The biology of Canadian weeds. 127. *Panicum capillare* L.

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Clements, D. R., DiTommaso, A., Darbyshire, S. J., Cavers, P. B. and Sartonov, A. D. 2004. **The biology of Canadian weeds. 127. *Panicum capillare* L.** Can. J. Plant Sci. **84**: 327–341. *Panicum capillare* L., witch grass, is an annual grass native to North America that infests field crops, small grains, grasslands, and a variety of other habitats. High seed production, a persistent seed bank, a tumble-weed seed-dispersing mechanism, and the ability to tolerate some herbicides contribute to the success of *P. capillare* in these habitats. Despite the widespread presence of *P. capillare* in crops, its actual impact on crop yield is not well documented. It is an additional host for several insect pests (e.g., cereal aphids) and diseases attacking crop species.

Key words: *Panicum capillare*, witch grass, panic capillaire, weed biology, native weed species

Clements, D. R., DiTommaso, A., Darbyshire, S. J., Cavers, P. B. et Sartonov, A. D. 2004. **Biologie des mauvaises herbes au Canada. 127. *Panicum capillare* L.** Can. J. Plant Sci. **84**: 327–341. Le panic capillaire, *Panicum capillare* L., est une graminée annuelle indigène de l'Amérique du Nord qui infeste les champs, les cultures de céréales secondaires, les prairies et une gamme d'autres habitats. La réussite de cette adventice repose sur la production d'une grande quantité de semences, un réservoir persistant de graines, un système de dispersion qui rappelle celui de l'anémone de Virginie et la tolérance à certains herbicides. Malgré son omniprésence dans les cultures, on connaît mal les incidences réelles du panic capillaire sur le rendement. L'espèce sert d'hôte à plusieurs ravageurs (notamment les pucerons des céréales) et maladies des cultures.

Mots clés: *Panicum capillare*, panic capillaire, witch grass, biologie des mauvaises herbes, adventice indigène

1. Name

Panicum capillare L. **witch grass**, **panic capillaire** (Darbyshire et al. 2000). Other common names include: old witch grass, common witch grass, capillary panic grass, switch grass, tickle grass, witchgrass, tumblegrass, mount au cul, mousseline, and panic (Scoggan 1978; Dore and McNeill 1980; Crompton et al. 1988; Marie-Victorin 1995; Bouchard and Néron 1999; Anonymous 2002). Poaceae (Gramineae), grass family, Graminées.

2. Description and Account of Variation

(a) *Physical description* —Caespitose annual (having a densely-clumped, tufted or cushion-like growth form) with erect or decumbent stems 20–100 cm tall; sometimes branched toward the base. Leaf sheaths and blades hispid (with bristly hairs), or pilose (hairy); the hairs may or may not have postulate or small-papillose bases; ligules a fringe of hairs, to about 2 mm long; blades 10–25 cm long, (2) 5–16 (27) mm wide, rolled in bud and becoming flat with maturity. Infloresence an open, diffuse panicle, (2) 9–30 (40) cm long (axillary inflorescences, when present, are smaller than terminal one); the lower portion of the internode below the infloresence becoming weak and eventually breaking; branches and pedicels widely spreading or the lower branches partly inserted in the flag leaf sheath (especially for axial inflorescences), strongly scabrous (rough with minute prickles). Spikelets with one fertile floret and one sterile floret (usually reduced to a lemma), primary disarticulation is above the glumes and with a secondary disarticulation zone below; glumes very unequal, with sparse bicellular microhairs; first glume broadly ovate, acute to acuminate (having a long tapering point), 1–2 mm long, 3 to 5 veins, usually sparsely scabrous on the midvein; second glume ovate-lanceolate, acute to acuminate, (2) 2.5–3.5 (4.5) mm long, 5–7 veins, usually sparsely scabrous on the nerves; sterile lemma very similar to the second glume but often a little shorter (palea lacking or reduced to a ridge of tissue); fertile lemma indurate (hardened), lustrous light brown or olive brown to dark brown, elliptic-ovate, (1.1) 1.2–2 mm long, 5–7 veins; palea indurate and tightly overlapped by the lemma; anthers (0.7) 0.8–1.1 (1.3) mm long.

Panicum capillare has a chromosome number of $2n = 18$ (Gould 1968; Hamoud et al. 1994). The chromosomes are primarily metacentric and submetacentric, exhibiting relatively high variation in length and arm ratio (Hamoud et al. 1994).

(b) *Distinguishing features—Panicum capillare* is part of a complex of five native annual species occurring in eastern Canada: *P. capillare*, *P. flexile* (Gattinger) Scribner, *P. gattingeri* Scribner, *P. philadelphicum* Bernh. ex. Trin., and *P. tuckermanii* Fernald (Darbyshire and Cayouette 1995). The genus *Panicum* contains more than 500 species worldwide, mostly occurring in the tropics (Crins 1991). Critical phylogenetic analysis of *Panicum* and its related genera is only in the early stages (Zuloaga et al. 2000), but even if many of the proposed segregate genera are recognized, *Panicum* remains one of the larger angiosperm genera.

