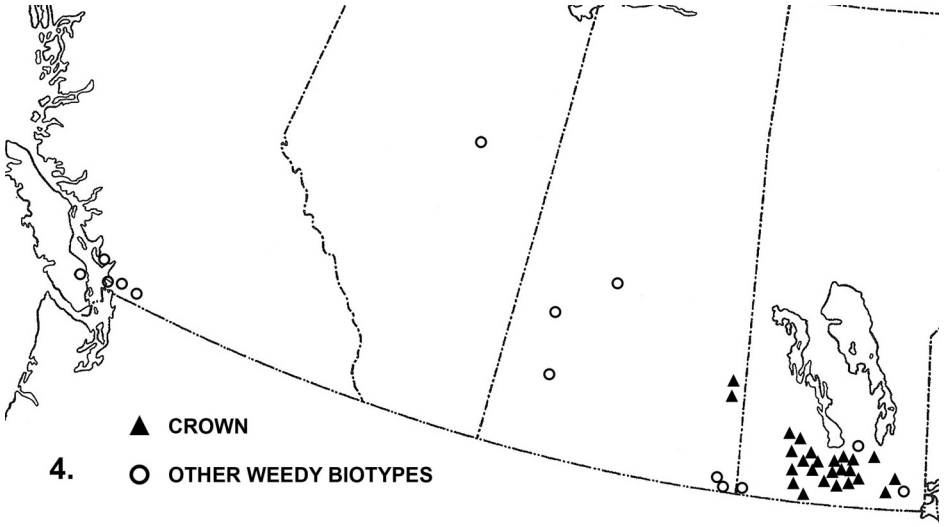


Fig. 4. The distribution of weedy proso millet (*Panicum miliaceum*) biotypes in British Columbia and the Prairie Provinces.



As a crop, proso millet is grown in parts of the United States [see section 3(b)]. The USDA PLANTS database (USDA and NRCS 2015) listed it as present in all continental states except Alaska, Arkansas, Oklahoma, South Carolina and West Virginia. Although *P. miliaceum* (other than growing as a crop) has been reported from many states within the United States by others (e.g., Small 1933; Gleason 1963; Steyermark 1963; Voss 1972; Wunderlin and Hansen 2008), the description has usually been that of an occasional weed of roadsides, field edges or waste places, or an adventive or crop volunteer bearing cream or golden seeds [e.g., Stevens (1946); Steyermark and Swink (1955)]. Lorence and Flynn (1997) reported that *P. miliaceum* was present in Hawaii growing from seeds spilled from a bird feeder on Kauai, and that it is naturalized on Oahu and Maui, and cultivated on Hawaii. The USDA PLANTS database (USDA and NRCS 2015) maps all of these occurrences as *P. miliaceum* subsp. *miliaceum* (see Table 3).

By the mid 1980s, however, a description by Cochrane (1984) of a widespread black-seeded weed in the mid-western United States, which was identified as *P. miliaceum* subsp. *ruderale*, wild-proso millet, matched a description of a type of proso millet from Manchuria

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Fig. 5. The distribution of weedy proso millet (*Panicum miliaceum*) biotypes in Ontario.

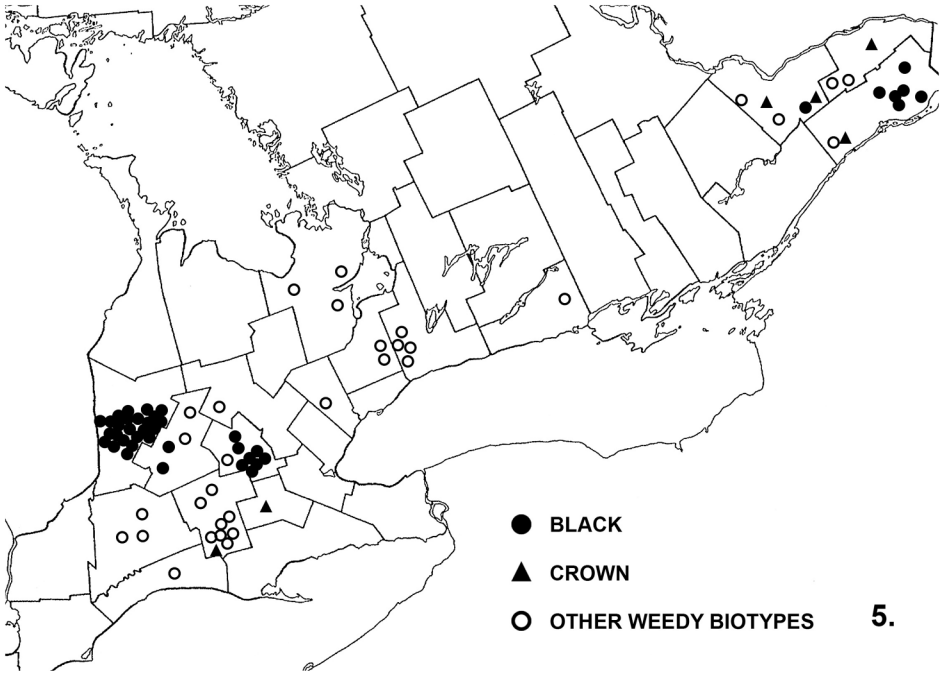
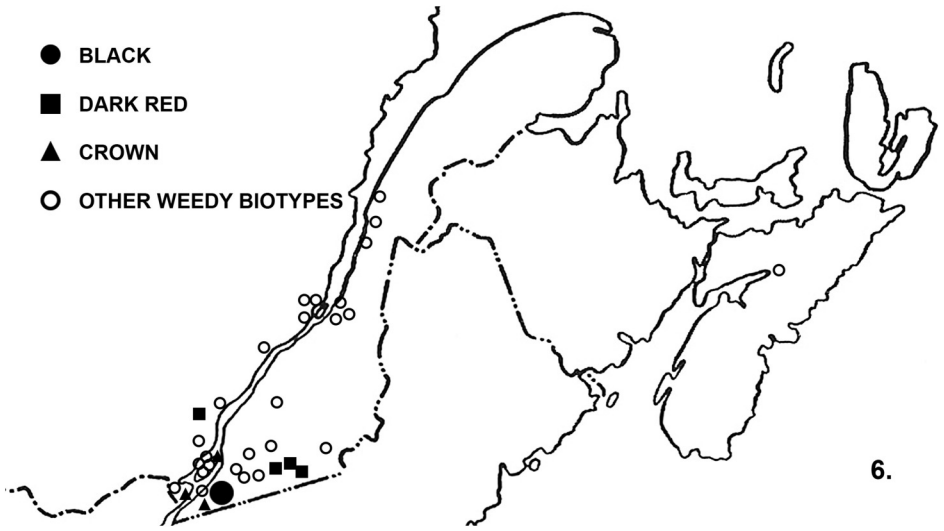


Fig. 6. The distribution of weedy proso millet (*Panicum miliaceum*) biotypes in Quebec and the Maritime Provinces. The large solid black circle represents several sites in south-west Quebec (Montérégie region).



(Kitagawa 1937) and Mongolia (Hilbig and Schamsran 1980). This weed corresponded to the wild-proso millet, which, at that time, was spreading rapidly in the corn-growing areas of the United States, in particular Wisconsin and Minnesota [see section 3(a); Table 3; USDA and NRCS (2015) map for *P. miliaceum* subsp. *ruderale*]. Cochrane (1984) suggested that the proso millet of older reports should be referred to as *P. miliaceum* subsp. *miliaceum*. Fortunately, the occurrence of wild-proso millet in the United States has been greatly reduced following the adoption of more effective weed-control treatments [see sections 3(a) and 11]. In Mexico, *P. miliaceum*, growing as an annual weed, was recorded for the first time in 1988, in the valley of Mexico (Herrera 1988).

We have noted in section 2(c) that the species *Panicum miliaceum* encompasses wild (progenitors), weedy and crop taxa. Tables 2 and 3 present information on the global distribution of crop and weedy proso millet.

In 1982, Joe Colosi, working in the Cavers laboratory in London, ON, received samples of 157 accessions of *P. miliaceum* from the Regional Plant Introduction Station, Iowa State University, in Ames, IA. These accessions, from

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Table 2. Worldwide geographical distribution of *Panicum miliaceum* being grown as a crop.

Continent and country	Reference(s) and comments
For details see sections 3(b), Economic Importance, Beneficial and 4, Geographical Distribution.	
North America	
Canada	Grown primarily in Manitoba and Ontario for hog and poultry feed, birdseed and as a rescue/catch crop.
United States	Produced primarily in Colorado, Nebraska and South Dakota (Lyon et al. 2008). Used for poultry and hog feed, as a catch crop and as a substitute for summer fallow.
Africa	
Algeria	Bertin et al. (1971)
Egypt	Currently a minor cereal in Egypt including the Arabian peninsula (Brown 1999).
Ethiopia	Ketema (1989)
Kenya	Minor crop (Mburu 1989); Reddy et al. (2007).
Malawi	Kaume (2006); Reddy et al. (2007). Kaume (2006) also lists Botswana, Zimbabwe, Madagascar and Lesotho.
Morocco	Bertin et al. (1971)
Nigeria	Uhegbu (1997)
South Africa	Bertin et al. (1971)
Asia	Grown extensively in temperate Eurasia (de Wet 1989). Bertin et al. (1971) mapped countries in S.E. Asia additional to those listed below.
Afghanistan	Lyon et al. (2008)
Bangladesh	Majid et al. (1989)
Bhutan	Shouliang and Renvoize (2006)
China	Semi-arid N, N-W and N-E. (Jiaju 1989); Shouliang and Renvoize (2006). Known as a crop for 10 000 yr (Lu et al. 2009*b*).
Former USSR [Asia/Europe]	Volga region [over 50% of all millet cultivation in Russia] and the Central Black Earth Belt. It is also grown in the non-Chernozem areas of Ryazan, Orei, Nizhni and Novgorod regions and in the autonomous republics of Chuvash and Mordovia (Gashkova 2003–2009). Parts of Kazakhastan (Ilyin and Zolotukhin 1989). Georgia (Akhalkatsi et al. 2012). Kühn et al. (1980) considered it an indigenous relic crop.
India	Mainly in areas S. of Krishna River, but occasionally in central or hilly parts of the north (Rachie 1975). Andhra Pradesh, Tamil Nadu, Maharashtra (Doggett 1989). Kerala and parts of Mysore (Karthikeyan 1971). Madhya Pradesh, Karnataka, Gujurat and Uttar Pradesh (Upadhyaya et al. 2008).
Iran	Gashkova (2003–2009)
Japan	Shouliang and Renvoize (2006)
Pakistan	Beg and Khan (1974)
Sri Lanka	Ponnuthurai (1989)
Turkey [Asia/Europe]	Gashkova (2003–2009); Lyon et al. (2008)
Australasia	
Australia	South Australia, Tasmania, Western Australia, Queensland,[a] New South Wales[a] and Victoria[a] (Simon and Alfonso 2014).
New Zealand	Evaluated as a crop on several occasions since 1944 but never adopted as a commercial crop for any reason (T. James, personal communication).
Europe	*Eastern Europe:* 'grown widely' (de Wet 1989). Romania (Lyon et al. 2008), Ukraine, Poland, Hungary and Bulgaria (Gashkova 2003–2009). Slovenia (Bavec and Bavec 2006). For Russia, see under Asia, Former USSR, above. *Western Europe:* All countries except Ireland, the British Isles, Northern Germany, Norway, Finland and Sweden (except for southern tip) Bertin et al. (1971).
South America	See Simon and Alfonso (2014).
Argentina	Sisterna and Wolcan (1987); Léder (2004)
Brazil	Tyler (1941)

[a]Also in Bertin et al. (1971).

17 countries on five continents, were included in a wide ranging study of the species. The sole Canadian accession was labelled 'crown'. This information illustrates how easily and how rapidly genotypes of *P. miliaceum* can be spread to new areas of the world where they might be able to establish weedy infestations.

5. Habitat

(a) Climatic requirements

(i) Primarily for crop populations

Proso millet is a warm-season annual adapted to temperate and subtropical areas. Komarov (1934) described it as a typical xerophyte. The ability of the species to

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Table 3. Worldwide geographical distribution of *Panicum miliaceum* occurring as a weed.

Continent and country	Reference(s) and comments
See further information in sections 3(a), Economic Importance, Detrimental and 4, Geographical Distribution.	
North America	
Canada	See Figs. 3–6, sections 3(a), Detrimental and 4, Geographical Distribution. Primarily in Manitoba, Ontario, and Quebec. Some parts of British Columbia (Anonymous 2015). Most records elsewhere are of single occurrences.
Mexico	First recorded by Herrera (1988) as an annual weed, in the valley of Mexico.
United States	The USDA PLANTS database (USDA and NRCS 2015) listed *P. miliaceum* subsp. *miliaceum* as present in all continental USA states except Alaska, Arkansas, Oklahoma, South Carolina and West Virginia. It is also present in Hawaii (Lorence and Flynn 1997). In states other than those where it is grown as a crop (Table 2), the plant would be present only as a weed.
	This same database shows *P. miliaceum* subsp. *ruderale* (the black seeded biotype) to be present in Wisconsin and Minnesota. In addition to these states, Westra et al. (1990) reported its presence in Colorado, Idaho, Michigan, Nebraska, Oregon, Washington and Wyoming. Colosi and Schaal (1997) used additional accessions obtained from North Dakota, South Dakota and Utah. It is also in Iowa and Illinois, (R.G. Harvey, personal communication).
Africa	
South Africa	'Part of the flora but status as a weed unknown' (Holm et al. 1979).
Asia	
Afghanistan	'Part of the flora but status as a weed unknown' (Holm et al. 1979).
China	Kitagawa (1937) described a wild plant, *P. miliaceum* var. *ruderale* Kitag., as part of the flora of Manchuria and Boreal China (see also section 6, History).
Former USSR [Asia/Europe]	Central-Boharian Oasis: Sakamoto (1987) noted a description by Popova (1926) of a plant seemingly corresponding to *P. miliaceum* var. *ruderale. Panicum miliaceum* present in many parts of the former USSR as an adventive weed, Komarov (1934).
India	'Part of the flora but status as a weed unknown' (Holm et al. 1979).
Iran	'In cornfields near Kermanshah' (Baghestani et al. 2007).
Japan	Described as a 'principal weed' by Holm et al. (1979).
Sri Lanka	'Part of the flora but status as a weed unknown' (Holm et al. 1979).
Turkey [Asia/Europe]	'Present and behaving as a weed' Holm et al. (1979).
Australasia	
Australia	An early collection was made by Mueller in 1851 [N. Walsh, personal communication].
	Bentham and von Mueller (1878) listed it as an escape in South Australia.
	Plants of cultivated biotypes with a wide variety of seed colours (not black) collected from many places (the late B.K. Simon, N. Walsh, M. Baker, T. Macfarlane and D. Panetta, personal communications).
New Zealand	Some 'later incursions' (since the 1990s) of weedy black-seeded *P. miliaceum*. Now established across the North Island and present in the South Island [T. James, personal communication; James et al. (2011)].
Europe	
Austria	Scholz (1983). *P. miliaceum* subsp. *agricolum* [subsp.*nova*][a] (Scholz and Mikoláš 1991).
Belgium	Verloove (2001) reported that both subsp. *miliaceum* and subsp. *ruderale* were present, and that subsp. *agricolum* was 'likely to occur'.
Croatia	Extremely competitive weed in corn but also in soybean (Hulina 1994). Hulina's description of '*P. miliaceum* subsp. *agricolum*' leads us (P. Cavers and M. Kane) to think that this may be subsp. *ruderale*.
Czech Republic	*P. miliaceum* described as an important weed of arable land (Holec et al. 2002).
	P. miliaceum subsp. *agricolum* ([subsp. *nova*][a] (Scholz and Mikoláš 1991).
Former USSR	See above under Asia.
France	Lauragais region (Sartori 1979). Alsace, *P. miliaceum* subsp. *agricolum* [subsp. *nova*][a] (Scholz and Mikoláš 1991).
Germany	Caspers (1976). *P. miliaceum* subsp. *agricolum* (subsp. *nova*)[a] in Bavaria (Scholz and Mikoláš 1991).
Hungary	Terpó-Pomogyi (1976); Brückner et al. (1997). *P. miliaceum* subsp. *agricolum* [subsp.*nova*][a] (Scholz and Mikoláš 1991). Magyar and Király (2012) mapped the distribution of subsp. *agricolum* occurring as a segetal and ruderal weed, and noted that it was often more locally dominant than subsp. *ruderale*.
Ireland	Rare casual (Reynolds 1998).
Italy	Holm et al. (1979). *Panicum miliaceum* is one of the commonest weeds in the northeast (Sartorato et al. 1996). *P. miliaceum* subsp. *agricolum* (subsp.*nova*)[a] in the northeast (Scholz and Mikoláš 1991).
Romania	Weed populations along roadsides by corn fields correspond to *P. miliaceum* subsp.*ruderale*, the "black-seeded biotype" a widespread weed in North America (Sakamoto 1987).
	One of the eight most dense weed species on an experimental farm (Slonovschi and Răutu 2004).
Slovenia	*P. miliaceum* subsp. *agricolum* [subsp. *nova*][a] (Scholz and Mikoláš 1991).
Sweden	Occurs in waste places and as a weed (Karlsson 1977).

[a]*P. miliaceum* subsp. *agricolum* (subsp. *nova*), mentioned above, is described by Scholz and Mikoláš (1991) [see Table 1] as having a similar to lighter grain colour and more contracted panicle than subsp. *ruderale*. Glumes remain on the inflorescence following disarticulation.

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complete its life-cycle within 60–90 days enables it to survive (or avoid) heat and drought in arid areas (Shanahan et al. 2000; Zohary and Hopf 2001). According to Hanna et al. (2004), *P. miliaceum* can grow at higher latitudes (up to 54°N) than other millets and is well adapted to plateau conditions and higher elevations (up to 1200 m in the former USSR and 3500 m in India). Akhalkatsi et al. (2012) noted that it is cultivated in high mountain regions (1000–1800 m) in parts of Georgia in the former USSR. During development the plants need temperatures of 18 °C–23 °C at various stages of growth (Gashkova 2003–2009; Kalinová and Moudrý 2005). Although the plant has a high water-use efficiency, it is the short growing season, rather than drought tolerance, that confers success in hot dry areas, because the species does not grow well under either water stress or, in fact, excessive moisture (Baltensperger 1996; Upadhyaya et al. 2008). In an experiment conducted in Iran to establish the stages of growth at which *P. miliaceum* is most susceptible to drought stress, Seghatoleslami et al. (2008) found the greatest reduction in seed yield and water-use efficiency at the ear-emergence stage.

In Germany, Öztürk et al. (1981) compared the growth of a C_3 grass, *Avena sativa*, with that of *Panicum miliaceum*, a C_4 grass, under a range of soil-water levels. They found that the length and dry weight of the above-ground parts of *A. sativa* increased, whereas the comparable values for *P. miliaceum* decreased, as soil water supply increased. The roots of *P. miliaceum* were longer than those of *A. sativa* under all water conditions. Also, the root length in *P. miliaceum* increased in the drier soils whereas root length in *A. sativa* did not change with changes in soil moisture.

In Wisconsin, Anderegg and Lichtenstein (1981) compared five C_3 species to four C_4 species for the amount of water transpired. All of the C_4 species transpired less than any of the C_3 species, and *Panicum miliaceum* (red proso variety) transpired the least of all the species.

Although it is described as a short-day species [Kumar et al. 1977; Baltensperger 1996; but see section 3(b)], Carpenter and Hopen (1985) found that both wild and cultivated proso millet flowered under all photoperiods (ranging from 10 to 24 h) under experimental conditions. They also found that dry matter production increased with photoperiod. Tayal (1972) reported that maximal values for the dry weights of whole plants were reached earlier under short days (8 h d^{-1}) than in natural day lengths or long days (18 h d^{-1}). However, the dry-weight increase, although slower, lasted longer and reached higher maxima in the latter two regimes. In a later paper, Tayal and Nanda (1980) reported that the size of the inflorescence and the number of spikelets were much reduced under short days but the size of floral organs and the embryo did not differ much under the three photoperiods. They concluded that the shorter vegetative period for plants sown later in the growing season (September) is primarily a result of exposure to shorter photoperiods.

In the western Great Plains of the USA where proso millet is grown as a crop, it is susceptible to hail damage. Simulations have demonstrated that seed number, rather than mass, is reduced by hail (Shanahan et al. 2000).

Proso millet plants are sensitive to low air temperatures (+2 °C to −3 °C), but can survive better in comparatively cooler climates than foxtail millet [*Setaria italica* (L.) P. Beauv.], so that, as a crop, proso millet can be grown in more northerly zones (Marinval 1992). Plants may be damaged by frost, in particular at both the germination and flowering stages (Gashkova 2003–2009). Kalinová and Moudrý (2005) found proso millet plants to be most sensitive to frost from the two-leaf to tillering stages in their experiments. They also noted that the specific temperatures (−1.5 °C to −4.1 °C) for frost sensitivity vary with crop variety.

Plants of *P. miliaceum* showed decreased biomass accumulation, and decreased grain quality and quantity when they were exposed to 0.08 ppm O_3, 0.5% SO_2 or a combination of 0.04% O_3 + 0.25% SO_2 under experimental conditions. The pollutants had a synergistic effect on the plants (Agrawal et al. 1983).

(ii) Weed populations

Patterson et al. (1986) compared the responses of wild-proso millet and Texas panicum (*Panicum texanum* Buckl.), grown separately or together, to different temperature/photoperiod regimes in a controlled environment. When the species were grown separately, height, tiller number, leaf number and leaf area, and plant dry weight for proso millet were all greater in a 30/24 °C day/night temperature regime than in a 24/18 °C regime over the first 31 days of the experiment. When the two species were grown together, Texas panicum was the superior competitor under the higher temperature regime and wild-proso millet outcompeted Texas panicum under the cooler regime. It was the authors' opinion that wild-proso millet would be competitively inferior to locally adapted grasses, including Texas panicum, in the southern United States.

Under experimental field conditions where the species was grown in either monoculture or in competition with corn, leaf area index (LAI) and radiation use efficiency (RUE) were greater under the competitive conditions where shading increased the proportion of diffuse light reaching the weed (Gramig et al. 2006). The nature of the crop canopy also affects the growth of the weed (see section 10).

Di Paola and Benvenuti (1993), using chlorophyll luminescence as an indicator of chilling tolerance, found proso millet to be the most sensitive to chilling of the eight weeds they studied.

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(b) Substratum

(i) Primarily crop information

To our knowledge, the species has no very specific substrate requirements. Marinval (1992) considered *P. miliaceum* to be less exacting in its soil requirements than *Setaria italica*. It thrives on the chernozems of Manitoba and the calcareous, clay and sandy soils found in its areas of distribution in Ontario and Quebec.

The loess plateau of Northern China seems to have been the site of origin of the species as a crop (Zeller 2000). It is still a major crop there (Chen et al. 2007), where it is grown in the semi-arid loess hilly region of the loess plateau. The soils in that region originate from calcareous loess included in the Calcic Cambisol group. It is currently grown as a crop in the Central Black Earth Belt in Russia as well as some non-chernozem regions of Russia and adjacent countries (Gashkova 2003–2009).

In a study of the effects of tillage systems on the growth of proso millet as a crop on the Central Great Plains of the USA, improved growth following autumn weed removal by tillage and/or atrazine was attributed to increased soil NO_3^- levels and increased water-use efficiency (Anderson et al. 1986). Investigations into microbial communities and enzyme activities under crop rotations in similar terrain in Akron, CO, were conducted by Acosta-Martínez et al. (2007). The soils there were described as Weld loam; fine smectitic mesic aridic paleustolls. They found that, among other rotation/tillage options, using a crop rotation of corn, wheat and proso millet increased microbial carbon and microbial biomass nitrogen at the 0–5 cm depth, compared with the traditional wheat/fallow rotation [see also Wright and Anderson (2000) in section 7(e)].

Rachie (1975) described the species as being nitropositive, but Senft (1978) reported that, as a crop, proso millet grown on good loam or silt-loam soils has a far lower requirement for supplemental nitrogen (28.02 kg ha^{-1}) than that needed for wheat (67.24 kg ha^{-1}). In the loamy argiustolls of eastern Colorado, Rodriguez et al. (1989) found that, for a proso millet crop, the critical level of supplemental nitrogen, below which a growth response would be expected, was 58 kg ha^{-1}. Phosphorus requirements ranged from 16 kg ha^{-1} for soils with very low soil phosphorus, to zero when phosphorus availability was naturally high (Rodriguez et al. 1989). Kalinová and Moudrý (2003) found that plants responded to nitrogen fertilization by an increase in leaf size; this in turn increased the LAI, which had a positive effect on grain/seed yield. In contrast, Anderson et al. (1986) found that adding nitrogen fertilizer decreased seed production in proso millet.

He and Dong (2001) demonstrated experimentally that in soil that is nutritionally heterogenous there is a plastic response by the fine roots (cf. the coarse 'framework' roots) of *P. miliaceum* in length and surface area, rather than a change in biomass to obtain nutrients. Later, He et al. (2004), using *P. miliaceum* and four soil-nutrient levels, controlled nutrient concentrations in the vicinity of the original plant and the surrounding patch and measured many parameters through the growth cycle of the plants. They demonstrated that plants of proso millet showed a plastic response to a number of fitness components, in addition to a response by fine roots.

Soil salinity is a problem in arid regions of the world and there is interest in salt-tolerant crops. In an experiment to assess variations in salt tolerance among cultivars of *P. miliaceum*, Sabir and Ashraf (2008) showed that two of 18 accessions from Pakistan had some tolerance to a salt concentration of 180 mM in Hoagland's solution at the germination and seedling stages, although weights of germinants and seedlings were less than in the control. The experiment did not continue to later growth stages. Salt is often present in irrigation waters and becomes concentrated in the irrigated soil solution. Magistad and Christiansen (1944) tested the salt tolerance of 48 crops grown on irrigated land west of the Mississippi in the United States. Proso millet was one of the eight least salt-tolerant crops tested.

Balan and Bară (2008) used roots from proso millet seedlings, which had been germinated in Petri dishes, to examine the cytotoxic effects on the root cells of copper acetate and ferrous sulphate solutions of varying strengths, for durations up to a maximum of 48 h. The highest concentration of copper acetate used (0.05%) led to a decrease in cell division. Roots treated for the longest time interval had the fewest cell divisions. Ferrous sulphate treatments resulted in only minor decreases in cell division.

Root length of proso millet seedlings was measured in an experiment by Bona et al. (1993*a*) in Hungary to examine acid-soil tolerance by fourteen genotypes of this species. Limed (pH 5.1) and unlimed (pH 4.1) versions of Porters soil were used; this is a soil type dominated by exchangeable aluminum ions. Of the genotypes used, four were tolerant and four intolerant. The remaining six were intermediate. In a ranking of acid-soil tolerance of cereal species, *Panicum miliaceum* was much less tolerant than rye (*Secale cereale* L.) and oats (*Avena sativa*), but slightly more tolerant than bread wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and durum wheat (*Triticum durum* Desf.) (Bona et al. 1993*b*). These results differ from a review by Bavec and Bavec (2006), which stated that proso millet does not tolerate acid soil and that it prefers sandy-loam soil.

(c) Communities in which the species occurs

(i) Weeds

In Canada, the authors have noted the presence of *Abutilon theophrasti* Medik in the same fields as *P. miliaceum* but assumed that the colonizations by the two species were independent of each other, as both of these warmth-tolerant species edged northwards.

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Setaria viridis (L.) P. Beauv., *Panicum capillare* and *P. dichotomiflorum* may be present in the same fields as *P. miliaceum* (although frequently they occur as separate infestations), but again the authors have assumed this to be partly coincidental and partly a consequence of selective herbicides allowing the build-up of a seed bank of resistant species rather than a formal assemblage of species constituting a community. In surveys of corn fields in Huron County, Ontario infested with Black proso millet in the early 1980s, other common weed species were *Convolvulus arvensis* L., *Equisetum arvense* L., *Asclepias syriaca* L., *Elytrigia repens* (L.) Desv. Ex B.D. Jacks [= *Agropyron repens* (L.) P. Beauv.], *Setaria viridis*, *Amaranthus retroflexus* L., *Abutilon theophrasti, Panicum capillare*, *Polygonum convolvulus* L., *Ambrosia artemisiifolia* L. and *Salsola kali* subsp. *ruthenica* (Iljin) Soó (P.B. Cavers and research associates, unpublished data). A subsequent survey conducted in the same decade in other counties of southern Ontario had the following weeds, starting with the species in the greatest number of fields (28) and progressing to those in the fewest (3): *Setaria viridis*, *Chenopodium album* L., *Asclepias syriaca*, *Equisetum arvense*, *Amaranthus retroflexus, Echinochloa crusgalli* (L.) P. Beauv., *Elytrigia repens*, *Cirsium arvense* (L.) Scop., *Convolvulus arvensis*, *Panicum capillare*, *Ambrosia artemisiifolia*, *Cyperus esculentus* L., *Polygonum convolvulus*, *Arctium minus* Bernh. subsp. *minus*, *Malva neglecta* Wallr. and *Phleum pratense* L. (P.B. Cavers and research associates, unpublished data). In Prairie Weed Surveys in Canada (Thomas et al. 1998; Leeson et al. 2002, 2005), proso millet was primarily listed as a weed of oat crops in Manitoba.

Cochrane (1984) described *P.miliaceum* subsp. *ruderale* in Wisconsin as being locally abundant in cultivated fields of *Zea mays* and *Glycine max*, where it is invariably associated with *Setaria faberi* Herrm., *S. viridis*, *P. dichotomiflorum* and *Abutilon theophrasti*.

In Hungary, Lehoczky et al. (2006) investigated the impact of weeds on soil moisture content in maize (corn) plots. Early in the growing season they found proso millet to be the second most abundant weed (after jimsonweed, *Datura stramonium* L.). Although proso millet increased its presence to about 10% of the weed flora as the season progressed, by the end of the season it was far behind jimsonweed (50%) and wild hemp, *Cannabis sativa* L. (25%). Most other weeds of the early floral assemblage had diminished to about 1.7% or less by the last sampling date. Proso millet has been reported as part of a plant community in a village in Eastern Saxony, Germany, together with *Ambrosia artemisiifolia, Malva neglecta* and *Urtica* sp. (Gehlken 1998).

In Mongolia, independent of soil conditions, the grasses *Panicum miliaceum, Setaria viridis* and *Avena fatua* L. were widely distributed in the Orchon-Selenga-Basin and were found in each of five listed weed associations from that area (Hilbig 1982).

6. History

(a) Weed/crop origins of *P. miliaceum*

The wild ancestor(s) of *Panicum miliaceum* were unknown as recently as the late 1980s (Sakamoto 1987; Nesbitt and Summers 1988). Hunt et al. (2014), using nuclear and chloroplast DNA sequences from *P. miliaceum* and four of its many diploid and tetraploid relatives, were able to construct phylogenies of these. Further molecular investigation based on these phylogenies supported the allotetraploid origin of the species, with the maternal ancestor being proposed as either *P. capillare* or a close relative. The other genome was described as shared with *P. repens* L., itself an allopolyploid (see section 9). This work indicates the need to characterize other genomes within the genus. Since *P. capillare* is a New World native, this poses questions beyond the scope of this paper.

The history of many crops is that of wild or weedy species being brought into cultivation through a process of selection for desirable characteristics, such as larger seeds/grains, non-disarticulating inflorescences and limited (to no) dormancy. Wild and weed types would have co-existed with these new crops, oats and wild oats being an example, and sometimes individual plants in the crop would have maintained some of the wild or weedy traits, such as seed dormancy, so that their genotypes would persist in the fields the following year or longer as volunteers [see for example Smith (1995) and Levetin and McMahon (2008)].

There is some discussion in the literature about whether this pattern of selection from and coexistence with wild or weedy relatives is true for proso millet as a crop. The plant we know as the Black biotype is very probably *P. miliaceum* var. *ruderale* Kitag., described by Kitagawa (1937), as a wild plant, and as part of the flora of Manchuria and Boreal China. de Wet (1992) considered this to be the progenitor of *P. miliaceum* race *miliaceum* (see section 2). In contrast, Scholz (1983) thought that this biotype, *Panicum miliaceum* subsp. (sic) *ruderale*, with its disarticulating spikelets, was the result of repeated reverse mutations in *P. miliaceum* subsp. *miliaceum* (see section 4). Bartsch et al. (1993) thus used this Black biotype as an example of a reversion of a cultigen to its wild-type form. In one paper, Harlan (1992) considered *Panicum miliaceum* to be a good example of a species where the weed was derived from crop biotypes. This was based on the suggestion that if disarticulation was controlled by one gene, reversion to a plant with shattering panicles was very possible. This does not take into account other weedy characteristics (see for example Cavers and Bough 1985) such as the dormancy and smaller seeds that *P. miliaceum* subsp. *ruderale* possesses. Barton et al. (2009) commented that we know very little about how domestication of this species occurred, since it appeared early and suddenly from an 'unidentified wild progenitor'. Hunt et al. (2008) also commented that

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the status of *P.miliaceum* subsp. *ruderale* as a wild species or a feral derivative of a crop remains an open question. Hunt et al. (2014) have been investigating possible progenitors (see section 9).

Weedy characteristics occasionally do appear in cultivated biotypes [e.g., seed dormancy in the Golden biotype, mentioned in section 8, and a tendency for shattering in at least one Crown population in Ontario (Bough et al. 1986)]. During the transition from hunter-gathering to agriculture, the distinction between crop and weed may not have been sharp or applied at all among Neolithic people (Harlan 1975; Hunt et al. 2008).

Globally, proso millet is amongst the oldest cereals. Its use as a food in India, China and Egypt preceded written records (Anderson and Martin 1949). However, in the literature, the term 'millet' is used broadly for up to 14 species, so not all references to 'millet' refer to *P. miliaceum*. Foxtail millet (*Setaria italica*) and proso millet were both cultivated as staple crops in the Far East (China, Japan, Russia and India), and distinguishing each in archaeological sites was difficult. Lu et al. (2009*a*) examined the phytoliths (silica bodies) of these two species, and found five key diagnostic characteristics by which to distinguish each. This will now enable investigators to determine which of the two was/is present in a particular site.

(b) Site(s) of origin

Proso millet may have been brought into domestication in more than one general area. Both Hunt et al. (2008) and Crawford (2009) noted that because *P. miliaceum* has been shown to occur contemporaneously in both Europe and North China at about 8000 cal BP (calendar years before present). The crop may have been brought into cultivation more than once. Harlan (1992) noted that the wild progenitors of both proso millet (*P. miliaceum*) and foxtail millet (*Setaria italica*) ranged across Eurasia and thus independent domestication seemed likely. Harlan (1976) had previously commented that species with very wide natural distributions, in which group he included proso millet, are very likely to have been domesticated more than once. Hunt et al. (2008) discussed the unusual geographic pattern for both of these species in the archaeobotanical record. Both are known from Yellow River Valley sites in China from 8000 to 9000 cal BP. *Panicum miliaceum* has been reported in Eastern Europe and the Caucasus from sites of a roughly similar age. So far, neither species has been reported for a similar time frame from central Asia, which separates these two areas. Neither of two proposed hypotheses, multiple domestications, or domestication in China or Eastern Europe and rapid spread, would explain the absence of contemporaneous sites between the two known areas of domestication [see Hunt et al. (2011) below].