Two of the species within the *P. capillare* complex, *P. philadelphicum* and *P. flexile*, are not found in arable fields (Darbyshire and Cayouette 1995). In both *P. flexile* and *P. capillare*, the terminal inflorescence is greater than or about equal to half the culm internode length, whereas it is usually shorter in the other species. *Panicum capillare* can be distinguished from *P. flexile* on the basis of a brittle culm internode at maturity (see section 3b), a relatively larger flag leaf blade (usually greater than 0.7× the upper culm length), the less attenuate spikelets, and the shorter anthers (usually greater than 1.1 mm in *P. flexile* and less than 1.1 mm in *P. capillare*). The key below provides several criteria for distinguishing the three species in agricultural habitats. See Darbyshire and Cayouette (1995) for a key to all five species.

1. Terminal inflorescence greater than or about equal to half the culm length; mature upper culm internode brittle, the lower part rapidly senescent and easily fractured; inflorescence branches stiff; second glume and sterile lemma tapering, acute; floret length usually less than twice the breadth; pedicels scabrous, the trichomes noticeably increasing in length apically (examine several pedicels); primary abscission zone on the rachilla, the indurate florets falling separately from the papery glumes and sterile lemma . . . . . .*P. capillare*

1. Terminal inflorescence usually less than half the total culm length; mature upper culm internode not brittle and breaking; inflorescence branches stiff or lax; second glume and sterile lemma more or less abruptly acute; floret length usually greater than twice the breadth; pedicels scabrous, the trichomes not noticeably increasing in length apically; primary abscission zone on the pedicel, the spikelets falling entire 2

2. Culms usually decumbent to prostrate; inflorescence branches usually thin and lax, readily bending under the weight of mature spikelets; spikelets usually less than 1.8 mm long; florets usually less than 1.2 mm long and 0.65 mm wide; anthers usually less than 0.9 mm long . . . . . .*P. tuckermanii*

2. Culms usually decumbent to erect; inflorescence branches stiffer, not readily bending under the weight of mature spikelets; spikelets usually greater than 1.8 mm long; florets usually greater than 1.2 mm long and 0.65 mm wide; anthers usually greater than 0.9 mm long . . . . . .*P. gattingeri*

Leptoloma cognatum (Schult.) Chase [= *Digitaxia cognate* (Schult.) Pilger], an uncommon grass in Ontario, is distinguished from *P. capillare* by its membranous ligule without a fringe of hairs, sparsely hairy leaf sheaths and flexible bracts of the mature fertile florets (Fassett 1951; Dore and McNeill 1980). *Panicum dichotomiflorum* (L.) Michx. is distinguished from *P. capillare* by virtue of a coarser panicle, zigzag appearance of somewhat flattened stems and lack of hair on the leaf sheaths and leaf blades in the upper half of the plant (Dore and McNeill 1980; Alex 1992). The spikelets of *Panicum miliaceum* L. (proso millet) are longer (> 4.5 mm) than those of *P. capillare* (< 4.5 mm). *P. miliaceum* has much larger [3.9 to 5.9 mg average for different populations (Bough et al. 1986)] and fewer seeds than *P. capillare* (0.15 to 0.29 mg, Sect. 8b), within a coarser panicle. The colours of *P. miliaceum* seeds, ranging from light cream, golden-yellow, orange-red, gray-green with lighter stripes, dark red to black, also distinguish most of them from the gray-brown seeds of *P. capillare* (Bough et al. 1986). However, some gray-brown seeds have been observed in US populations of *P. miliaceum* (Dr. P. Westra, personal communications).

(c) *Intraspecific variation—Panicum capillare* exhibits substantial phenotypic variation, often due to differences in substrate or climate between localities where the species is found (Darbyshire and Cayouette 1995). In its natural habitat along beaches, it rarely exceeds 30 cm in height and its panicles are usually less than 15 cm across (Dore and McNeill 1980). In gardens, cultivated fields and waste areas, however, *P. capillare* attains a height of 20–80 cm or higher. Variations in size of all major morphological structures are common, except for structures associated with the spikelets. Various ecotypes or taxa associated with particular climatic regions are distinguished on the basis of features such as colour and size of spikelets and vestiture of inflorescences and leaves. Dore and McNeill (1980) report that in Ontario populations these characteristics are maintained under different growing conditions but are not consistently correlated. The typical form was described from the eastern United States, and one or more western forms, with somewhat larger spikelets, have been recognized at various taxonomic ranks (species, subspecies or varieties) by different authors. McGregor (1984b) recognized 2 western forms as varieties. He felt that because all forms have become sympatric through human activity, subspecies rank was not warranted. The following key to these varieties is adapted from McGregor (1984b).