(c) Archaeological history of *P. miliaceum*

(i) 10 000–5000 cal BP

China

In a posthumous translation, Vavilov (1992) stated that 'the native land of the millet', both *P. miliaceum* and *Setaria italica*, was Eastern Asia, in China and contiguous countries. He also mentioned that in Mongolia there are *P. miliaceum* plants characterized by easily shed seeds. Proso millet is known to have been grown in Yang-shao sites in southern Shensi and Shansi provinces 6000 cal BP (de Wet 1981). Later, de Wet (1989) stated that the species' progenitor is native to Manchuria. Bishop (1933), Harlan (1992) and Zeller (2000) each reported that proso millet was present in the Chinese Neolithic. It is one of the oldest crops and has played a major role as a foodstuff in the development of Chinese civilization and culture Hu et al. (2008).

The precise location of the centre of proso millet domestication in China is still debated (Hunt et al. 2011). Evidence to date suggests that the centre of origin and place of earliest domestication might be the Loess Plateau of northern China. Li (1970) considered this loess region, of which the Tsin-ling mountain range forms the southern boundary, to be the area in which millet, Huang Mi — "yellow grain", originated. Lu et al. (2009*b*) dated broomcorn [proso] millet material, including phytoliths, from Cishan, a village in the Yellow River area of North China to 10 000 cal BP, which provides the oldest clear evidence of millet cultivation to date. Large amounts of *P. miliaceum* were found in storage pits at this site, showing it to have been an important grain crop. Crawford (2009) pointed out that this dating places the timing of agricultural origins in North China at the Pleistocene–Holocene transition, similar to that of early agriculture in Southwest Asia, Mexico, and South America.

Barton et al. (2009), using isotopic analysis, demonstrated that by 5900 cal BP *P. miliaceum*, a C_4 grass with high δ^{13} C values, formed part of the diet of humans, dogs and pigs at the Dadiwan site in northwestern China, an area in which climate restricts growth of C_4 plants to the summer months. The implication is that millet would have had to have been planted and stored in order to provide a consistent and significant part of their diet.

Hunt et al. (2008), in an extensive and thorough review of pre-7000 cal BP sites in the Old World, encompassing the early to late Neolithic, documented a range of sites in which proso millet has been recorded. *Panicum miliaceum* (and not just '*Panicum* sp.') was recorded as being present at 31 sites. Three of these were in China, one at the Dadiwan site in northwest China (the loess region), one in Inner Mongolia and one in the Shangdong province, which is bordered by the ocean and the eastern edge of the north China plain. The other sites were to the west of China [see following subsection, *Eastern Europe, including the Caucasus and beyond*].

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Following the publication of 25 microsatellite loci for *P. miliaceum* by Cho et al. (2010), Hunt et al. (2011) were able to use these markers to conduct analyses of 98 accessions of *P. miliaceum* landraces from across Eurasia in an attempt to elucidate the centre(s) of domestication of this species. Although the task was complicated by the tetraploid genome and lack of sequence data, their results showed two geographic clusters with either an eastern or western focus, with moderate genetic differentiation between the two groups. The eastern group has a centre of distribution in China, which is in accordance with the archaeobotanical evidence that proso millet was first cultivated in northern China, even though the precise location within this area is still being debated.

Both Hunt et al. (2008, 2011) and Crawford (2009) noted that because *P. miliaceum* has been shown to occur contemporaneously in both Europe and North China at about 8000 yr cal BP, there may have been an independent domestication event in Europe.

The western cluster is described in the following subsection.

Eastern Europe, including the Caucasus and beyond

Hancock (2012), citing Hunt et al. (2008), noted that the evidence of domestication dating from 8000 to 7500 cal BP found in Europe and the Caucasus supports the concept that proso millet was brought into domestication independently in at least two regions.

Lisitsyna and Prishchepenko (1976, 1977) stated that in the arid Caucasus regions of the former USSR, proso millet was cultivated from 7000 cal BP. The 28 non-China (European + Caucasus) sites listed by Hunt et al. (2008) within this time frame were in Azerbaijan, Bulgaria, the Czech Republic, Georgia, Germany, Greece, Moldova, Poland, Romania, Slovakia and Ukraine. Some of these sites were represented by only one or two seeds, thus we should use caution in interpretation.

Beyond these areas, in Africa, one *P. miliaceum* find was recorded in Egypt in this time frame (Litynska-Zajac 1993).

The western [cf. eastern, see subsection *China* in 6(c)(i)] geographic clustering of sites revealed by Hunt et al. (2011) was less genetically diverse. The data can be interpreted as an area of independent domestication in eastern Europe/central Asia or as the possibility that domesticated proso millet was taken westward as farming societies expanded. Their accessions did not include any of *P. miliaceum* subsp. *ruderale*, but the techniques they used could allow inclusion of this subspecies in future work.

Excavations in Poland showed *P. miliaceum* to have been used both in the Neolithic period and early Middle Ages (Klichowska 1972) and it was present at Gomolava, a settlement near Beograd (Belgrade), Yugoslavia, from 5800 to 4400 cal BP, by which time it was well represented (van Zeist 1975).

Hunt et al. (2008) also acknowledged the difficulties of inferring the status (domesticated/wild; crop/weed) of *P. miliaceum* at these sites. Because some of the records are for single grains, the speculation might be that these were not widespread crops, or could, in fact, have been weeds in the crops. The timing of these events is roughly at the end of the last glacial period. Cunniff et al. (2008) postulated that increasing ambient CO_2 levels in the warmer post-glacial period provided a 'global trigger' that caused increases in the growth rates of wild crop progenitors. Their experiments, using controlled environments on *P. miliaceum* subsp. *ruderale* and other early C_4 crop species, resulted in such an increase in biomass. There was also an accompanying reduction in transpiration rate, which would confer better water-use efficiency on the plants. No such increase in biomass occurred when Cunniff et al. (2008) compared post-glacial to current CO_2 levels experimentally.

(ii) 5000 to 2000 cal BP

China and Asia

Proso millet, along with foxtail millet, was important to the Chinese agricultural societies that developed into the earliest urban societies in China between 4500 and 3800 cal BP (Crawford 2009). An et al. (2014) noted that the Qijia Culture, based on millet agriculture, was distributed throughout the western China Loess Plateau (WLP) from 4300 to 3800 cal BP. Remains of cultivated *P. miliaceum* were present in the High Himalayas (western Nepal) in a burial cave used from 2400 cal BP to 1900 cal BP and were more abundant in later sites in the same area (Knörzer 2000).

The Middle East

By 3550 cal BP, proso millet (broomcorn millet) was being grown in Iran as a crop (Nesbitt and Summers 1988) and in Northern Iraq by 2700 cal BP (Helbaek 1966). However, in the list of records that Nesbitt and Summers considered reliable, the status of the species at two of the earliest sites listed (Early Bronze Age, 5000 cal BP, Macedonia; and 4400–3800 cal BP, Iran) was that of a 'scarce weed' and 'a few grains of broomcorn millet: weed', respectively. Later records referred to it as a crop.

Africa

Alphonse De Candolle (1806–1893), described as an 'armchair plant geographer' in Barbour et al. (1987), considered the wide-ranging ancient literature on the possible crop origins of proso millet and decided that it probably had an Egypto-Arabian origin (De Candolle 1886). Subsequent work [outlined in subsection *China and Asia* in 6(c)(ii) above] has discounted this possibility but this grain crop did appear early in the Egyptian archaeological record. Copley et al. (2004), using $\delta^{13}C$ analysis, have shown proso millet to be the earliest C_4 grain grown at a Nubian site (Qasr Ibrim) in Egypt by the Napatan period (2700–2300 cal BP). The site in Egypt at Nabta Playa, mentioned by Hunt et al. (2008), was earlier [about 9500–8500 cal BP, see the *Eastern*

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Europe, including the Caucasus and beyond subsection in 6(c)(i)]. Weber and Fuller (2008) found it curious that the earliest finds of a domesticated millet in Nubia were not of an indigenous African species. *Panicum miliaceum* plant material has also been found in a Neolithic site in Amiant, Upper Egypt (Litynska-Zajac 1993). We could not find any archaeological records of this species being grown elsewhere in Africa during this time frame, nor in India where it is now grown as a crop in many areas.

Europe

In Europe, archaeological studies document the presence of proso millet at many excavation sites from 5000 yr ago. These are presented briefly, by country/area, in roughly chronological order below.

Italy: Bellini et al. (2008) found seeds of *P. miliaceu*m at Bronze-age sites in Tuscany. Middle to late Bronze Age would be ~4000–3000 cal BP. Arobba et al. (2003) discovered remains of *P. miliaceum* in Early Iron Age (2800–2700 cal BP) hill forts at Monte Trabocchetto, Liguria.

French Alps: Jacob et al. (2008) inferred that millet was being cultivated around 3700 cal BP, from the discovery of a fossil molecule of miliacin (synthesized by *P. miliaceum*) in sediment cores from Lake Le Bourget in that area.

Austria: Heiss and Oeggl (2005) found carbonized caryopses of *P. miliaceum* dated to the late Bronze Age (approximately 3410–2930 cal BP) at a site in the Inn valley.

Portugal: Pinto da Silva (1976) noted the presence of proso millet from the late Bronze Age until about 2100 BP.

Southern France: Bouby et al. (2005) found seeds dating to the Late Bronze Age as components of grain stores in two caves at Balme Gontran and Baume Layrou. In contrast, Marinval (1992) reported that the Iron Age was the period in which *P. miliaceum* apparently reached this area.

Sweden: Hjelmqvist (1955) reported grain/seed impressions of *P. miliaceum* on pottery dated from the Late Bronze Age.

Hungary: Dálnoki and Jacomet (2002) reported that spelt wheat and proso millet were the dominant cereals at a "Late Iron Age" (no time frame given) site in Budapest.

Switzerland: King (1966) documented evidence of millet in lake dwellings 2000 cal BP.

Greece: Nesbitt and Summers (1988) stated that evidence of this species has been found in Hellenistic (2066 cal BP) sites.

(iii) 2000 cal BP–present
Europe — later sites

Scandinavia: Hultén (1964) stated that 2000 yr ago *P. miliaceum* was cultivated this far north in Europe.

Turkey: Nesbitt and Summers (1988) reported the presence of *P. miliaceum* at an Asian Turkish site (Aşvan Kale) in Roman times (1900 cal BP).

France: Bouby and Marinval (2004) recorded the presence of the species at a Roman cremation site (the Bernard Maître site) in Beaumont, Limagne from late 1900–1800 cal BP.

Italy: Meyer (1980) noted that carbonized seeds of proso millet were found at Pompeii and Herculaneum — sites destroyed by the eruption of Mount Vesuvius in 1936 cal BP (79AD).

England: Willcox (1977) reported that seeds from 1800 cal BP were found in waterlogged Roman sites in London, England.

Poland: Bieniek (1999) reported remains of cultivated *P. miliaceum* from a Roman Iron Age (approximately 2000 cal BP) site in central Poland. Szydłowski and Wasylikowa (1973) reported that proso millet seeds were found in 1200–1100 cal BP sites at Lubomia, southern Poland. These were present in small amounts in samples of rye and thus possibly contaminants or weeds. Dembińska (1976) found millet seeds dating from the Middle Ages (1100–700 cal BP), at sites in Gdansk.

Bohemia (Czech Republic): Holý (1975) reported that seeds of proso millet were found in 600 cal BP refuse pits.

Hungary: Lágler et al. (2005) successfully extracted DNA from seed remains of proso millet found in a 15th century (500 cal BP) site in Budapest. Of the 20 modern cultivars with which this material was compared, it most closely resembled a Russian cultivar (Omszkoje) that has red and yellow seeds.

Russia: Panicum miliaceum is still an economically important crop long grown in the former USSR (Europe and Asia). It was one of the "major" species collected by N. Vavilov on his collecting missions between 1916 and 1940 (Loskutov 1999).

North America
As a crop

The crop made its way to North America more recently. It was recorded as a crop grown in Canada as early as 1600 AD [Bertin et al. (1971) in O'Toole (1982)]. Borodin (1929) wrote of immigrants who came from Southern Russia and Ukraine in the mid-nineteenth century, looking for lands similar to their native Steppes, and who "found their Kieff" in North and South Dakota in the United States, and in Manitoba, Canada. There they were able to grow their wheat, flax, sunflowers and 'proso'. Seventeen varieties that the Russian immigrants grew are listed by Borodin (1929), some named "black" or "red" but no potentially weedy characteristics are mentioned. Hinze (1972) also thought that proso millet was probably brought to the United States by Russian immigrants. R. Néron (personal communication) reported that it was grown in Canada in the 17th century. He believed that proso millet, including the Dark red biotype, was probably brought to Quebec by early

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settlers (it was reported as a crop in France in the period from 1500 to 1750).

Proso millet was used in Canada as a forage crop in the early 1900s (Dekker et al. 1981). The description of 'Crown' proso millet, accompanying its registration in 1937 (supplied by the breeder, T.M. Stevenson, Dominion Experimental Farms Service, Ottawa, ON) said that its breeding resulted from repeated mass selection from seed stocks obtained from Manchuria in 1928 [see sections 3(b) and 3(c)].

As a weed

Canada

In the early 1970s, there were scattered reports of a black-seeded grass, resistant to herbicides used in arable crops in southern Ontario (Dekker et al. 1981). There is strong evidence to suggest that the Black biotype entered Canada from the United States on used farm machinery in the 1970s (O'Toole 1982; Bough et al. 1986); the colloquial local name ascribed to the weed is the name of the farmer who imported the equipment. It has spread rapidly in southern Ontario and southwestern Quebec from that time until the present. A few years later, when farmers in Southern Ontario were experiencing serious infestations, the present authors described the complexity of the crop/weed nature of proso millet to the Canadian Pest Management Society (Anonymous 1988*b*). This biotype was undoubtedly the "wild-proso millet", which was spreading rapidly in the United States Corn Belt at that time (see below).

United States

References to *P. miliaceum* as a new weed in the USA, present as a volunteer in crop fields and along fencerows and roadsides began to appear in the 1920s. Hansen (1926) reported it from Fulton County, Indiana, Stevens (1946) noted its appearance in North Dakota and Steyermark and Swink (1955) included it in a list of taxa new to the Chicago region in Illinois (see Table 3). Descriptions matched those of crop-like biotypes.

Wide-scale infestations of a weedy proso millet in Minnesota and Wisconsin dating from 1970 were reported by Strand et al. (1973) and Strand and Behrens (1979) as "wild proso millet". Their descriptions corresponded to the black-seeded plant described by Kitagawa (1937) as a wild variety, (*P. miliaceum* var. *ruderale*) growing in Manchuria and as a weedy species (*P. spontaneum*), by Zhukovsky (1964). Similar reports of weedy populations of proso millet in Eastern Europe (e.g., Mansfeld 1952; Terpó-Pomogyi 1976) led us to conclude that this weed originated in Asia or Eastern Europe and probably reached the United States as a contaminant of seed grain. By 1979, wild-proso millet was described as the greatest single threat to row crop production in southern Wisconsin and Minnesota (Harvey 1979). By 1990, wild-proso millet had infested millions of hectares in Wisconsin, Minnesota and Michigan as well as 11 000 ha in Colorado and 20 000 ha in Nebraska (Westra et al. 1990). At that time, Colorado represented the southern boundary of wild-proso millet infestations in the United States, but there were also small spreading populations in Wyoming, Idaho, Oregon and Washington (Westra et al. 1990). Since then, Colosi and Schaal (1997) have reported additional accessions from North Dakota, South Dakota and Utah (see Table 3).

New Zealand

A very recent invasion by black-seeded proso millet has occurred in New Zealand. It was first recorded after 1995 and is now widespread (James et al. 2011), especially on the North Island (T. James, personal communication). There were multiple introductions of proso millet in the 30–40 yr period before 1995 but all of these were thought to be crop biotypes and none of them has persisted in New Zealand (James et al. 2011).

Globally, current distributions of the crop and weed are described in section 4.

7. Growth and Development

(a) Morphology

(i) Mostly weeds

Plant height and amount of tillering depend on the crop with which the weed is growing. The Black biotype can reach 2 m or more in corn but only becomes 15–40 cm tall in barley (Bough et al. 1986). Black-seeded plants tend to be about 100 cm tall in white beans (*Phaseolus vulgaris*) (Dekker et al. 1981). Bough et al. (1986) found that tillering is most extensive in low crops such as soybeans and at low weed-plant densities and, in general, is least in corn crops.

Bough et al. (1986) described height and tillering in the biotypes they studied. A typical stand of the Golden biotype is 80–90 cm tall but one Ontario population was at least 160 cm tall. Tillering is prevalent in this biotype. Height of the Crown biotype is fairly uniform, about 110–140 cm in corn and slightly shorter in soybeans. The Orange-red biotype is comparatively short, rarely more than 40 cm in Ontario but about 70 cm in Manitoba and Quebec. It tillers profusely, particularly towards the end of the growing season. The White biotype grows to 100–110 cm tall and has sparse tillering. The Elgin biotype is the largest and most robust but also the slowest to mature. Its height is 140–160 cm. It has large leaves, large strong culms, and is strong enough to support seed-eating finches (*Carpodacus* spp.) while they feed.

The Dark red biotype is unique in that flowering stems lying horizontally (after lodging, etc.) can produce vertical shoots from the nodes (Bough et al. 1986).

In young seedlings of *P. miliaceum*, the first internode lengthens, which enables successful germination and emergence from depths of 5 cm or more (Strand et al. 1973).

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Proso millet has a fibrous root system that penetrates the soil to a depth of up to 150 cm and spreads laterally to between 100 and 120 cm. Most of the root system is formed prior to panicle emergence (Gashkova 2003–2009).

(b) Perennation

Proso millet is an annual grass, arising from seed each year (Dekker et al. 1981).