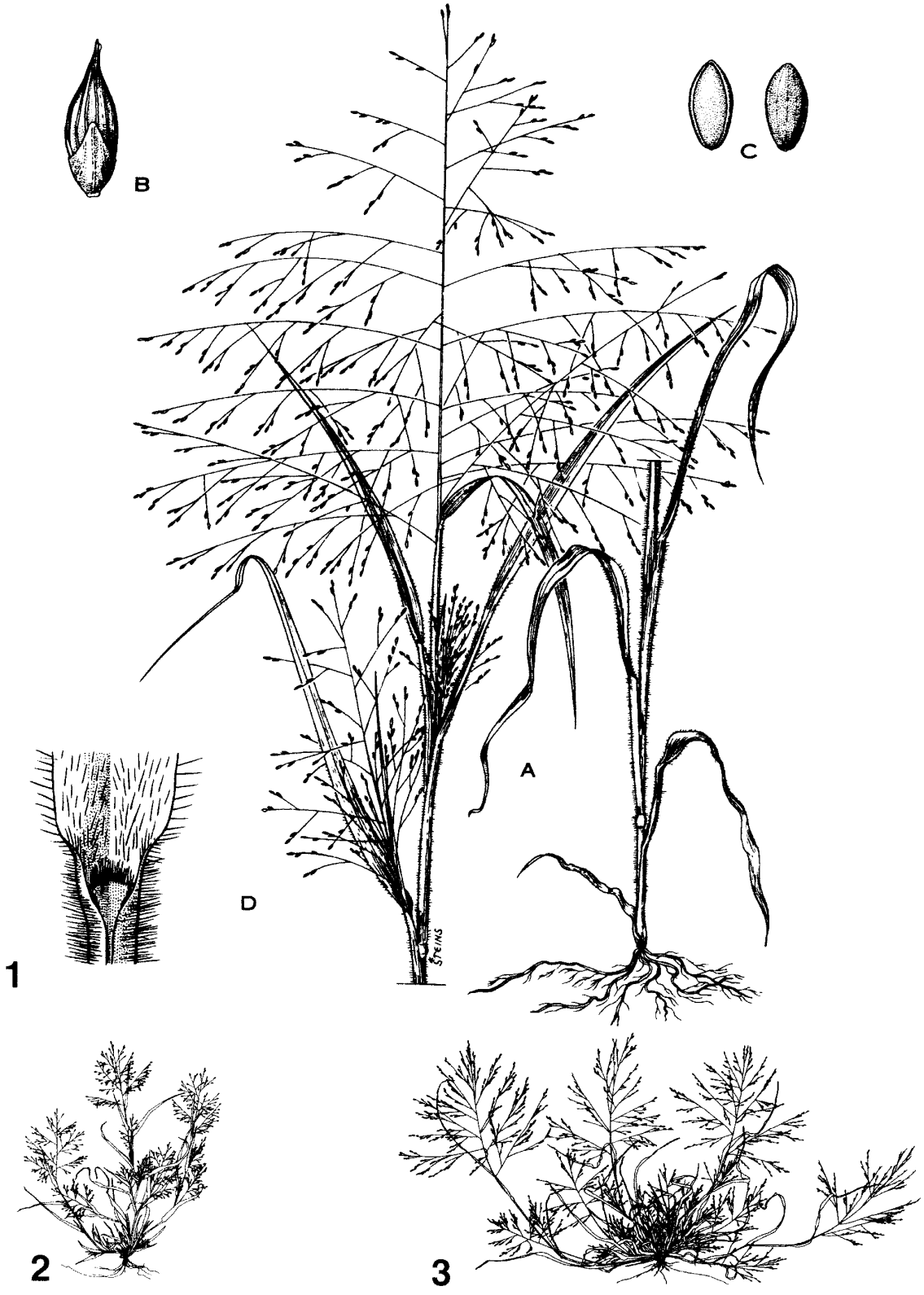
1. Mature spikelets 1.8–2.3 mm long ……var. *capillare*
1. Mature spikelets 2.4–4.5 mm long ……2
2. . . . . .Mature spikelets 2.4–2.9 (3.1) mm long; seeds 1.5 times as long as wide ……var. *brevifolium* Vasey ex Rydb. & Shear
2. Mature spikelets 3.0–4.0 (4.5) mm long; seeds 2 times as long as wide …… var. *barbipulvinatum* (Nash) McGregor

If varieties *brevifolium* and *barbipulvinatum* are taxonomically grouped together, the former name should be used. As pointed out by McGregor (1984a), the commonly used name, *P. capillare* var. *occidentale* Rybd. is illegitimate and must be discarded.

(d) *Illustrations – Panicum capillare* is illustrated in Fig. 1. Illustrations of the closely allied species, *P. gattingeri* and *P. tuckermanii* are given in Fig. 2 and Fig. 3, respectively. Illustrations are also published by Darbyshire and Cayouette (1995). Excellent colour photographs of mature plants and seedlings are found in Bouchard and Néron (1999).

3. Economic Importance

Detrimental—P. capillare is a native species in North America, adapted to areas of natural disturbance, but it



Figs. 1–3. Weedy species in the *Panicum capillare* complex. Fig. 1. *P. capillare*: A, habit of mature plant; B, spikelet showing first glume and sterile lemma; C, floret containing achene showing the palea (left) and lemma (right); D, junction of the leaf blade and sheath showing the ligule of hairs. Fig. 2. *P. gattingeri* mature plant habit. Fig. 3. *P. tuckermanii* mature plant habit.

assumes a weedy habit in cultivated crops and even in less disturbed habitats such as managed grasslands. Field crops commonly infested by *P. capillare* include corn, soybeans, winter wheat, and sorghum (Wax et al. 1981; Harman et al. 1989; Frick et al. 1990; Swanton et al. 1996; Unger et al. 1999). Wax et al. (1981) listed *P. capillare* as one of the seven most common annual grasses found in corn and soybeans. In small grain crops, *P. capillare* was among the three most common summer-annual-grass weed species in Nebraska where *P. capillare* and *Echinochloa crus-galli* (L.) Beauv. were the most difficult to control (Wicks et al. 1995). Despite the widespread presence of *P. capillare* in crops, the actual impact of *P. capillare* infestations on crop yield is not well documented.

P. capillare may also infest grasslands, particularly in conjunction with management practices that make use of fertilizers or herbicides (Morrow and Canode 1982; Berg 1995). These infestations result in decreased range quality and reduction of biodiversity, through displacement of perennial grasses. *P. capillare* is a nitrate accumulator and has been found to contain levels potentially toxic to livestock under certain conditions (Kingsbury 1964).

The other species within the *P. capillare* complex that is considered a serious weed is *P. gattingeri*. Mainly a problem in the northeastern United States, *P. gattingeri* is not yet widespread or common within Canada (Darbyshire and Cayouette 1995). Nevertheless, in the last 25 yr, both *P. gattingeri* and *P. tuckermanii* have become much more common as weeds in ruderal and agricultural habitats of southern Ontario and Québec.

Seeds of *P. capillare* may contaminate crop seeds (Tanji and Taleb 1997). *P. capillare* has been found associated with grain elevators in Canada and in Belgium (Lindsay 1977; Verloove 2001). *P. capillare* may also act as an alternative or transitional host for cereal aphids such as *Rhopalosiphum padi* L. and *R. maidis* Fiotch (Kieckhefer and Lunden 1983). It may also serve as a host for the planthoppers *Sogatodes oryzicola* Muir and *S. cubanus* Crawford which are vectors of the rice hoja blanca virus, one of the most destructive rice diseases in the Western hemisphere (Thresh 1981).

(b) *Beneficial*—Seeds of *P. capillare* are consumed by seed-eating birds, such as game birds and ground feeding songbirds and mammals (Baumgras 1943; Martin et al. 1951). It is an important component in the diet of at least two voles with broad distributions in North America, *Microtus pennsylvanicus* Ord and *M. ochrogaster* Wagner (Zimmerman 1965). Weaver and Albertson (1944) referred to *P. capillare* as an important ground cover under drought conditions in Kansas. It has been suggested that *P. capillare* may have potential for bioremediation of atrazine contaminated soils as mineralized ^{14}C-atrazine has been detected in microbial-rich rhizosphere soils around roots of *P. capillare* growing in highly contaminated areas (Anderson et al. 1995).

(c) *Legislation*—Québec lists *P. capillare* as a noxious weed under the Agricultural Abuses Act when it is growing in cultivated or pasture lands (Anonymous 1981), but it is not listed as a noxious weed in any other province. All *Panicum* species are listed as Class 5 noxious weeds under the federal seeds Act (Agriculture Canada 1986). The name "*Panicum vulgaris*" (sic) listed under Class 4 may apply to this species.

4. Geographical Distribution

Within Canada, *P. capillare* is found in all provinces except Newfoundland (Fig. 4). The most northerly locations mapped are at Dawson Creek, British Columbia (55°46′N, 120°14′W) and Pinehouse Lake, Saskatchewan (55° 32′N, 106° 36′W). Its distribution is somewhat limited in northern areas; e.g., within the clay belt just south of James Bay it occurs only as a weed of railway ballast and is not found elsewhere (Baldwin 1958). Lindsay (1977) found *P. capillare* growing among grain elevators at Thunder Bay, ON. Within North America, *P. capillare* var. *capillare* originally occurred indigenously from Florida to Texas north to southeastern Maine, southwestern Québec, southern Ontario; and west to southern Manitoba, and Montana (Hitchcock and Chase 1910; Fernald 1950).

The western var. *barbipulvinatum* ranged from Texas north to Illinois westward to the Pacific Ocean (Hitchcock and Chase 1910). *P. capillare* tends to be less common in western Canada than in eastern Canada. In a weed survey of cultivated land in Manitoba, it had a synthetic relative abundance value of less than 0.1 (Thomas 1978). By 1981, the relative abundance had increased to 0.4 (Thomas and Wise 1982). In a more detailed study of cereal and oilseed crops, Thomas et al. (1998) recorded a relative abundance for *P. capillare* of 0.2 for all fields in the Northwest Agricultural Region of Manitoba, and 0.4 in the Eastern Agricultural Region of the Province. A survey of 631 Manitoba cereal and oilseed fields in 2002 ranked *P. capillare* as the 92nd most common weed species (Leeson et al. 2002). It was only detected in the Interlake Plain and Lake of the Woods Ecoregion where it was encountered in oat fields. Although it is widely distributed across southern Manitoba (Fig. 4) it is an agricultural weed of significance primarily in the Red River Valley. It now occurs across southern Canada and throughout the United States (Fig. 4; Scoggan 1978; Häfliger et al. 1980).