(c) Physiology and biochemistry

(i) Mostly crops, weed information near the end of this subsection

In general, darker seeds have heavier husks and suffer less imbibition damage, measured as electrolyte leakage (Khan et al. 1996). According to Lorenz (1983), dark-husked crop varieties have higher tannin content in the grains than those of lighter-husked varieties. Phytate and tannin contents of the grain diminish when the husks are removed. Lorenz (1983) also recorded large differences in crude fibre content among the crop varieties he studied. Lorenz and Hinze (1976) compared the functional characteristics of starches from six proso millet varieties, two foxtail millet (*Setaria italica*) varieties and one variety each of wheat and rye. All proso millet starches had higher values for water-binding capacity and gelatinization than wheat starch. Four proso millet varieties produced swelling-power values that were similar to that of wheat starch; the other two proso millet varieties had higher values, similar to that from rye starch. Percent solubility values at 90 °C for proso millet varieties were lower than that of wheat starch, with one exception, which had more than twice the solubility of any other proso millet variety.

In a comparison of 20 commercial grain products from eight grain species, whole-grain grits of *P. miliaceum* had comparatively low values for total phenolic acids but a similar composition of the different phenolic acids (Mattila et al. 2005). The value for caffeic acid was the lowest of all the samples.

Rudramuniyappa and Panchaksharappa (1978) made a detailed histochemical study of seed development in *Panicum miliaceum*. They found that the zygote is rich in RNA and proteins, as are the shoot and root apices during differentiation, but these substances decline in other tissues as the seeds mature. In the proembryo, RNA and proteins increase and persist in the embryo proper. Lipid bodies are abundant and distributed uniformly in all layers of the embryo from the quadrant to the globular stage, but at later stages they are more confined towards the basal region. The early endosperm is rich in lipids but, as it develops, lipids decline to a low level. The embryo proper is rich in reducing sugars, as are the young shoot-root apices and their axis. They also found that the early endosperm is rich in lipids, but these decline to a low level as it develops.

The reported nutritional composition of proso millet seeds varies slightly. Anderson and Martin (1949) compiled data from three sources, which show approximately 10%–12% protein, 1%–3.4% fat and 71%–75% carbohydrate. Data from Kaume (2006) are similar: 11% protein, 4.2% fat and 72.9% carbohydrate, together with 8.5% dietary fibre. Kaume's paper also gives details of the mineral and essential amino acid composition of the seeds.

Kalinova and Moudry (2006) evaluated seven Eastern European varieties of proso millet and they agreed that the usual protein content of proso millet seeds is between 11.3% and 12.7%, but the highest value they obtained was 17%. Wheat has similar protein content, around 11%, but proso millet seeds are significantly richer in the essential amino acids leucine and methionine. Leucine content was twice that of wheat and methionine content was three times higher (Kalinova and Moudry 2006). There were significant differences among the seven varieties in protein quantity and quality (Kalinova and Moudry 2006).

Cell wall composition and biogenesis in crop plants of *Panicum miliaceum* were studied by Carpita et al. (1985). They found that the composition of tissues and cell suspensions of *P. miliaceum* was similar to those of other graminaceous species. Also, walls of embryonal cells contained much higher proportions of total hemicellulosic sugars than walls of developed or elongated cells, very similar to the pattern in corn coleoptiles. Carpita (1989) made a more detailed study of the chemical composition of the pectin fraction of growing cells of corn and proso millet. He found that the neutral sugar profiles of the two preparations were similar. Both had about 5% rhamnose and a total of about 30% arabinose and xylose. The corn pectin fraction contained about 36% uronic acid, which was mostly converted to galactose during chemical reduction. In contrast, the proso millet pectin fraction was only about 25% uronic acid, which was primarily compensated for by slight enrichment of arabinose and galactose.

The principal components of leaf waxes of *Panicum miliaceum* are hydrocarbons, esters, aldehydes and alcohols (Tulloch 1982). The esters include esters of triterpene alcohols and the major free alcohol is dotriacontanol. Free triterpene alcohols were also found.

In India, Sinha and Saran (1992) examined the leaves of six C_4 *Panicum* species to determine the anatomical structure of the photosynthetic pathway. All of these species possess a chlorenchymatous bundle sheath. In *P. miliaceum* and three other species, there are intervening cells between the metaxylem and the chlorenchymatous bundle sheath cells. This type of anatomical arrangement implies that the species has a NAD-malic-enzyme type of C_4 metabolism. In such NAD-ME type C_4 plants, the bundle sheath mitochondria are functionally differentiated into photosynthetic organelles, containing some enzymes involved in the C_4 dicarboxylate cycle.

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Taniguchi et al. (1995) studied three isozymes of aspartate aminotransferase (AspAT) in proso millet. The cytosolic and mitochondrial isozymes (cAspAT and mAspAT) are major components whose activity and protein levels increased selectively during recovery from a nitrogen deficit. The third isozyme (pAspAT), localized in plastids, is considered a minor isozyme and its level remains unchanged during recovery from a nitrogen deficit. A group of C_4 species, including *Panicum miliaceum*, utilize three compounds (a NAD-malic enzyme, the mitochondrial isoenzyme mAspAT and a NAD-malate dehydrogenase) to decarboxylate C_4 acids (Kagawa and Hatch 1975). These three compounds are localized in the mitochondria of bundle sheath cells. A more detailed study of regulation of the NAD-malic enzyme in proso millet is found in Chapman and Hatch (1977).

In Japan, Ohnishi and Kanai (1987, 1988) measured the uptake of glycerate and pyruvate into intact chloroplasts isolated from mesophyll and bundle sheath protoplasts of proso millet. Chloroplasts from both sources had similar rates of light-enhanced glycerate uptake even though glycerate kinase, the glycerate metabolizing enzyme, was undetectable in bundle sheath chloroplasts, whereas kinase activity in mesophyll chloroplasts was significant (Ohnishi and Kanai 1988). Chloroplasts from both sources had similar slow rates of pyruvate uptake when they were incubated in darkness, but when incubated in the light the mesophyll chloroplasts had a very rapid and greatly enhanced pyruvate uptake, whereas the bundle sheath chloroplasts did not show this enhancement (Ohnishi and Kanai 1987).

Samples of fresh and decomposed dissolved organic matter (DOM) from ten different plant (crop) sources were compared by Hunt and Ohno (2007) in Maine. Proso millet had the highest fresh weights and highest DOM apparent molecular weight (MW_{AP}) of the five crop species that were field-weathered. It also had the highest humification index (HIX).

Aarati et al. (2003) found that finger millet (*Eleusine coracana* Gaertn.) and *Panicum miliaceum* are relatively tolerant to increasing levels of salinity [in contrast to findings of Magistad and Christiansen (1944) and Sabir and Ashraf (2008); section 5(b)] and both of them have higher levels of expression of an ABA responsive 21 kDa protein than cucumber (*Cucumis sativus* L.) and other salinity-sensitive species. In fact, cucumber did not show any detectable level of expression of this protein.

Animal wastes from intensive farming are usually spread on fields for fertilization in many parts of the world and these wastes contain drugs that pollute the soil (Migliore et al. 1995). One such drug, sulphadimethoxine, altered normal post-germination development and growth in three species, the C_4 plants *Panicum miliaceum* and *Zea mays* and the C_3 plant *Pisum sativum* L. The magnitude of the toxic effect depended on the bioaccumulation rate and was higher for the C_4 species.

Linoleic acid was isolated from methanol extracts of proso millet as a histone deacetylase inhibitor that showed noncompetitive inhibitory activity towards histone deacetylase and potent cytotoxicity towards human leukemia and prostate cancer cells (Aburai et al. 2007). These authors concluded that millets containing linoleic acid might have anti-tumor activity.

(ii) Crops and weeds

Panicum miliaceum is one of a few species that cause hepatogenous photosensitizations in lambs that graze upon their foliage [Miles et al. 1993; see also section 3(a)]. The resulting condition is similar to alveld, a disease appearing in grazing pastures where lambs ingest leaves of *Narthecium ossifragum* (L.) Huds. Both *P. miliaceum* and *N. ossifragum* contain steroidal saponins. The saponins in proso millet are derived mainly from diosgenin and yamogenin. The diseases appear after the saponins are ingested by the sheep and crystalloid material is deposited in and around the bile ducts of the liver; this leads to photosensitization (Miles et al. 1993). Of more importance to humans are the infrequent but severe anaphylactic reactions that individuals may suffer after consuming millet-containing food (Bohle et al. 2003). In their study, these authors found that all of the affected people kept cage birds. They concluded that proso millet plays an important role as an inhalant allergen for people with a predisposition to this allergy. A sensitization to proso millet may subsequently also cause the food allergy.

Chlorophyll fluorescence was measured as an indicator of chilling tolerance in eight weed species by Di Paola and Benvenuti (1993). *Panicum miliaceum* had the least chilling tolerance of the eight species (i.e., was the most sensitive). Zauralov et al. (1994) exposed 9-d-old seedlings of two cultivated varieties of proso millet, differing in cold resistance, to chilling at 2 °C for periods of 0.5 to 24 h. Chilling enhanced exosmosis and lipid peroxidation, decreased intracellular pH and reduced plant height and weight as well as leaf surface area. The magnitude of the observed changes depended on the inherent cold resistance of the cultivar and the duration of chilling.

(iii) Weeds

In a greenhouse study, the responses of two crop species, corn and soybean, and three weed species, velvetleaf (*Abutilon theophrasti*), redroot pigweed (*Amaranthus retroflexus*) and wild-proso millet, to applications of five naturally occurring allelopathic chemicals, salicylic acid, *p*-hydroxybenzoic acid, caffeine, hydroquinone and umbelliferone, were tested (Shettel and Balke 1983). At an application rate of 11.2 kg ha^{-1} the allelochemicals inhibited the weed species more than the crop species. At that rate, wild-proso millet was reduced significantly by *p*-hydroxybenzoic acid, caffeine and umbelliferone. The authors suggested that in agro-ecosystems these

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chemicals could inhibit the growth of weed, but not crop, species. Some cucumber accessions have shown allelopathy to proso millet in the field [see section 13(c)].

Peterson et al. (1997) tested 12 different synthetic sucrose esters for their ability to inhibit the germination of seeds of *Panicum miliaceum* and velvetleaf. Tests in Petri dishes revealed that ten of the synthetic sucrose esters could cause more than 90% inhibition of germination in *P. miliaceum* when applied at a concentration of 100 ppm and one of these esters could cause 80% inhibition at a concentration of 10 ppm. Seeds of velvetleaf were affected to nearly the same extent at a concentration of 100 ppm but had less effect at lower concentrations. These authors pointed out that field evaluation is necessary to determine whether the synthetic sucrose esters could be used to control *P. miliaceum* when it occurs as a weed in crops.

(d) Phenology

(i) Weeds

Most seeds of the Black biotype remain dormant on or in the soil during their first winter in Ontario, then germinate and emerge between mid-May and mid-June (O'Toole 1982). Seedling emergence of the Black biotype continues intermittently throughout the growing season (Bough and Cavers 1987). Emergence of Canadian biotypes (Black and crop-like weeds) that set viable seeds occurred from May to August, however emergence in early June resulted in optimal growth (P. Cavers and M. Kane, unpublished data). In New Zealand, late-germinating (autumn) plants were able to set seeds within 5 wk of emergence (James et al. 2011). In Ontario, some seeds of the Golden biotype germinate shortly after dispersal during mild autumn weather (Bough et al. 1986) but they do not produce viable seeds (M. Kane and P. Cavers, personal observations). A few seeds of other crop-weed biotypes can survive one winter in or on the soil and they typically germinate with the crop the following spring. The White biotype exhibits the least overwinter survival in the field but its seeds, like those of other biotypes can survive as impurities in crop seed collections and then be sown and germinate with the crop in the following growing season (Bough et al. 1986).

In Colorado, Anderson (1994*a*) recorded the emergence pattern of a weed community of 16 species in wheat stubble for each of seven successive years from 1 Apr. to 31 Aug. Wild proso millet was one of six species that emerged each year and comprised over 80% of the total seedlings counted. There were two peaks of emergence, late April-early May and late May-early June. Wild proso millet, *Setaria viridis*, *Amaranthus retroflexus* and *A. hybridus* L. predominated in the second peak of emergence.

There is very little published information on the date of panicle emergence. However, in barley and corn fields in Huron County, Ontario the first panicles of the Black biotype appeared between 7 and 21 July in 1980 (O'Toole and Cavers 1983). In the white bean field of this study, planted later, panicles did not appear until 5 Aug.

(e) Mycorrhizae and bacterial symbioses

(i) Crops and weeds

Plenchette et al. (1983), used soils collected from a nursery in Pont-Rouge, Quebec, Canada in which *P. miliaceum* had been grown the previous year. The root fragments of this species in the soil were described as 'intensely mycorrhizal' but no species were named.

The presence of arbuscular mycorrhizal fungi (AMF) can be inferred by the concentration of glomulin, an AMF product, in soils (Wright and Anderson 2000). These authors measured soil glomulin content under different crop rotations in the Central Great Plains regions of the USA and found that soils from a rotation of wheat–corn–proso millet had significantly higher glomulin values than soils from other rotations.

Mycorrhizal fungi need a compatible host to complete their life-cycle and sporulate. They are not generally considered host-specific, but some host-fungus combinations may be better (Silva et al. 2005). In a greenhouse experiment conducted in Brazil to evaluate the effects of nutrient solutions and buffers on AMF sporulation, Silva et al. (2005) used inocula of *Gigaspora margarita* Becker and Hall, *Scutellospora heterogama* (Nicolson & Gerdemann) Walker & Sanders and *Glomus etunicatum* Becker & Gerdemann and two hosts, *P. miliaceum* and sorghum. These plants were grown in a sterile substrate. *P. miliaceum* as a host elicited higher sporulation in all treatments than those in which sorghum was the host. Their results show that the three fungal species used are able to colonize *P. miliaceum*.

Rhizophagus fasciculatus (Thaxt) C. Walker & Schuessler (=*Glomus fasciculatum*, MUCL 46100) was found to be the predominant AMF in soils of the Dharwad region of India (Channabasava et al. 2015). It was shown experimentally to form a host–fungus relationship with *P. miliaceum*, a relationship that could be harmed by some fungicides.

Working with mine-spoil waste in the Uttara Kannada region of India, Channabasava and Lakshman (2013) added inocula of two locally abundant mycorrhizal fungi, *Glomus fasciculatum* (=*Rhizophagus fasciculatus*) and *Acaulospora laevis* Gerdemann & Trappe, to potting mixtures containing different proportions of mine waste in which plants of *P. miliaceum* and *Jatropa curcas* L. were grown. In soils with 25% mine-spoil waste, both growth and potassium uptake were increased for both plant species in the presence of the mycorrhizal inocula. We infer from their results that each of the two plant species and each of the two mycorrhizal fungal species form good host-fungus relationships.

In a study conducted in Germany, Maier et al. (1997) grew 61 species of Poaceae, including *P. miliaceum* in a defined nutrient medium. These were inoculated with

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the AMF *Glomus intraradices* Schenk & Smith. Although the percentage mycorrhization of roots of these species was as low as 5% in one of the *Poa* species used, 80% of *P. miliaceum* roots became infected.

In Israel and India, *Azospirillum brasilense* Tarrand & Krieg, a bacterium, fixes nitrogen in association with the roots of *P. miliaceum* (Kapulnik et al. 1981; Rai 1985). Under controlled environments in a phytotron and a greenhouse, plants of *P. miliaceum* inoculated with *A. brasilense* as seedlings had faster development to the heading stage, higher shoot and root weights and higher total N weight than uninoculated controls (Kapulnik et al. 1981). In India, one high-temperature-adapted strain of *P. miliaceum* had more growth and greater nitrogenase and hydrogenase activity at 30 °C to 42 °C than parental or other temperature-adapted strains (Rai 1988).

8. Reproduction

(a) Floral biology

(i) Crop biotypes

Proso millet is self-fertile (Kane and Cavers 1992) and is ordinarily self-pollinated (Ayyangar and Rao 1938). It is considered a self-pollinated crop (Baltensperger 1996) but natural cross-pollination may exceed 10% (Popov 1947). In Russia, Gashkova (2003–2009) linked self- or cross-pollination to ambient temperatures and anther protrusion. In cool and cloudy weather flowers do not open and only self-pollination occurs. Under 'optimal' conditions, the anthers dehisce at the time that they emerge from the opening flower; most of the pollen falls on the stigmas inside the flower but some pollination of other flowers in the same panicle is possible. In hot and dry weather, the anthers open after they have emerged, the pollen is released into the air and cross-pollination occurs. Nelson (1984) described techniques to improve the effectiveness of cross-pollination methods in *P. miliaceum*.

Treatment of plants of *Panicum miliaceum* growing under continuous light with 100 mg L^{-1} of gibberellic acid caused flowers to form. However, the spikelets remained short and sterile (Kumar et al. 1977).

In Madras Province in India, flowers of *P. miliaceum* open between 1000 and 1200 with individual flowers opening and closing within five to seven minutes (Ayyangar and Rao 1938). In their plant breeding studies, Ayyangar and Rao (1938) found that finger-thumb pressure on flowers induces opening about one hour before normal and this procedure permits emasculation. In Russia, Gashkova (2003–2009) reported flowers opening between 0800 and 0900, with a peak of flowering between 1000 and 1200, and flowering was over by 1500. She found that an individual flower can stay open from five to ten or from 20–40 min, depending on weather conditions. Under warm dry conditions, for early-maturing and mid-season cultivated varieties, anthesis (flower opening) begins on days two or three after the emergence of the panicle. Late-maturing varieties begin anthesis on days four to six, and very late-maturing varieties on days five to eight. At peak flowering, 50–100 flowers may open simultaneously on a single panicle.

In northern cultivation areas in Russia, varieties with loose, spreading and widely branched panicles are most suitable because they have more light penetration and moisture evaporation, whereas in more arid southern areas, biotypes with compact, dense panicles have reduced moisture evaporation and are more suitable (Gashkova 2003–2009).

(b) Seed production and dispersal

(i) Mostly weeds but some crop information

Seeds of *P. miliaceum* ripen in basipetal succession (from the top down) on each inflorescence (Kane and Cavers 1992). In crop populations in the central United States, the seeds in the upper portion are ripe and liable to shatter while lower seeds are still green and ripening (Baltensperger 1996), although in Ontario most crop populations have little or no shattering before harvest [see also sections 2 and 13(a)(i)]. Crop populations tend to produce a single panicle from the apical bud, even when the plants are widely spaced. In contrast, plants of the Black biotype and those of the Orange-red crop-like weed have the greatest tendency to produce inflorescences on tillers arising from lateral bud development (Cavers and Bough 1985).

In a field study conducted in India, on two crop varieties of proso millet, Rao et al. (1977) assessed the importance of the upper leaves of the main shoot in their resource contribution to seed development. They concluded that almost 50% of seed development was contributed by the stem and leaf sheaths, with the ear and flag leaf contributing a further 33%. Each of the second, third and fourth leaves contributed about 6%–7%.

Seed production of the Black biotype averaged 92 seeds m^{-2} (1.5 million ha^{-1}) in a barley crop, 2354 seeds m^{-2} (34 million ha^{-1}) in corn and 38 247 seeds m^{-2} (426 million ha^{-1}) in white beans (O'Toole and Cavers 1983).

Mean seed weights for three Black populations, from Huron County, Waterloo County and Glengarry (now Stormont, Prescott and Glengarry) County in Ontario, were 3.69, 3.75 and 3.72 mg, respectively. Mean seed weights for six populations of crops and crop-like weeds ranged from 4.90 to 6.23 mg (Moore and Cavers 1985). In a more detailed study, Bough et al. (1986) provided mean seed weights for Canadian weed and crop-like weed biotypes. They found that average seed weight for the Black biotype ranged from 4.2 mg for seeds ripening early in the season, to 3.9 mg for seeds ripening in mid-season, to 3.0 mg for late-ripening seeds; ranged from 4.3 to 6.0 mg for different populations of the Crown biotype; ranged from 4.9 to 5.9 mg for different populations of the Golden biotype; averaged 6.2 mg for the Orange-red biotype; averaged "about 6 mg" for the

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White biotype; averaged 5.2 mg for the Dark red biotype; and averaged 6.5 mg for the Elgin biotype. In the mid 1980s, the Crown biotype was the only one with large weed populations in both Southern Ontario and Southern Manitoba (Cavers and Bough 1985). The crop and weed populations in Manitoba had average seed weights from 6.1 to 6.2 mg, whereas the weedy Crown populations from Southern Ontario averaged 4.7 to 5.5 mg per seed.

Motuzaite-Matuzeviciute et al. (2011) studied variation in the lengths and widths of seeds from individual plants of cultivated populations of *P. miliaceum*. They found variation of 20% or more in both length and width but there was no clear relationship between seed dimensions and position of the seed on the panicle. Kane and Cavers (1992) found for the Black biotype that there was no relationship between the date of seed ripening and the total seed viability.

Seeds of the Black biotype in Ontario shatter readily as they mature and thus seeds are dispersed from early August (O'Toole and Cavers 1983) until the time of the first frost, usually in October (Bough et al. 1986). Seed dispersal of this biotype occurred first in corn fields, next in white-bean (*Phaseolus vulgaris*) fields and latest in barley fields in Southern Ontario (O'Toole and Cavers 1983). In contrast, also in Ontario, crop-like weed biotypes have little shattering and most crop populations have almost no shattering (Bough et al. 1986). Consequently, most ripe seeds from crop and crop-like weed populations are retained on the parent plant until crop harvest or post-harvest cultivation (McCanny 1986; M. Kane and P. Cavers, personal observations). One exception is a crop-like weed population of the Crown biotype from the former Carleton County, Ontario (near Ottawa), whose seeds shatter more readily than those of other Crown populations (Bough et al. 1986).

Wind has little effect on the dispersal of proso millet seeds (Cavers and Bough 1985). For example, if Black seeds are not dispersed by human action, the vast majority fall within the maximum lateral spread of the parent plant (O'Toole and Cavers 1983).

Panicum miliaceum was one of 146 species recorded as adventive at terminal grain elevators and adjacent railway yards in a 1975 survey at Thunder Bay, Ontario, but none of these adventive species appeared to pose a threat to local agriculture (Lindsay 1977). Jehlik (1995) implicated railway freight transport in the Czech Republic as a means whereby alien weeds, including *P. miliaceum*, were introduced to that country.

There is strong circumstantial evidence that the Black biotype was brought to southern Ontario from Wisconsin on used farm equipment (J. O'Toole, personal communication). Initial infestations in Huron County, Ontario were all on farms where farm equipment was shared and at least one of these machines had been imported from an area in Wisconsin with dense infestations of Black proso millet (J. O'Toole, personal communication). A later intensive study by Stephen McCanny confirmed that seeds of *P. miliaceum* were being moved between and within fields on combine harvesters (McCanny 1986). Experimental evidence demonstrated that, on average, 3.3% of seeds from plants of the Black biotype were carried more than 50 m by combines. Earlier preliminary studies in Huron County, Ontario had shown that isolated patches could be spread to more or less complete coverage in a field within two years (J.J. O'Toole, unpublished data). McCanny et al. (1988) confirmed that much of this spread could be attributed to combine harvesters. McCanny and Cavers (1988) reported that combines carry up to 13 000 seeds at a time out of a field. McCanny et al. (1988) also showed that combines could distribute seeds of the Golden biotype between fields and that 0.9% could be carried more than 50 m within a field on combines. We have observed that farm equipment in Manitoba can be infested with large numbers of seeds of the Crown biotype and that anyone walking through fields contaminated with Crown or Black proso millet on a warm summer day can pick up hundreds of ripe seeds sticking to skin and sweat-moistened clothing (P. Cavers and M. Kane personal observations). Proso millet seeds are also transported in mud that has stuck to footwear and vehicle wheels (Cavers and Bough 1985).

J.F. Alex and R.D. McLaren of the University of Guelph supplied additional information on the dispersal of proso millet by means of their "Weed Alert Program" and through personal consultations. In 1979, Alex and McLaren isolated nine different seed colours from weed populations and regrowth from crops of proso millet in Ontario (O'Toole 1982). In 1980, they reported proso millet as a weed on 72 Ontario farms (O'Toole 1982). Our research group at the University of Western Ontario contacted more than 100 farm operators in Ontario who had reported weed populations of proso millet before 1985. Many of them believed that their infestation originated on farm equipment brought into their fields from infested farms (P. Klumpers, S. McCanny, M. Kane, and P. Cavers, unpublished data).

James et al. (2010) reported that infestations of *Panicum miliaceum* in New Zealand in the 1960s and 1970s were probably of crop varieties that originated from imported birdseed and as a contaminant in imported seeds of choumollier (*Brassica oleracea* L.). It is unknown how the black-seeded weed was brought to New Zealand, but it has spread throughout much of that nation on agricultural equipment (T. James, personal communication).

In west-central Minnesota, Forcella et al. (1996) found that for early-maturing weed species, including wild mustard (*Sinapis arvensis* L.) and possibly wild proso millet, rapid maturation during warm growing seasons resulted in almost complete dispersal of seeds prior to crop harvest by combine. In cool growing seasons, some seeds of these species were retained on the parent plant

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until combine harvest. They recommended that this information be considered in devising better systems of weed management.

(c) Seed banks, seed viability and germination

(i) Predominantly weed populations

In 1989–1990, Yenish et al. (1992) examined the distribution of weed seeds in the upper 10 cm of two soils in Wisconsin, a silt loam in Arlington that had been sown to a corn/soybean rotation from 1984 to 1988, and a loamy sand in Hancock that had been sown to continuous corn since 1982. Most of the weed seeds were *Chenopodium album*, *Amaranthus retroflexus*, *Panicum dichotomiflorum*, *Panicum miliaceum*, *Setaria pumila* (Poir.) Roem. & Schult. and *Cenchrus longispinus* (Hack.) Fernald. At both sites, over 60% of the weed seeds in the top 10 cm were found in the top one cm in no-till plots and the concentration of weed seeds declined logarithmically with increasing depth. In chisel-ploughed plots, more than 30% of the weed seeds were in the top centimetre and weed-seed density declined linearly with depth.

The longevity of seeds in the seed bank varies from very brief, less than one year and often only a few weeks, to strongly persistent over several to many years (Bough et al. 1986; Colosi et al. 1988; Cavers et al. 1992; J.J. O'Toole, personal communication). At one extreme, in Ontario, seeds of the White biotype of *P. miliaceum* almost never survive in the soil for more than a few weeks and more than 99% cannot overwinter successfully in the field (Cavers et al. 1992). Most crop-like weeds have little or no survival in the soil over winter but approximately 20% of the seeds of one Golden population collected from Durham County, Ontario survived overwinter in the soil and were still viable but ungerminated in June of the following year (Cavers et al. 1992). This is also one of the very few crop-like weed populations that has spread naturally into neighbouring fields from the original infestation (Cavers et al. 1992; M. Kane and J.C. Colosi, personal observations). Another crop-like weed with appreciable seed survival over winter is the Dark red biotype from Quebec (Bough et al. 1986; R. Néron, personal communication).

In Canada, the one crop population that also became a serious weed was the Crown biotype in Manitoba [Bough et al. 1986; see section 3(a)]. This population has heavier seeds than other weedy Crown populations from Ontario and Quebec (Cavers and Bough 1985). We examined approximately 30 populations of the Crown biotype from a wide geographical range in southern Manitoba, as well as plants arising from a crop population grown at Plum Coulee, Manitoba, all of which appeared to be of an identical type (Bough et al. 1986). These large populations occurred despite the fact that they had transient seed banks (Cavers et al. 1992). Several factors led to this result; more or less continuous corn crops with regular use of atrazine, a herbicide to which proso millet is resistant; slow breakdown of atrazine in Manitoba soils; large numbers of proso millet seeds persisting on the parent until winter; and long cold winters with few periods when seeds could germinate or rot (Cavers et al. 1992).

The earliest study of seed banks of the black-seeded biotype in North America was initiated in 1977 by McNevin and Harvey in Minnesota (McNevin and Harvey 1980*b*). They buried approximately 400 seeds at a time (first sample counted and weighed, remaining samples weighed) in a 15 cm long piece of PVC (polyvinyl chloride) drainage pipe covered at both ends with plastic mesh and placed upright in the soil at a depth of 25 cm. They used two different soils, a silt loam and a sandy loam. Samples were removed at different dates and set to germinate (conditions not specified). After one year, 212 seeds from the silt loam and 170 from the sandy loam germinated. These values declined after two years to 73 and 84 seeds germinating from the silt and sandy loam treatments, respectively.

The Black biotype forms large persistent seed banks in Ontario. Early studies by our team in London, Ontario revealed that Black seeds could remain dormant in the soil for at least four years when stored at a depth of 20 cm (Bough et al. 1986). Similar results were obtained by a farmer in Huron County, Ontario who had a large newly-established population of the Black biotype. He worked effectively to prevent any new seed production by this biotype for five years, but in the sixth year he had a large infestation of proso millet in his corn crop and it had to have come from the seed bank (Cavers et al. 1992). In an experiment in London, Ontario, seeds of the Black biotype were stored for various periods at three depths: surface, three cm deep and 20 cm deep. No seed remained viable on the surface for more than two years but some seeds of this biotype remained alive for 30 months at the three and 20 cm depths (Cavers et al. 1992). The pattern of viable seeds in arable soils is exceedingly variable, even from different soil samples taken from a single arable field (O'Toole and Cavers 1981). To study seed distribution, we established a 100 m × 100 m area in a field in Huron County, Ontario that had had dense infestations of the Black biotype for at least three years. At 50 randomly selected points within this area, a 1000 cc soil sample was collected in June 1981, when the field had an almost uninterrupted lawn of proso millet seedlings. There was a range of viable millet seeds per sample from 0 to 180, with no obvious pattern. Almost half of the seed bank in this field had died over the previous winter (Cavers et al. 1992; see also section 10).

In a very large experiment run at eleven sites across the US Corn Belt from Ohio to Colorado and from Minnesota to Missouri, field emergence of weed species was monitored from 1991 to 1994 (Forcella et al. 1997). Seedling emergence of wild-proso millet ranked eighth

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of 15 species, with emergence in three or more site years and an average of 6.6% emergence per site.

Williams and Harvey (2002) conducted a field experiment in the United States to determine how many wild-proso millet seeds could be returned to the soil each year without increasing future seed-bank populations. Their original seed bank, in 1988, averaged 15 000 seeds m^{-2}. Starting that year, they added a seed rain of 0%, 3%, 6%, 12%, 24% and 48% of the original seed bank each autumn for five years. After the fifth year, more than 90% of the original seed bank had been lost in all treatments. They estimated that 77% of the seed rain and 68% of the spring seed bank had been lost each year. This meant that the wild-proso millet had to return approximately three times the number of seeds in the soil each year to maintain a constant seed-bank population.

Lloyd and Cavers (2002) compared dormancy, viability and seedling vigour from fresh seeds of the Black biotype, several crop-like weed biotypes and a white-seeded crop with seeds from the same populations that had been stored for 15 yr at 5 °C and 40% relative humidity. In a greenhouse study, seedling emergence from aged seeds of the most weedy biotypes (Black, Dark red), planted 1 and 3 cm deep, was faster and more complete than from fresh seeds, demonstrating that seeds of these biotypes lost dormancy, but not viability, during storage. Aged and fresh seeds of the Crown and White crop-like weeds emerged equally quickly and with no loss of viability during storage. In contrast, aged seeds of the white-seeded crop had 70% viability or less (compared with 100% for fresh seeds). Seeds sown on the soil surface had the most variable seedling emergence patterns. Fresh and aged seeds of the Crown biotype had rapid complete emergence. In contrast, the Black biotype had slow and intermittent emergence, reaching 77% for aged seeds and 28% for fresh seeds after three months. In a separate study, emerged seedlings from aged crop seeds had up to 70% mortality before flowering, whereas seedling mortality from aged seeds of five weed and crop-like weed biotypes was negligible.

In a germination test in an incubator, the low threshold temperature for germination of wild proso millet in the USA was 6.9 °C (Wiese and Binning 1987). In Iran, Kamkar et al. (2006) found that the base (lowest) temperature for germination of cultivated *P. miliaceum* seeds was 9.9 °C, the optimum temperature for fastest germination was 40.2 °C and the ceiling (highest) temperature for germination was 47.8 °C. In the United States, crop seeds of proso millet germinate well between 10 °C and 45 °C but do not germinate at 5 °C or 50 °C (Theisen et al. 1978, cited in Baltensperger 1996).

Van der Kley and Schelwald (1987) tested germination of seven weed biotypes of proso millet in incubators under complete darkness and with 15 h d^{-1} of light. There were two diurnal temperature regimes; 25/10 °C and 35/20 °C with a 15/9 h day/night in each case. The seven biotypes were Black, Golden, White, Orange-red, Dark red, Crown and Elgin. For five biotypes, germination under the higher temperatures was rapid and over 80% in both light/dark and completely dark regimes within two days. The Dark red seeds had slightly less germination (70% vs. 80%) and the Black seeds much less (15% in light and 30% in darkness). A few Dark red seeds and a large proportion of the Black seeds remained dormant but viable. Germination under the lower temperature regime proceeded more slowly but after five days had reached close to 100% for the Elgin, Crown, Golden and White biotypes in both light regimes. The Orange-red seeds germinated to over 90% in darkness after five days but only to 60% in light/dark conditions. The Dark red seeds had 80% germination in complete darkness after five days, but only half that much in the light/dark regime. Approximately half of the Black seeds had germinated after five days in both the darkness and light/dark regimes.

Di Paolo (1995) investigated the role of the husk (lemma and palea) in causing dormancy in seeds of proso millet. She tested germination of freshly ripened Black seeds in Petri dishes in an incubator set at diurnal cycles of 25 °C, light for 14 h and 10 °C, dark for 10 h. Intact seeds did not germinate but remained dormant and viable. Black seeds with the husk removed (i.e., the caryopses) and huskless seeds placed in a Petri dish with their removed husks had 98% and 96.6% germination respectively and the few ungerminated seeds were dead. She concluded that the seeds had a husk-induced dormancy. Khan et al. (1996) tested germination from seven weed biotypes and the Crown crop biotype of proso millet and found that the darker the husk, the more dormant were the seeds. They discovered that the darker seeds had heavier husks, imbibed and germinated more slowly and suffered less imbibition damage (measured as electrolyte leakage).

Mándy and Szabó (1973), working in Hungary with crop varieties of proso millet, found that the optimum temperatures for seedling emergence were 18 °C–21 °C at five cm depth. Freshly ripened seeds gave "poor" germination but after a rest period of three to five months, differing for varieties, full germination was achieved. Exposure of fresh seeds to cold stratification had no effect. In contrast, Striegel and Boldt (1981), working with black-seeded proso millet, found that optimum germination occurred at 30 °C and that dormancy could be overcome by the absence of light during germination, by moist pre-chilling at 5 °C or by nine weeks of dry storage at 22 °C.

Beres (1993) reported that germination of weed populations of proso millet in Hungary was unaffected by sodium chloride concentrations of 50, 100 or 150 mM but in a concentration of 200 mM there was a 15%–16% reduction in germination. This author also reported that seeds of proso millet can germinate at pH values from three to eight and that during germination

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these seeds are less sensitive to drought than those of *Chenopodium album*.

In Argentina, De Caire et al. (1976) found that aqueous and ether extracts from an algal mass of *Nostoc muscorum* Ag. significantly accelerated germination of seeds of *Panicum miliaceum*; a lower concentration of the ether extract was most effective.

(d) Vegetative reproduction

Vegetative reproduction does not occur in proso millet.

9. Hybrids

There are no reports of (spontaneous) interspecific hybridization involving *P. miliaceum*.