P. capillare has been introduced to numerous temperate areas throughout the world, including Argentina, Chile, Europe, Asia, New Zealand, and Australia (Holm et al. 1979; Häfliger et al. 1980). It occurs in southern (Spain, Italy and Portugal), central (Germany, Switzerland, Hungary, Poland, and Romania) and eastern Europe (Russia) (Tutin et al. 1980). It is also found to a lesser extent in subtropical areas such as Hawaii (Holm et al. 1979) and Morocco (Tanji and Taleb 1997).

5. Habitat

(a) *Climatic requirements*—A warm season annual grass (Berg 1995), *P. capillare* occurs across a broad range of moisture levels and temperatures (Darbyshire and Cayouette 1995). Comparison of locations where it occurs in Canada provides an indication of the range of climates tolerated by *P. capillare*. The plant is found in Medicine Hat, AB, which receives an average of 347 mm of annual precipitation and

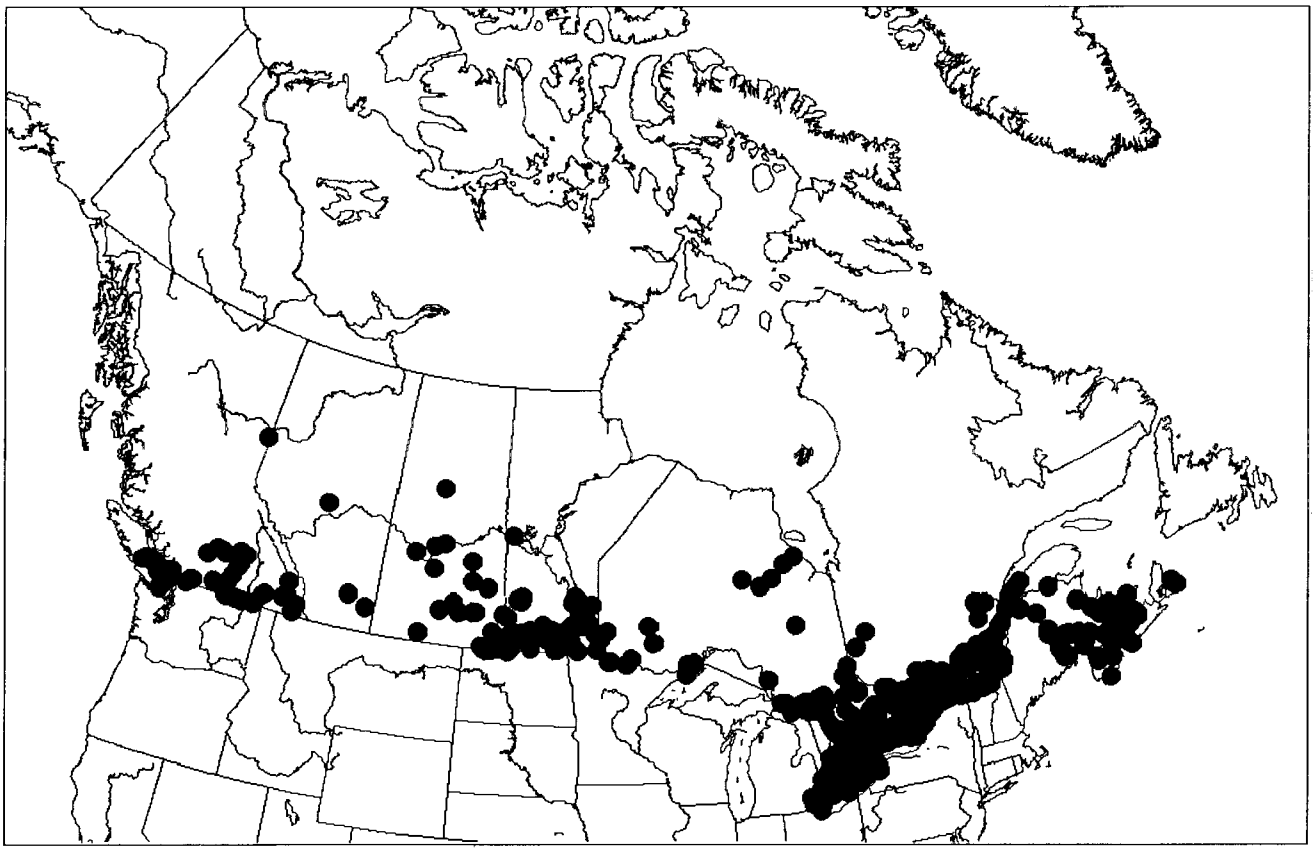


Fig. 4. The Canadian distribution of *Panicum capillare*. Mapped from over 1500 specimens from the following herbaria: ACAD, ALTA, CAN, DAO, MMMN, MT, MTMG, NFLD, NSAC, NSPM, OAC, QFA, QUE, SASK, SFS, UBC, UNB, UWO, V, WAT, WIN, with supplemental specimens from GH, NY and US. For abbreviations see Holmgren et al. 1990.