Colosi and Schaal (1997) used Random Amplified Polymorphic DNA (RAPD) to assess relationships among 97 genotypes; 69 were black-seeded weeds (B), 26 were crops (C) and crop-like weeds (CL) and two were hybrids between B and C or CL genotypes [see also section 2(c)(iii)]. Both of the hybrids were collected from Minnesota where *Panicum miliaceum* is grown as a crop and where the black-seeded weed has been found since at least 1970. Their results suggest that hybridization between crop and weed biotypes does occur in North America, but the hybrid genotypes also could have been brought to North America from other continents. The production of hybrids within proso millet is discussed in section 3(b). In Europe, Scholz (1983) stated that the weedy biotype of proso millet is a result of repeated reverse mutations in a crop biotype (see section 6).

There is a program in China to produce hybrid seeds of *P. miliaceum* (Cui 2008). Kashin et al. (1997) described interspecific crosses between *P. miliaceum* and a distant millet species.

10. Population Dynamics

(a) Seed populations

(i) Predominantly weeds

For all biotypes, input of seeds to the soil depends on the crop with which the weed was growing and the weed-control measures used during the season (Cavers et al. 1992). Cavers et al. (1992) found that in Ontario very few Black seeds were produced in barley or winter-wheat crops but large numbers could be found in corn and white-bean crops. The greatest numbers of Black seeds were dispersed in September in Huron County, Ontario (O'Toole and Cavers 1983). The timing of seed production and dispersal also were governed by the crop and by weed-control measures. For example, Cavers et al. (1992) found that small plants in a barley field produced very few seeds by early September in Huron County, but more seeds ripened after crop harvest and were shed later in September and in October, after seed dispersal in other crops was almost complete.

Although there is often a huge increase in the proso millet seed bank following a dense weed infestation, there is usually a large decrease in the seed bank before the onset of the next growing season. In a field of white beans in Huron County, the seed bank of the Black biotype increased to 28 470 seeds m^{-2} in October 1980 but this number had decreased by more than 10 000 m^{-2} by April 1981 (Cavers et al. 1992). Many seeds on the soil surface were destroyed by rodents, which left only fragments of lemmas and paleas on the soil surface in the spring, and many other seeds rotted over the winter. Seed banks of the crop and crop-like weed biotypes seldom persist beyond one winter, with the exception of the Dark red biotype in Quebec and one Golden population from Durham County in Ontario (Cavers et al. 1992).

(b) Crop biotypes

(i) As weeds

In Minnesota, Robinson (1985) noted that crops of *P. miliaceum* gave rise to volunteer plants for several ensuing years. In a field with silt-loam soil, seeds of seven proso millet cultivars, five white-seeded and two red-seeded, were sown in October 1978 following harvest of a crop of 'Minsum' proso millet. After these seeds had been sown, crops of sorghum were grown for five successive years. Eight tillage treatments, including a no-till control, were applied to plots within the field for the five years. In all plots, volunteer proso millet plants were removed before seed production from 1979 to 1983 inclusive. In all treatments, a total of more than 700 000 seedlings ha^{-1} of volunteer proso millet emerged over the five years. The no-tillage control was the only treatment where emergence was reduced to zero after four years. In contrast, 73 and 254 volunteer seedlings ha^{-1} emerged in the fifth year after spring and fall moldboard-plough treatments, respectively. Robinson (1985) provided evidence that volunteers of crop biotypes can emerge in several successive years after a proso millet crop in the USA (although in his study seed colours of the emerged volunteer plants were not determined).

(c) Seedling populations

(i) Weeds and crops

Moore and Cavers (1985) compared seedling vigour in crops, Black biotype weeds and crop-like weeds of proso millet. Most differences in seedling vigour could be attributed to dissimilar seed weights among the various biotypes. Seedlings of crop-like weeds, with larger seeds, had greater seedling vigour than those of the Black biotype. However, early-season growth in the absence of competition from crops is extremely rapid in all biotypes (Bough and Cavers 1987). In Australia, Murray (1998) focussed on the role of density-dependence during the seed germination period of the life cycle for twelve phylogenetically-diverse plant species. *Panicum miliaceum* (purchased crop seeds, biotype not specified) was one of four species that had a significant decrease in the proportion of seeds germinating at higher densities of conspecifics. These four species subsequently were

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each treated at low densities with a leachate solution obtained from high-density conspecifics. For *P. miliaceum*, this resulted in a significant decrease in the proportion of seeds germinating at the simulated high densities. Murray concluded that the reduced germination percentages caused by the leachate would benefit the species by reducing high-density effects and possibly enabling some seeds to delay germination until a more-favourable time of lower conspecific density. A problem with this study is that Murray identified *P. miliaceum* as a perennial.

Anderson and Nielsen (1996) studied seedling emergence of weeds in winter wheat stubble in Colorado for three years. Wild-proso millet emergence was greater in tilled than in no-till plots, whereas the reverse was true for kochia [*Kochia scoparia* (L.) Schrad.], volunteer wheat and green foxtail. In this study, emergence of wild-proso millet began in late May and continued until August.

(d) Plant populations

(i) Predominantly weeds

Carpenter and Hopen (1985) grew plants of the black-seeded weed and a cultivated white-seeded variety of proso millet in pure stands at different densities in a greenhouse experiment in Illinois. Plant height of both biotypes decreased linearly with increasing planting density. Both biotypes exhibited decreased shoot dry mass per plant at higher densities and the percentage of plants with panicles also was lower at higher densities. Nevertheless, there was still substantial panicle production by both biotypes even at the highest density of 5540 plants m^{-2}. In Ottawa, Ontario, Warwick and Thompson (1987) ran a similar but much larger experiment using the White, Golden, Orange-red, Crown and Black biotypes of proso millet. Pure stands of each biotype were grown in trays in a greenhouse at densities equivalent to 111, 237, 474 and 978 plants m^{-2}. The Golden biotype had more than 10% mortality at all four densities, with a maximum of 20% at the two highest densities. The White biotype had increased mortality at the two highest densities but the other three biotypes only had increased mortality (less than 12%) at the highest density. All biotypes had decreased biomass per plant and delayed flowering with increasing density. The White and Golden biotypes also had reduced weight per seed with increasing density. Van der Kley and Schelwald (1987) grew seedlings of four biotypes, Black, Orange-red, White and Crown at different densities in pure stands in a greenhouse in London Ontario. The treatments involved seedlings sown (planted) at spacings of 25, 10, 5, 4, 3 and 2 cm. The experiment was harvested 42 days after seedling emergence, when virtually all plants had grown out of the seedling stage. There was almost no mortality at the two lowest densities (widest spacings) but up to 25% died at the highest densities, with the greatest mortality for the Black biotype. At the end of the experiment, the Crown biotype had the highest mean weight per plant. Black had the lowest values but the differences were only significant at the lowest density. Plants from all biotypes tillered at the lowest density, but only the Black biotype tillered at the second-lowest density and no seedlings tillered at the four highest densities. The Black biotype did not flower at any density; the Crown biotype flowered at the lowest density and only in the last three days of the experiment. The White and Orange-red had 80% and 84% flowering, respectively, in the 10 cm spacing and less at all other densities.

Eberlein et al. (1990) studied growth and development of three "wild-proso millet biotypes" and one cultivated biotype (Crown) under non-competitive conditions in the field in Minnesota. All of the "wild" biotypes had greater leaf area and dry weight at maturity than Crown. They also produced more seeds per plant than Crown, up to twice as many for one wild biotype. Crown headed earlier than all of the wild types. Although all of the "wild" biotypes could be classed as the Black biotype of Bough et al. (1986), they did differ in plant height, seed shattering, reproductive potential, seed size and seed dormancy characteristics. Eberlein et al. (1990) concluded that two of these wild biotypes had more weedy characteristics than the third one.

The "escape hypothesis" (Howe and Smallwood 1982) predicts that a seed's chance of survival increases with distance from its parent, in situations where the parent is an isolated single plant. McCanny and Cavers (1987) tested this hypothesis in Ontario using six weedy biotypes of proso millet growing in two different crops, corn and soybeans. Although there were no clear differences among the different biotypes or between crops, the overall results supported the escape hypothesis. McCanny and Cavers interpreted these findings to have been the result of density-dependent mortality. In a later paper, McCanny and Cavers (1989) examined the effects of parent plant size and fecundity on the seed shadows and mature offspring patterns around isolated parent plants of six biotypes of proso millet. The most important result, irrespective of biotype, was that the more fecund groups had more distant cohorts of mature offspring. The two prime causes of this pattern were greater density-dependent mortality near the most fecund parent plants and the larger seed shadows of the larger sized parents.

In a greenhouse experiment, Warwick and Thompson (1987) grew five weed biotypes (Black, White, Golden, Orange-red and Crown) together at three densities, 30, 60 and 90 seeds of each biotype per tray (equivalent to just over 1000, 2000 and 3000 seeds m^{-2}). All biotypes had reduced survivorship with increasing density but, in contrast to the experiment with pure stands described in the same paper, the Black biotype had the greatest mortality at all three densities, whereas the White and Golden biotypes had the highest survivorship at the two higher densities. In terms of total fresh weight per

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tray, the taller-growing, later-flowering White biotype totally dominated the mixture and the Golden biotype had the second highest fresh weight at each density. The Crown and Black biotypes had very low fresh weights at all densities. The Crown biotype had the highest percent allocation to reproductive weight, whereas Orange-red had the lowest allocation.

In general, early-maturing sweet corn hybrids were less competitive with wild proso millet than later-maturing ones (So et al. 2009*a*). Williams II et al. (2012), using four morphologically different sweet-corn hybrids, found that characteristics of the crop (the maternal crop environment) influenced the seed characteristics of wild-proso millet. The weed plants were more productive and their seeds were larger, with greater germinability, in crops that matured faster and had a smaller canopy. Under these latter crops, the seed colour of wild-proso millet was also slightly lighter. Conversely, an early crop-canopy spread at the time of weed emergence, and an almost complete crop canopy later, suppressed weed fitness (So et al. 2009*b*). Wilson (1993*a*) studied the effects of different densities of wild-proso millet on the yield of dry beans in Nebraska. He found that it was most important to remove wild-proso millet plants during the first four weeks of the dry-bean growing season. In contrast, if the dry-bean crop was kept free of proso millet for four weeks after planting, then the yield was comparable to the yield for dry beans kept weed-free all season. In a four-year experiment with corn, also in Nebraska, Wilson (1993*b*) tested the effects of different pre-plant tillage methods on densities of six major weed species. The most effective of these methods on proso millet was 'ridge-till' where 50% of the weed seeds were left in the topmost 0–7 cm, 92% of weed seeds directly over the corn row were removed and 50% of the weed seeds were moved to an area 25 cm away from the corn row. After this treatment, proso millet plant density was much lower than it was after other pre-plant tillage treatments.

(e) Population dynamics

(i) Crops

There have been numerous studies of population dynamics in crops of proso millet. Agdag et al. (2001) grew proso millet using six different row spacings, three tillage regimes (irrigated, dryland and no-till) and with either no weeds or under weedy conditions in the United States Great Plains. Row spacing had little effect on seed weight, but narrower rows improved seed yield and weed control. In areas of limited moisture, a row spacing of 19 cm appeared optimal. In Southern Germany, Gebauer et al. (1987) grew two C_3 crop grasses, barley and oats, and two C_4 crop grasses, proso millet and barnyard millet (*Panicum crus-galli* L. [= *Echinochloa crusgalli* (L.) P. Beauv. var. *frumentacea* (Link) W. Wight (see Small 2009)] in pure and mixed cultures in field plots. Low and high nitrogen fertility levels were incorporated in the experiment. In mixed cultures, *P. miliaceum* was least able to compete; its shoot biomass, but not its shoot length, was drastically reduced when compared with its performance in pure stands. In North Dakota, Berglund (2007) also reported that crops of proso millet are known for their poor seedling vigour and are poor competitors with weeds. One exception is the crown variety in Manitoba [see section 3(a)]. Also, Anderson (2000*b*) hypothesized that, in a semi-arid area with erratic precipitation, sowing a crop of proso millet during a period of minimal weed emergence and using a combination of cultural weed-control methods would enable producers to control weeds in that proso millet crop without herbicides.

11. Response to Herbicides and Other Chemicals

(a) Crops

The literature on proso millet response to herbicides in North America changed dramatically in the 1970s. Before that time, proso millet was known as a crop that was used for animal feed, for feeding wild birds in the winter and occasionally for human uses such as baking and brewing [see section 3(b)]. In that era, atrazine was the favourite chemical for weed control in proso millet crops (Dekker et al. 1981). A detailed study of weed control in proso millet crops in Nebraska was made by Grabouski (1971). Grabouski tested eight post-emergence herbicide treatments at three growth stages of the millet. Plots treated with the dimethylamine salt of 2,4-D applied at 0.56 kg ha^{-1} had significantly higher grain yields than the weedy check plots. All herbicides used, except the amine of 2,4-D at 0.28 kg ha^{-1}, appeared to injure the proso millet plants but yields were not greatly reduced. In Nebraska, Burnside (1974) found that proso millet crops could be severely affected after trifluralin herbicide had been used in three successive years.

Additional papers reporting herbicide studies in crops of proso millet have been published intermittently over the past 40 years, both in the USA (e.g., Robinson 1973; Lyon and Anderson 1993; Lyon and Baltensperger 1993; Lyon et al. 2007) and overseas (e.g., Kasasian 1977). A seed treatment with a herbicide safener, CGA-43089 developed by CIBA-GEIGY, provided crops of proso millet with improved tolerance to metolachlor (Nyffeler et al. 1980).

(b) Weeds

Control of weedy proso millet has been the main focus of herbicide trials on this species since 1975. The most extensive early trials to control black-seeded wild-proso millet in the United States Corn Belt were conducted in the late 1970s by R.G. Harvey and associates in Wisconsin. They tested many herbicide treatments for proso-millet control in field and sweet corn and soybeans, but even the better treatments gave only partial suppression of wild-proso millet (McNevin and Harvey 1980*a*, 1980*c*, 1982). In contrast, in Austria,

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Discus et al. (1976) tested CL 11.344 (fenpyrate), a new contact herbicide, and found that it provided control of proso millet if applied up to the 5-leaf stage in corn (maize) crops. An application rate of 1.0 kg a.i. ha^{-1} proved to be sufficient. They did not state which biotype(s) of proso millet were tested in their study, but they did identify the species as one of four hard-to-kill grass weeds in corn crops in Austria. In Spain, after chemical weed control had been adopted for corn crops, *Panicum miliaceum* was one annual weed that could appear 'suddenly' (Guillerm and Maillet 1982).

An early Canadian study of the responses of weedy proso millet to herbicides was done by Jensen et al. (1977). Unfortunately, they did not specify which biotype of proso millet was used. By 1981, in a Fact Sheet on proso millet issued by the Ontario Ministry of Agriculture and Food, black-seeded proso millet was recognized as a major problem in corn and bean fields in central and western Ontario (Dekker et al. 1981). At that time, EPTC [S-ethyl dipropyl carbamothioate] with the protectant gave adequate early-season control in most corn fields but without further control measures the weed escaped and set seeds (Bandeen et al. 1979). The only herbicide treatment recommended as one of these "further control measures" was Linuron applied with skid-mounted nozzles (Dekker et al. 1981; based on research of Anderson and Harris 1980), but with many provisos (e.g., do not apply to proso millet taller than 20 cm; corn must be at least 38 cm tall to the highest free-standing leaf; allow at least 60 days between the date of application and harvest). Crop rotations with alfalfa (*Medicago sativa* L.), small grains or "possibly" soybeans were also recommended although proso millet might escape and set some viable seeds after these crops had been harvested (Dekker et al. 1981). These authors pointed out that the "grassy weed herbicides" used with soybeans and recommended in the Guide to Chemical Weed Control (Ontario Herbicide Committee 1983) could also be a good control measure. When the Fact Sheet was revised six years later, the same recommendations for herbicide control in corn were given, but the authors emphasized that if post-emergence chemical control of proso millet with Linuron was attempted, "the applicator must be aware of the potential for crop injury" (Bough and Cavers 1987). A new development by 1987 was that sethoxydim (Poast®) had been registered for use on canola [(rapeseed) *Brassica napus* L. subsp. *napus* or *Brassica rapa* L. subsp. *oleifera* (DC) Metzg.], flax (*Linum usitatissimum* L.), soybeans, dry beans (*Phaseolus vulgaris*), peas, onions (*Allium* spp.), tomatoes and potatoes. It was recommended for use against proso millet at rates of 0.8 to 4.4 L ha^{-1} along with Assist oil concentrate at 2 L ha^{-1} (Bough and Cavers 1987).

Tridiphane [2-(3,5-dichlorophenyl)-2-(2,2,2-trichloroethyl)oxirane] can function as a potent synergist of atrazine to provide postemergence control of some important grass weeds (Ezra et al. 1985). These scientists, working in Ontario, tested tridiphane with four herbicides to see if any of these herbicide-synergist combinations could provide control of Black proso millet. Both EPTC and alachlor [2-chloro-2′,6′-diethyl-*N*-(methoxymethyl) acetanilide] were synergized effectively by tridiphane but atrazine and CDAA (*N*-*N*-dially-2-chloroacetamide) were not. They concluded that tridiphane, in combination with EPTC or alachlor, might provide improved control of proso millet in corn.

There have been continuing studies to improve control measures for Black proso millet. In a laboratory study in Ontario, Swanton and Chandler (1990) evaluated imazethapyr, a member of the imidazolinone class of herbicides, and found that seedlings of Black proso millet were controlled at the 1- to 5-leaf stage by 50 g a.i. ha^{-1} of this herbicide. Higher doses were required to control older seedlings. In a field study, imazethapyr, applied pre-emergence or post-emergence, provided effective control of Black proso millet in soybeans, with soybean yields comparable to those obtained with the recommended post-emergence treatment with sethoxydim.