in Sydney, NS, where annual precipitation totals about 1400 mm. It occurs at Duncan, BC, which experiences a mean average temperature of 9.4°C and at The Pas, Manitoba, with a mean annual temperature of 0.3°C. Since this is a C_4 (NAD-ME type) species (Hattersley 1984), populations of *P. capillare* would be expected to be most successful under shorter day and higher temperature conditions towards the southern parts of its range. The lower water requirements of plants with the C_4 photosynthetic pathway, along with higher optimal temperatures, will facilitate competition with C_3 plants in open habitats having dry and hot microclimates. However, a lack of summer moisture is limiting. On the prairies, *P. capillare* is most common in mesic or irrigated areas (S. Darbyshire, unpublished observations).

(b) *Substratum—P. capillare* is capable of growing in a variety of soil types, ranging from dry mineral soils to rich loams characteristic of agricultural soils (Darbyshire and Cayouette 1995). Favourable soil types include the humid, cool boreal, brunisolic soils of the west coast; the semi-arid chernozenic soils of the prairies and the perhumid, cryboreal, podzolic soils of the Maritime Provinces. It particularly thrives in dry (Runnels and Schaffner 1931) or sandy soils (Weaver and Albertson 1944; Scoggan 1978). In southwestern Ontario, Frick et al. (1990) recorded the greatest frequency (21–25%) of *P. capillare* on Huron clay loam and Guelph loam soils. It was rare on clay and silt loam soils.

(c) *Communities in which the species occurs*—In general, *P. capillare* does not thrive in communities with dense shade (Fassett 1951). Natural habitats are open areas of disturbed or eroded soils including beaches and floodplains (Dore and McNeill 1980), loess prairies (Nicholson and Hulett 1969), alvars (Steyermark 1940) and burned Jack pine (*Pinus banksiana* Lambert) forests (Abrams and Dickman 1982). It is found in a wide variety of anthropogenically influenced communities including cultivated fields, meadows, gardens, and waste areas (Wax et al. 1981), roadsides and clearings (Dore and McNeill 1980), ditches and alkali flats (Cronquist et al. 1977), over-grazed native prairie pastures (Weaver and Albertson 1944), abandoned cultivated areas in the prairie region (Costello 1944), and burned-over bracken grassland (Vogl 1964).

In old fields, *P. capillare* tends to be an early successional species occurring in fields aged less than 5 yr (Costello 1944). In an old field community in Michigan, *P. capillare* was found growing with *Ambrosia artemisiifolia* L., *Elytrigia repens* (L.) Nevski (= *Agropyron repens* L.), *Plantago lanceolata* L., *Chenopodium album* L., *Trifolium repens* L., *Lepidium campestre* L., and *Daucus carota* L.

(T. Miller, personal communications). An Ohio community populated by *P. capillare* included *Amaranthus retroflexus*, *Chenopodium album*, *Polygonum persicaria* L., *P. pennsylvanicum* L., and *P. convolvulus* L. (Smith 1986).

In corn (*Zea mays* L.) fields in Québec, the most common species (found in more than 50% of fields surveyed) associated with *P. capillare* were: *Agropyron repens*, *Agrostis alba* L. (= *A. gigantea* Roth), *Amaranthus retroflexus*, *Ambrosia artemisiifolia*, *Asclepias syriaca* L., *Chenopodium album*, *Cirsium arvense* (L.) Scop., *Digitaria ischaemum* (Schreb.) Muhl., *Echinochloa crusgalli* (L.) P. Beauv., *Equisetum arvense* L., *Euphorbia helioscopia* L., *Galeopsis tetrahit* L., *Gnaphalium uliginosum* L., *Leucanthemum vulgare* Lam. (= *Chrysanthemum leucanthemum* L.), *Matricaria discoidea* DC. [= *M. matricarioides* (Less.) Porter], *Medicago sativa* L., *Oxalis stricta* L., *Phleum pratense* L., *Plantago major* L., *Polygonum convolvulus* L., *Polygonum persicaria* L., *Polygonum hydropiper* L., *Ranunculus acris* L., *Ranunculus repens* L., *Rumex acetosella* L., *Setaria pumila* (Poir.) Roem. & Schult. [= *S. glauca* (L.) P. Beauv.], *Setaria viridis* (L.) P. Beauv., *Solidago canadensis* L., *Solidago graminifolia* (L.) Salisb., *Taraxacum officinale* L., *Trifolium repens* L. and *Vicia cracca* L. (Lemieux et al. 1988b). In cereal fields in Québec, the most common associates were: *Acalypha rhomboidea* Raf., *Achillea millefolium* L., *Elytrigia repens*, *Agrostis gigantea*, *Ambrosia artemisiifolia*, *Sinapis arvensis* L. [= *Brassica kaber* (DC.) L.C. Wheeler], *Brassica rapa* L., *Capsella bursa-pastoris* (L.) Medik., *Cerastium fontanum* subsp. *vulgare* (Hartm.) Greuter & Burdet (= *C. vulgatum* L.), *Chenopodium album*, *Cirsium arvense*, *Echinochloa crusgalli*, *Equisetum arvense*, *Erysimum cheiranthoides* L., *Euphorbia helioscopia*, *Festuca rubra* L., *Fragaria virginiana* Mill., *Galeopsis tetrahit*, *Gnaphalium uliginosum*, *Hieracium aurantiacum* L., *Juncus tenuis* Willd., *Leucanthemum vulgare*, *Oxalis stricta*, *Matricaria discoidea*, *Medicago sativa*, *Phleum pratense*, *Plantago major*, *Poa annua* L., *Poa compressa* L., *Poa pratensis* L., *Polygonum aviculare* L., *Polygonum convolvulus*, *Polygonum hydropiper*, *Polygonum persicaria*, *Polygonum scabrum* Moench, *Potentilla norvegica* L., *Ranunculus acris*, *Ranunculus repens*, *Rumex acetosella*, *Setaria pumila*, *Silene vulgaris* (Moench) Garcke (= *S. cucubalus* Wibel), *Solidago canadensis*, *Solidago graminifolia*, *Spergula arvensis* L., *Stellaria graminea* L., *Stellaria media* (L.) Vill., *Taraxacum officinale*, *Trifolium pratense* L., *Trifolium repens*, *Vicia cracca*, and *Viola tricolor* L. (Lemieux et al. 1988a).

In southwestern Ontario, Frick et al. (1990) found that within no-till managed fields, *P. capillare* occurred most frequently in continuous corn fields, and in mixed annual and perennial crop rotation. It was less common in bean (soybean, white bean) fields and in fields under conventional tillage systems.

6. History

P. capillare is indigenous to the New World, and subsequent to European settlement of the Americas has become a cosmopolitan weed (Tutin et al. 1980; Baskin and Baskin 1986). Dore and McNeill (1980) report that *P. capillare* was originally found in areas within North America that were naturally open, such as beaches and river banks but its range quickly extended to fields, roadsides and gardens as human settlement advanced.

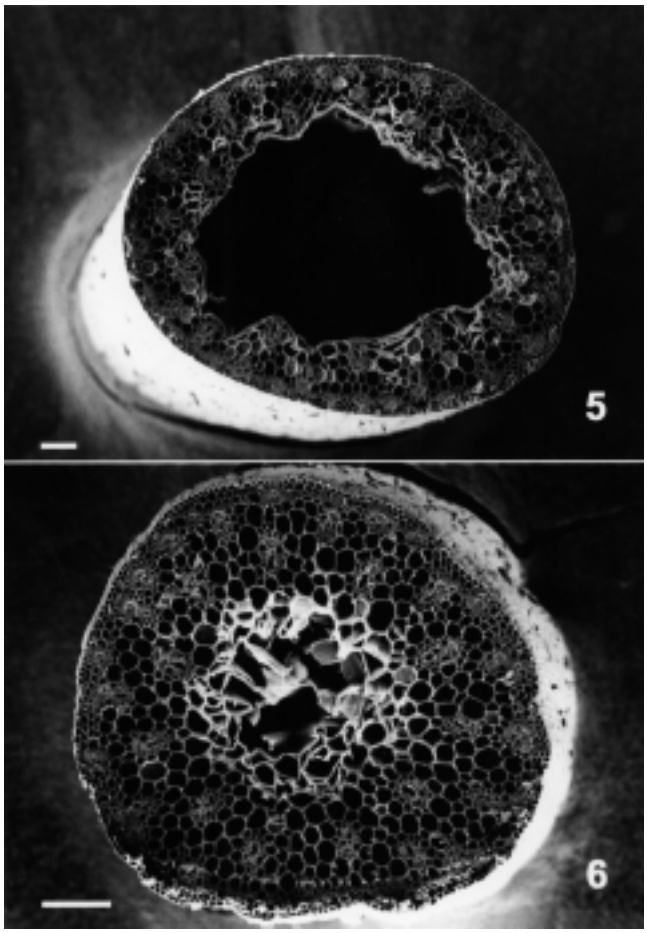
The earliest herbarium specimens indicate that by the 1870s it was already a common weed in eastern Canada. Well before the end of the 19th Century, Macoun (1888) documented it as a common weed in eastern Canada, although still restricted to lake and river shores in the west. According to Dore and McNeill (1980), it has become one of the most prolific weedy grasses in North America. Its invasiveness is largely accredited to its tumbleweed-like habit and association with seeds of timothy and clover that facilitate seed dispersal. The latter mechanism has been seen as a means of introduction of *P. capillare* into areas of Britain (Salisbury 1964). In addition, Verloove (2001) reports that occurrences of *P. capillare* in Belgium are mostly associated with grain importation.