In a Quebec study, Mekki and Leroux (1994) tested the responses of seven weed species including proso millet (biotype not specified) to the herbicides rimsulfuron and nicosulfuron, plus a 1:1 mixture of these herbicides, DPX-79406 (Ultim), under greenhouse conditions. These herbicides, developed originally in France, cause impairment of biosynthesis of essential amino acids. They also studied the effects of these herbicides on acetohydroxyacid synthase (AHAS), also known as acetolactate synthase (ALS). They found that proso millet was "very susceptible" to rimsulfuron and DPX-79406 (the 1:1 mixture) with a 90% reduction in dry weight caused by 6–7 g a.i. ha^{-1}, but only "susceptible" to nicosulfuron, with a 90% reduction in dry weight caused by 16 or more g a.i. ha^{-1}.

Swanton et al. (1996) tested DPX-79406, the 1:1 premix of nicosulfuron and rimsulfuron, on corn and five annual-grass weeds in both greenhouse and field trials in southern Ontario. In the greenhouse, green foxtail (*Setaria viridis*) was the most susceptible to this chemical, yellow foxtail (*Setaria pumila*) was the least susceptible and barnyard grass (*Echinochloa crusgalli*) and proso millet were intermediate in susceptibility. In the field, when this herbicide was applied soon after the corn crop had emerged (early postemergence), 12.5 g ha^{-1} was required to reduce the dry shoot weight of Black proso millet seedlings by 93% in 1990 and 90% in 1991. In 1991, late application to more mature (four- to eight-leaf stage) Black proso millet seedlings was less effective. A treatment of 22.1 g ha^{-1} was needed to reduce dry-shoot weight by 77%.

In Ontario, McNaughton et al. (2004) noted that proso millet could cause great reductions in dry beans (*P. vulgaris*) if it was present in densities of ten plants m^{-2}. At that time, none of the registered soil-applied

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herbicides could control proso millet in this crop. They tested several newer herbicides and found that clethodim and quizalofop-P, both applied postemergence, could be effective in controlling Black proso millet in snap beans (also *P. vulgaris*). In tests in Huron County, Ontario, quizalofop-P injured snap bean plants but did not reduce plant height or yield, whereas clethodim did not injure, stunt or reduce yield of snap beans.

From 1982 to 1999, there were many papers published on research to control proso millet in a variety of crops in the United States (e.g., McNevin and Harvey 1982; Harvey et al. 1986, 1987; Fawcett and Harvey 1988; Harvey 1990, 1991; Harvey and McNevin 1990; Harvey and Porter 1990; Westra et al. 1990; Kleppe and Harvey 1991*a*, 1991*b*; Rabaey and Harvey 1997*a*, 1997*b*; Van Wychen et al. 1999). One important result noted by several different researchers was that repeated annual applications of the same herbicide (thiocarbamate herbicides in particular) led to reduced control of several "difficult-to-control" weeds such as proso millet (Harvey et al. 1987). They found that repeated applications of the same herbicide led to more rapid degradation of the herbicide in the soil. When rotations using different herbicides in a three- or four-year rotation were initiated the enhanced degradation did not occur (Harvey 1991). Further experiments revealed that incorporation of the chemical extender "SC-0058" with the herbicides Butylate or EPTC prevented enhanced biodegradation, even on soils treated for three successive years with the same herbicide (Harvey 1990). A contrasting problem was that the use of herbicides, such as atrazine, that can persist for several years in the soil can allow atrazine-resistant weeds such as wild proso millet to increase in the years following an atrazine application (Miller and Callihan 1995). These authors found that sowing atrazine-resistant oilseed rape (*Brassica napus* cv. Triton) at a high rate in the year following a corn crop given a high atrazine rate could provide early season control of proso millet. By 1999, several reports of greatly increased control of proso millet with newly introduced herbicides led to reduced crop losses. For example, Van Wychen et al. (1999) found that glufosinate, followed by cultivation gave 80% or greater control of wild-proso millet in sweet corn transformed by the incorporation of the phosphinothricin-N-acetyl transferase gene (PAT).

Shenk et al. (1990) examined the role of seed depth of wild-proso millet on the effectiveness of several herbicide treatments in sweet corn crops. They found that shoot exposure of the *P. miliaceum* seedlings to herbicides caused significantly greater phytotoxicity than root exposure.

Tests in Ontario to evaluate the responses of different biotypes to herbicide application have yielded variable results. In a growth room study, Swanton and Chandler (1990) sprayed seven biotypes (White, Golden, Orange-red, Black, Dark red, Crown and Elgin) with different concentrations of imazethapyr and found no significant differences among biotypes in shoot dry weight. M. Bough and P. Cavers (unpublished data) ran a field experiment in which established non-flowering plants of the White, Golden, Orange-red, Black, Crown and Elgin biotypes were treated with four herbicides. Two of the herbicides were undergoing evaluation and were never registered in Ontario. The other two herbicides were sethoxydim and fluazifop-P-butyl (Fusilade). Sethoxydim caused huge reductions in plant numbers, surviving plant size and seed production in all biotypes, but the two Black populations were the most severely affected. Fluazifop-P-butyl was also very effective against the Black biotype but gave only partial control of the other biotypes. All of the herbicides were least effective against a population of the Golden biotype from Durham County, Ontario; a population that also had the greatest seed survival over winter of all the crop-like weed populations that we studied [see section 8(c)]. It appears that this population could become a serious weed problem in the future if current herbicide regulations change.

Although the evaluation of economic thresholds for weed densities in different crops has become more common, we have found only one paper where thresholds were presented for proso millet. In Italy, Sartorato et al. (1996) found that the economic threshold for proso millet in soybean was 4.18 plants m^{-2} in 1989 and 0.67 plants m^{-2} in 1990.

Over the past 20 yr there has been a huge reduction in infestations of Black proso millet in Ontario (P. Sikkema, D. Robinson and C. Swanton, personal communications, University of Guelph; personal observations by the authors). Two critical developments have caused this reduction: (a) the introduction of the sulfonyl urea (rimsulfuron and nicosulfuron) herbicides in corn in 1994 (and later foramsulfuron), which provide excellent control of proso millet, and more importantly, (b) the introduction of glyphosate-tolerant soybeans in 1997 and corn in 2001 with the concomitant increase in the use of glyphosate, which provides near perfect control of proso millet and also reduces weed-seed return to the soil (P. Sikkema, personal communication). For the few growers not using glyphosate-tolerant corn, field-corn growers usually rely on Accent [nicosulfuron, 750 g kg^{-1}], Option [foramsulfuron, 22.5 g L^{-1}] or DPX-79406 [rimsulfuron 37.5%, nicosulfuron 37.5%] (D. Robinson, personal communication). In non-glyphosate-resistant soybeans, edible beans and most broad-leaved vegetable crops, growers use Poast Ultra [sethoxydim, 450 g L^{-1}], Excel [fenoxaprop–p-ethyl, 850 g L^{-1}], Select [MCPB 375 g L^{-1}, MCPA 25 g L^{-1}] and Venture [fluazifop–P-butyl and S isomer, 125 g L^{-1}] (D. Robinson, personal communication). At present, some seed-corn growers in southwestern Ontario still have some questions about control of proso millet (R. Nurse, personal communication).

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Much information has been published in Europe on the incidence and problems caused by weedy proso millet [see section 3(a)] and there also have been numerous reports of recommended herbicide treatments to control this weed.

In New Zealand, black-seeded proso millet has become a major weed problem in sweet corn crops within the past 20 years. James and Rahman (2009) tested a variety of pre-emergence herbicides against three annual grass weeds. *Panicum miliaceum* was the least affected and none of these treatments provided effective control of it on any of a wide range of soil types.

12. Response to Other Human Manipulations

(a) Weeds and cv. Crown as a weed

It is important to determine which biotype of proso millet is causing a particular weed problem. For example, crop rotation is a most effective means of controlling almost all the crop-like weed biotypes. In the early 1980s, we suggested that the numerous dense populations of the Crown biotype in corn-growing farms in Manitoba could be controlled by initiating a pattern of crop rotation to replace the preference for continuous corn crops. Since the only biotype causing a weed problem in Manitoba at that time was Crown [see section 3(a)], the proso millet populations could be greatly reduced during rotations into small grains, alfalfa or other crops (Bough and Cavers 1987), but the farmers also had to keep their mobile equipment clean of Crown seeds, which could survive overwinter on contaminated equipment and then be reintroduced when a corn crop was sown the next spring [see section 8(b)]. In addition, assiduous cleaning of all mobile farm equipment before it is moved from field to field will greatly reduce lateral dispersal of any weedy proso millet. After nearly 20 years, proso millet remained as a very minor weed in Manitoba (Leeson et al. 2002). This procedure worked because the transient seed banks of the Crown biotype could not survive for more than one year in the soil [see section 8(c)]. In contrast, infestations of the Black biotype in Huron County, Ontario persisted in seed banks for more than five years and crop rotation reduced but did not eliminate them [Cavers et al. 1992; section 8(c)].

In Wisconsin, Harvey and McNevin (1990) had similar results; corn yields were higher and seedling populations of wild-proso millet were reduced when corn was planted after one to four years of alfalfa.

Weedy proso millet may be suppressed in small grain crops or alfalfa except in patches where the crop has grown poorly. Nevertheless, depauperate (small but mature) weed plants are still able to set a few seeds that can contribute to seed banks, so that in these crops the weed may be reduced but not eradicated (M. Kane and P. Cavers, unpublished data).

In field experiments near London, Ontario, most seedlings of Black and Crown proso millet were killed by discing and rototilling treatments, but mowing and compression under tractor wheels caused very little mortality (Cavers and Kane 1990). In greenhouse experiments conducted at the same time, recently emerged seedlings suffered the greatest mortality after raking and desiccation treatments, but few were killed by shoot or root damage (Cavers and Kane 1990).

There have been few studies of the effects of weed management success in one crop on weed management success in a succeeding crop in the same field (Davis and Williams II 2007). These authors found that wild proso millet fecundity in a sweet-corn crop could have a significant influence on wild proso millet seedling establishment in a snap-bean crop the following year.

There are large differences among crops in their weed suppressive ability (WSA) for proso millet, in particular their ability to suppress the seedling emergence, growth and/or fecundity of black-seeded proso millet. In southern Ontario, O'Toole and Cavers (1983) found that barley had a much greater WSA for Black proso millet than corn, which, in turn, had a greater WSA than white beans. Even among hybrids of sweet corn, there are differences in their WSA for weedy proso millet (Williams II et al. 2007). These differences are due to known variation in canopy properties among sweet-corn hybrids.

In Wisconsin, Harvey and McNevin (1990) found that sweet-corn yields were higher when the crop was planted in rows 76 cm apart than in rows 108 cm apart. They also obtained better control of wild-proso millet and higher yields of both field and sweet corn for late-season planted crops (17 May) than for crops planted earlier (27 Apr.).

In areas of dense infestations of the Black biotype, there was a much greater decline in viable seeds overwinter in fields with no-till management (P. Cavers, personal observations). In these fields, a very large proportion of seeds on the soil were eaten, probably by small rodents, before the next crop was planted [see section 13(a)].

Sartorato et al. (2006) described field tests in Italy of a prototype microwave-based weed-killing machine. This "thermal" method uses microwave radiation to cause heating of plant tissue moisture, which eventually kills the plant. *Panicum miliaceum* and *Abutilon theophrasti* were tested, along with two crops, alfalfa and oilseed rape. Alfalfa was least affected but the other three species had increased dry weight reductions with increasingly strong microwave doses. The estimated microwave dose needed to cause a 90% dry weight reduction ranged from 1015 kJ m^{-2} for *A. theophrasti* to 3433 kJ m^{-2} for *P. miliaceum*. The authors concluded that this method could overcome the limitations of other thermal methods but it must be refined to give increased efficiency.

In New Zealand, James et al. (2010) found that sweet-corn residue passed through a "wilter", a 15 m long steam-heated enclosed conveyer belt, for seven minutes

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will not have any remaining live seeds of *P. miliaceum*, whereas untreated residue retains live seeds. In another test, seeds of *P. miliaceum* were all killed by three months of storage in ensiled sweet corn or in ensiled grass.

(b) Crop populations

Daugovish et al. (1999) studied the long-term effects of two- and three-year rotations in Nebraska for the control of downy brome (*Bromus tectorum* L.), jointed goatgrass (*Aegilops cylindrica* Host) and feral rye (*Secale* spp.). The most profitable of all the different rotations was a three-year one of winter wheat, proso millet (crop) and fallow. It gave the best profitability and provided excellent control of the winter-annual grass weeds.

A major and rapid change in cropping systems in the semi-arid Great Plains of the United States is that the adoption of no-till practices has led to great reductions in simple winter wheat-fallow rotations and their replacement by a diverse variety of cropping systems (Anderson 2003). However, there are problems with many of these systems because of herbicide-resistant weeds and low profit margins. Anderson pointed out that ecologically based weed-management practices utilizing cropping systems designed to lower weed community densities and improve crop competitiveness to weeds should be considered. He singled out crops of proso millet where he found that cultural control systems can be effective enough to preclude the need for herbicides for in-crop weed control (Anderson 2000*b*). In contrast, a simple rotation of winter wheat and proso millet was the least effective for weed control of eight crop rotations tested in South Dakota (Anderson et al. 2007).

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) Herbivory

(i) Mammals

Weed populations

In a field near Brucefield in Huron County, Ontario containing one of the most dense infestations of Black proso millet that we have seen, there was a large population of small rodents. By early autumn, many of the seeds on the ground had been eaten and local agronomists agreed that the damage was clearly caused by these mammals (P. Cavers and student assistants, unpublished data). Evidence for this conclusion came from the many rodent holes in these fields and the abundance of partially eaten proso millet seeds.

Crops

Seeds of *Panicum miliaceum* are fed to hogs, sheep, cattle, poultry and other livestock (Elliott 1923; Robinson 1962). The seeds should be ground before feeding to livestock other than poultry (Robinson 1962). In Canada, proso millet can be grown for swath grazing (McCartney et al. 2008) and as a forage crop (McCartney et al. 2009) but it is usually grown for seed (Lardner et al. 2011). However, Johns (2015) stated that proso millet is not suited to grazing, but he did say that it can be made into acceptable silage. Lardner et al. (2011) grew red proso millet in Saskatchewan in 2009. They obtained a very good yield of high quality for use as swath grazing by beef cows. The proso millet crop had slightly better forage quality than oats even though the millet was left in swath for nearly 60 d before it was grazed. However, they cautioned that crop performance by proso millet will vary from year to year, depending on the growing conditions. To alleviate the problem of harvest timing caused by uneven ripening within proso millet plants [see section 8(b)], Baltensperger (1996) recommended that swathing be done when most of the panicle is no longer green.

Feeding proso millet to horses is not recommended since it can cause kidney irritation and excessive urination (Johns 2015).

(ii) Birds and other vertebrates

Crops and weeds

In Ontario, crops of proso millet are grown for birdseed mixtures used in winter feeding stations, for parakeet seed packages and as a means of attracting birds into Conservation Authority areas (O'Toole 1982). Proso millet is a popular ingredient for many birdseed mixes for backyard feeders in North America (Mayntz 2013), with white-seeded varieties being the most popular for these mixes. Mayntz (2013) gave a long list of birds known to eat seeds of *P. miliaceum*. "Dove" proso millet is a variety introduced from India and planted in the southeastern United States to attract mourning doves (*Zenaidura macroura*) for hunting (Robinson 1971). In Minnesota, proso millet seeds are fed to a variety of cage birds, as well as wild birds (Robinson 1962).

Proso millet is fed to laying hens in North America with good rates and efficiencies of egg production (Sell 1977). Luis et al. (1982*c*) agreed, stating that "proso millet, either ground or whole, is an excellent ingredient for layer diets". It is also recommended for the diets of broiler chickens (Luis et al. 1982*a*) and turkey poults (Luis et al. 1982*b*).

McCanny (1986) ran a laboratory experiment in which ring necked doves (*Streptopelia rosegrisia*) were fed samples of seeds from six different biotypes of proso millet. Orange-red seeds proved to be the most palatable, but not significantly more so than White, Elgin or Golden seeds. Black seeds were the least palatable and they were the only seeds that were regurgitated after consumption by the doves. With the exception of the Orange-red seeds, there was a trend towards a decrease in the mean weight of consumed seeds with increasingly dark seed pigmentation. Few Crown seeds were eaten but there was no sign that they were distasteful to the birds. In a small feeding experiment in the field, Elgin seeds were

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favoured by American goldfinches (*Carduelis tristis*) (Cavers 1985).

In South Dakota, an analysis of the gizzard contents of red-winged blackbirds (*Agelaius phoeniceus*) revealed that seeds of proso millet had been eaten, but in smaller quantities than corn, oats and wheat, and in much smaller quantities than a weed, bristle grass (*Setaria* spp.) (Mott et al. 1972). In South Africa, Soobramoney and Perrin (2007) studied the effects of bill morphology and seed characteristics on the feeding behaviour of five species of granivorous passerines. They found that the birds husked all seeds, including *P. miliaceum*, before ingestion and that monocotyledenous seeds were handled significantly faster than dicotyledenous seeds. Their results also indicated that nutrition is less important than morphological traits of seeds, since the birds generally selected food items that were easiest to handle and could be processed faster. This behaviour enabled the birds to gain nutrients quickly.

(iii) Insects and other arthropods
Weeds and crops

The only reference that we found of insects living on *Panicum miliaceum* in Canada was a study of proso millet interference in field corn in Ontario (Alex et al. 1980). The total number of corn plants hosting larvae of European corn borer (*Ostrinia nubilalis* Hübner) during silking increased with increasing density of proso millet (a golden seeded biotype; probably a crop-like weed), as did the total number of proso millet plants infected per unit area.

In our discussions of damage from proso millet to corn fields in Manitoba with representatives of the Manitoba Department of Agriculture, they mentioned that corn stalk borer (*Helotropha reniformis* Grt.) will move to corn plants from proso millet and other grassy weeds and then kill the corn.

In North Dakota and New York State, Anderson et al. (2003) tested three millet species as possible "trap crops" for management of European corn borer (*Ostrinia nubilalis*). Of the three species, proso millet had the highest infestation rate and the widest distribution of *O. nubilalis* developmental stages. Both old and young females of *O. nubilalis* aggregated in proso millet during the day but at night the young females moved out of proso millet to oviposit, whereas old females remained in the millet.

Wilson and Burton (1980) stated that little is known about the responses of proso millet to insects, especially in the United States. They tested five insect pests of cereal grains in Oklahoma; fall armyworm (*Spodoptera frugiperda* J.E. Smith), southwestern corn borer (*Diatraea grandiosella* Dyar), corn earworm (*Heliothis zea* Boddie), chinch bug (*Blissus leucopterus leucopterus* Say) and yellow sugarcane aphid (*Sipha flava* Forbes); for oviposition and feeding responses on nine different cultivars of *P. miliaceum*. In 1978, field populations of chinch bug caused damage to all nine cultivars but only one was totally susceptible (killed). However, in 1979, chinch bug infestations were heavier and field populations of all nine proso millet cultivars were killed. In feeding preference tests in the greenhouse, there were significant differences among proso millet cultivars and it was not possible to predict how a particular cultivar would be damaged since the damage patterns caused by one insect often differed from the pattern for another insect (Wilson and Burton 1980). In North Dakota, grasshoppers (family Acrididae) have caused the most serious insect problems in crops of proso millet (Berglund 2007). Grasshoppers and armyworms can be controlled by the insecticide Sevin [carbaryl, 42.8% by weight] (Berglund 2007).

In the United States, Simmons et al. (2008) reported that *P. miliaceum* was one of three cultivated crops that was a new host of the sweetpotato whitefly (*Bemisia tabaci* Gennadius). It was acceptable to this insect for feeding, oviposition and development to the adult stage. In a greenhouse study, they did not see immature individuals of *B. tabaci* on *P. miliaceum* in an open-choice test, but they did record oviposition and development to the adult stage in a no-choice laboratory test. The authors emphasized that this whitefly spreads numerous viruses to and among cultivated plants.

In Colorado, Armstrong et al. (1995) recorded large numbers of blasted seed heads at maturity of a crop of 'Sunup' proso millet. The damage was caused by two chloropid flies, *Rhopalopterum carbonarium* Loew and the wheat stem maggot *Meromyza americana* Fitch.

Proso millet was one of seven non-preferred alternative host plant species (out of 15 species tested) for the feeding of early-instar larvae of the range caterpillar, *Hemileuca olivae* Cockerell, in a greenhouse study in Colorado (Capinera 1978).

Western corn rootworm, *Diabrotica virgifera* subsp. *virgifera* LeConte (Coleoptera), is an invasive pest of corn fields in Europe. Moeser and Vidal (2004) investigated the performance of this pest on eleven alternative host plants, including *Panicum miliaceum*. They found that the corn rootworm larvae had the highest weight gain on *P. miliaceum* but, conversely, it was not among the species that were fed on most by these larvae.

Grasses are important hosts during the life cycles of the hop vine borer (*Hydraecia immanis* Guenée) and the potato stem borer (*H. micacea* Esper), both Noctuidae: Lepidoptera. Wild-proso millet was one of eight grass species and corn on which both borers were reared successfully under greenhouse conditions in the United States. Thus, these species were recognized as possible food for these potentially serious agricultural pests (Giebink et al. 1999).

Stem flies and shootflies (*Atherigona* spp.) are important pests on millets and sorghums in India and Pakistan. In a field experiment in Coimbatore, India, Natarajan et al. (1974) tested nine varieties of *Panicum*

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miliaceum for damage from the shootfly *Atherigona miliaceae* M. and obtained different results from the different millet varieties. Plant mortality ranged from 5.1% to 12.9% and percent loss in yield ranged from 11.6% to 36.4%. Also in India, where proso millet can be sown throughout the year, damage from the shootfly, *Atherigona destructor* M. [considered a synonym of *A. pulla* Weidemann (S. Darbyshire, personal communication)] is lowest for proso millet crops sown from November to May and high for crops sown in the other months (Santharam and Venugopal 1978). In Pakistan, Moiz and Naqvi (1968) recorded the sorghum stem fly, *Atherigona varia* var. *soccata* Rondani, on *P. miliaceum* at Tando Jam.

(iv) Nematodes and other non-vertebrates
Crops and possibly weeds

Panicum miliaceum was found to be an excellent host in South Carolina for the Columbia lance nematode, *Hoplolaimus columbus* Sher. (Fassuliotis 1974). Tyler (1941) reported that *P. miliaceum* is usually "immune", or only slightly infested, to the root knot nematode in Florida; had no infestation in a pot experiment in India; and could be grown on soils that were the worst infested with this nematode in Brazil. Roy (1977) reported that *P. miliaceum* is highly susceptible to the rice root-knot nematode, *Meloidogyne graminicola* Golden and Birchfield, in India and is rated as a good host for this nematode.

(b) Diseases

(i) Fungi
Weed biotypes

In London, Ontario, S. Legeza and M. Kane (unpublished data) used potato dextrose agar to culture fungal spores present on the outer surfaces of seeds of weedy proso millet biotypes that had failed to germinate in germination tests. Six fungal genera were identified: *Alternaria, Cladosporium* and *Fusarium*, which are known to be either parasitic or saprophytic on plant material, *Helminthosporium*, a genus that is predominantly parasitic, and *Epicoccum* and *Aspergillus*, whose members are predominantly saprophytic.

Crops and weeds

In Canada, Conners (1967) listed five fungi from *Panicum miliaceum*; *Fusarium equiseti* (Cda.) Sacc. and *F. poae* (Pk.) Wr. [listed as *Fusarium equiseti* (Corda) Sacc. and *Fusarium poae* (Peck.) Wollenw. in Farr and Rossman (2013)] from seeds in Ontario, *Pythium debaryanum* Hesse from Saskatchewan, *Pythium graminicola* Subram. (*P. arrhenomanes* Drechsl.) a cause of browning root rot in Saskatchewan and Manitoba and *Ustilago destruens* Schltdl. [= *Sphacelotheca destruens* (Schltdl.) Stevenson & A.G. Johns., *Sorosporium panici-milacei* (Pers.) Tach. and *S. syntherismae* auct. non (Pk.) Farl.] a cause of smut in all Canadian provinces except Newfoundland. Dr. J.A. Traquair (personal communication) collected *Ustilago destruens* from Black proso millet in Essex Co., Ontario in 1992. Ginns (1986) listed a report of *Ustilago destruens* on *Panicum miliaceum* in British Columbia. Farr and Rossman (2013) listed the following smut fungi reported on *P. miliaceum* in Canada: *Ustilago syntherismae* (Schwein.) Peck. [= *Sorosporium syntherismae* (Schwein.) Farl.]; *Sporisorium destruens* (Schltdl.) Vánky [= *Sphacelotheca destruens* (Schltdl.) J.A. Stev. & Aar.G. Johnson]; *Ustilago destruens*; *Ustilago panici-miliacei* (Pers.) G. Winter, [for which Farr and Rossman claim that the worldwide host is *Panicum* (Poaceae)]; and *Ustilago crameri* Körn.

Farr and Rossman (2013) also listed many other fungal species that have been found on *P. miliaceum* in the USA. These are: *Colletotrichum graminicola* (Ces.) G.W. Wilson; *Curvularia geniculata* (Tracy & Earle) Boedijn; *Fusarium acuminatum* Ellis & Everh. [= *Fusarium scirpi* var. *acuminatum* (Ellis & Everh.) Wollenw.]; *Fusarium bulbigenum* Cooke & Massee; *Fusarium equiseti* (Corda) Sacc.; *Fusarium moniliforme* J. Sheld.; *Fusarium oxysporum* Schltdl.; *Fusarium poae* (Peck.) Wollenw.; *Microdochium bolleyi* (R. Sprague) de Hoog & Herm.-Nijh. (= *Gloeosporium bolleyi* R. Sprague); *Exserohilum rostratum* (Dreschler) K.J. Leonard & Suggs (= *Helminthosporium halodes* Dreschler); *Exserohilum monoceras* (Dreschler) K.J. Leonard and Suggs (= *Helminthosporium monoceras* Dreschler); *Bipolaris sorokiniana* (Sacc.) Shoemaker (= *Helminthosporium sativum* Pammel, C.M. King & Bakke); *Exserohilum turcicum* (Pass.) K.J. Leonard and Suggs (= *Helminthosporium turcicum* Pass.); *Penicillium expansum* Link; *Periconia circinata* (L. Mangin) Sacc.; *Phyllachora graminis* (Pers.:Fr.) Fuckel; *Puccinia emaculata* (Schwein.) Kuntze; *Setophoma terrestris* (H.N. Hansen) Gruyter, Aveskamp & Verkley [= *Pyrenochaeta terrestris* (H.N. Hansen) Gorenz, J.C. Walker & Larsson]; *Pyricularia grisea* Sacc.; *Pythium arrhenomanes* Drechsler; *Globisporangium debaryanum* (R. Hesse) Uzuhashi, Tojo & Kakish (= *Pythium debaryanum* R. Hesse); *Pythium graminicola* Subraman; *Pythium monospermum* Pringsh.; *Globisporangium ultimum* (Trow) Uzuhashi, Tojo & Kakish [= *Pythium ultimum* Trow]; *Schizonella melanogamma* (DC.) J. Schröt.; *Sclerophthora macrospora* (Sacc.) Thirum., C.G. Shaw & Naras; *Sclerospora graminicola* (Sacc.) J. Schröt.; and *Sporisorium cenchri* (Bref.) Zundel. Farr and Rossman (2013) also listed another 44 species that are found on *Panicum miliaceum* in countries other than Canada and the United States.

The proso millet crop has been identified as a host of the fungus disease "blast" [*Pyricularia grisea* (Cke.) Sacc.] in Australia (Simmonds 1947 *cited in* Singh and Prasad 1981; see above paragraph also).

The fungus *Aspergillus parasiticus* Speare (ATCC 15 517) produces flavacoumarins that cause growth delays in roots and small plant size in *Panicum miliaceum* and a variety of other plant species (Jacquet et al. 1971). These flavacoumarins also inhibit germination of *P. miliaceum* when present in water at a minimum concentration of 20 mg mL^{-1} (Jacquet et al. 1971).

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Nelson and Kerr (1984) reported that an infection of head smut (*Sphacelotheca destruens* = *Sporisorium destruens*) of proso millet in Nebraska could be reduced by 93% by a seed treatment with fungicides. In North Dakota, Berglund (2007) pointed out that seed treatment with thiram reduces infection by head smut spores in the soil and also may increase seedling survival. Kovacs et al. (1997) tested several cultivated varieties of proso millet for susceptibility to head smut (*Sporisorium destruens*) in Hungary and found that infection varied from 3% to 87%.

Misra et al. (1972) reported new records of three *Helminthosporium* diseases affecting crops of proso millet in India; leaf stripe (*Helminthosporium oryzae* Breda de Haan), leaf spot (*H. yamadai* Nisikado) and leaf blight (*H. panici miliacei* Nisikado). All of these fungi attack living leaves of proso millet and *H. panici miliacei* is found on almost all aerial parts of the plant, with severe infestations able to kill the plant.

Broomcorn millet (*P. miliaceum*) is a much more effective host than aphid cadavers for cultures of the aphid-pathogenic fungus *Pandora neoaphidis* (Zygomycetes: Entomophthorales). This is the basis of a possible cheap method for preparing and storing large quantities of *P. neoaphidis* inocula (Feng and Hua 2005) [see also section 3(b)].

(ii) Bacteria

Primarily crops

In Canada, Conners (1967) listed one bacterium from *Panicum miliaceum*; *Pseudomonas syringae* van Hall [= *Phytomonas panici* Ch. Elliott, *Phytomonas holci* (Kendr.) Bergey et al.], a cause of bacterial leaf spot in Alberta, Manitoba and Ontario.

Elliott (1923) described a bacterial stripe disease of *Panicum miliaceum* in South Dakota and Wisconsin. This disease developed only on *P. miliaceum* and not on barnyard millet (*Echinochloa crusgalli*), foxtail millet (*Setaria italica*), or cultivated varieties of sorghum, including "kafir corn". The disease caused narrow brown water-soaked streaks on the leaves of young plants and could spread to kill the entire above-ground part of the plant. However, even in the latter situation some plants could regrow from shoots arising from the below-ground portion. In field plots in Maryland, one variety of *P. miliaceum* had abundant infection in three successive years, two varieties had traces of the disease in one year but had abundant infection in a second year, one had a few scattered lesions in the one year it was tested and the fifth variety showed no trace of the disease.

(iii) Viruses

Crops and weeds

Brunt et al. (2013) reported that *P. miliaceum* is susceptible to eleven seed- and vector-transmitted viruses. Of these, cocksfoot mild mosaic (?) sobemovirus (CMMV) and wheat American striate mosaic nucleorhabdovirus (WASMV) are listed as spreading in Canada; barley stripe mosaic hordeivirus (BSMV) has a worldwide distribution; and foxtail mosaic potyvirus (FoMV), Johnsongrass mosaic potyvirus (JGMV), maize chlorotic dwarf waikavirus (MCDV), maize chlorotic mottle machlovirus (MCMV), maize dwarf mosaic potyvirus (MDMV), and Panicum mosaic (?) sobemovirus (PMV), are listed as spreading in the USA. *Panicum miliaceum* displayed systemic symptoms for two serotypes of maize chlorotic mottle virus (MCMV); one (MCMV-K) from Kansas and one (MCMV-P) from Peru (Bockelman et al. 1982). Maize streak monogeminivirus (MSV) and rice dwarf phytoreovirus (RDV) are not listed as spreading in North America, although *P. miliaceum* is listed as a diagnostically susceptible host species for RDV. *Panicum miliaceum* is an assay host (whole plant) for Panicum mosaic (?) sobemovirus (PMV) and is a diagnostically susceptible host species (symptoms: mosaic, reddening and dwarfing for maize dwarf mosaic potyvirus (MDMV). Brunt et al. (2013) also reported that *P. miliaceum* is not susceptible to Araujia mosaic potyvirus (ArjMV), Cynosurus mottle (?) sobemovirus (CnMoV) or Digitaria striate mosaic monogeminivirus (DiSMV).

Nault et al. (1976) described maize chlorotic dwarf virus (MCDV), to which *P. miliaceum* is susceptible, as the most damaging corn virus in the United States. In Ohio, it is transmitted by the leafhopper vector *Graminella nigrifrons* (Forbes).

Lee and Toler (1972) and Toler (1973) reported that *P. miliaceum* is a host species for the virus named St. Augustine decline (SAD). St. Augustine grass (*Stenotaphrum secundatum* Walt. Kuntz) has been the most important lawn grass in Texas and by 1972 96% of the lawns in the Gulf Coast area of that State were in that grass (Toler 1973). The symptoms of SAD on *P. miliaceum* were severe mosaic followed by death (Lee and Toler 1972). Toler (1973) tested four cultivated varieties of *P. miliaceum* and two of them were susceptible. In a more extensive study, Lee and Toler (1977) tested nine cultivars of proso millet; seven were susceptible to SAD but symptoms varied from mosaic (one), mosaic and dieback (four), stunted deformed heads (one), stunted blasted heads (one, cultivar "Crown") and mosaic and death (one). Samah and Holcomb (1975) found that reaction to SAD within a single cultivar, "Turgai", ranged from definitive mosaic symptoms to questionable mosaic symptoms to no symptoms at all. They obtained this range of responses from tests in greenhouses and growth chambers at different times during the year.

(iv) Other diseases

No information has been found.

(c) Higher plant parasites

Crops and weeds

Witchweeds (*Striga* spp.) are parasites on many cereal and leguminous crops (Weerasuriya et al. 1993) and they can cause devastating losses (Sugimoto et al. 1998). In the

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United States, Siame et al. (1993) found that seed germination of *Striga asiatica* (L.) Kuntze is stimulated by active compounds in root exudates of host crop plants. They identified strigol from proso millet and corn root exudates as the major stimulant of germination in seeds of *S. asiatica*.

In the United States, Putnam and Duke (1974) hypothesized that the predecessors of many species now grown for food or fibre may have possessed allelopathic substances that would have allowed them to compete effectively with other species in their native habitat. They tested this possibility by collecting 526 accessions of cucumber (*Cucumis sativus*) from 41 nations and grew them under controlled conditions with two indicator species, *Panicum miliaceum* and *Brassica hirta* Moench, as representatives of genera with economically important weed species. There was a wide variety of responses from *P. miliaceum*, with some accessions greatly reducing fresh weight but other accessions having no effect and one actually causing increased fresh weight. Putnam and Duke (1974) then took leachates from two cucumber accessions that had significantly reduced fresh weight in *P. miliaceum* and used leachate from one accession that had no effect as a control. The leachates from the "toxic" accessions inhibited seedling emergence and subsequent growth in *P. miliaceum* but the "non-toxic" accession had no effect. They concluded that it would be possible to produce crop genotypes that could compete successfully with weeds by means of allelopathic interactions. In a subsequent field study, Lockerman and Putnam (1979) tested two cucumber accessions against *P.miliaceum* and found that one accession reduced fresh weight by 58% and population numbers by 84% whereas the other accession was only half as effective against this weed. The allelopathic effects were suppressed during periods of increased rainfall.

In an experiment under simulated no-till conditions in the greenhouse, Barnes and Putnam (1986) reported that weedy proso millet had 35% less emergence when exposed to rye residues than in a control treatment. The effects on radicle elongation were greater than on percent germination. In another study in the United States, *Kalanchoe daigremontiana* Raym.-Hamet & H. Perrier caused allelopathic reductions in seed germination and reduced seedling development in *P. miliaceum* (Groner 1975).

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