Considered a serious agricultural and ruderal weed in Canada for more than 100 yr (Macoun 1888; Dore and McNeill 1980), *P. capillare* is probably the indigenous grass species of greatest abundance in eastern Canada (Dore and McNeill 1980). By contrast, other species within the *P. capillare* complex have only been reported as economically important relatively recently (Bouchard and Néron 1991). Analysis of herbarium specimens indicates that *P. tuckermanii* and *P. gattingeri* have only begun invading Canadian agricultural fields within the past 25 yr (S. Darbyshire, unpublished data).

7. Growth and Development

(a) *Morphology*—Vengris and Damon (1976) reported an average height at maturity of 96 cm, and an average of 8.5 tillers and 45.4 panicles per plant for *P. capillare* plants emerging on May 21 in Massachusetts, USA. Values for these growth parameters declined with later dates of emergence. For example, plants emerging on Jul. 6 averaged 53 cm in height, with 4.9 tillers, and 12.8 panicles, whereas plants emerging on Aug. 25, averaged 11 cm in height, with 2.5 tillers, and 2.6 panicles. However, maximum growth rates were observed when emergence was between Jun. 23 and Jul. 7 (Vengris and Damon 1976). Miller (1987) noted that aboveground biomass at the end of the growing season (late September) in a Michigan, USA, field was greatest for individuals emerging three to ten d after the first cohorts emerged. Gross et al. (1992) reported that roots of *P. capillare* began to branch 7 d after seeding.

Gross et al. (1992) found that roots of 12-d-old *P. capillare* seedlings exhibited a herringbone topology (i.e. magnitude = altitude, *sensu* Fitter 1985). This root pattern is thought to favour plants growing in water-limited habitats. Moreover, the proportion of dry biomass comprised by roots in these 12-d-old seedlings was 0.21 and the average specific root length was approximately 30 cm mg^{-1} (Gross et al. 1992). Darbyshire and Cayouette (1995) found that decumbent or prostrate stems of *P. capillare*, when elongated, frequently developed a zig-zag pattern to the internodes. Zgierska (1986) reported that *P. capillare* was resistant to trampling due to strong stem ramification.



Figs. 5–6. Cross sections of *Panicum* species in the lower region of the culm internode below a terminal inflorescence. Bar = 100 µm. Fig. 5. *P. capillare*, (Collection: Cody 35541). Fig. 6. *P. gattingeri*, (Collection: Cayouette and Darbyshire 6835).

Under controlled conditions, Brecke (1974) observed that *P. capillare* plants subjected to day-lengths of 8 or 10 hours formed rosettes rather than developing upright as was observed for plants subjected to day-lengths of 14 or 16 h.

(b) *Perennation* — No perennial growth of this annual grass has been reported. It overwinters only as seeds.

(c) *Physiological data*—As mentioned previously, *P. capillare* is a C_4 grass. The presence of the Kranz syndrome has been determined using carbon isotopic ratios (Smith and Brown 1973), leaf anatomy (Tregunna et al. 1970) and carbon dioxide compensation measurements (Downton and Tregunna 1968). Because of its C_4 photosynthetic pathway, *P. capillare* has often been used in comparative physiological studies evaluating the photosynthetic ability of mesophyll and bundle sheath cells or efficiency of C_3 versus C_4 plants (e.g., Edwards et al. 1974; Gutierrez et al. 1974a; 1974b; Ku et al. 1974; Ohnishi and Kanai 1983; Usuda et al. 1984; Gupta et al. 1994). Edwards et al. (1974) reported similar chlorophyll a/b ratios in mesophyll (3.85) and bundle sheath (3.20) cells. Moreover, the distribution of the photosynthetic enzyme, phosphoenolpyruvate (PEP) carboxylase was largely confined to mesophyll protoplast cells (562 µmoles mg^{-1} chl h^{-1}) compared with bundle sheath cells. In contrast, another key photosynthetic enzyme, ribulose-1,5-diphosphate (RuDP) carboxylase was mostly confined to bundle sheath cells (282 µmoles mg^{-1} chl h^{-1}).

Edwards et al. (1974) found that light-dependent fixation of CO_2 by *P. capillare* bundle sheath cells (103 µmoles CO_2 fixed mg chl h^{-1}) was the highest of six grass species tested. In addition, Gutierrez et al. (1974b) demonstrated that bundle sheath cells in this species were capable of performing photosynthetic CO_2 assimilation independent of mesophyll cells. Singh et al. (1974) reported that the response of *P. capillare* to increased light intensity did not follow typical patterns in terms of photosynthetic rate, light saturation, and extracted RuDP carboxylase activity. Photosynthetic rates and light saturation were the same at 50, 70, and 100% of full sunlight, but slightly reduced at 30% of full sunlight. However, *P. capillare* does not seem to thrive in shaded habitats. Further research is required to better elucidate the relationship between light intensity and growth in *P. capillare*.

Wilson and Tilman (1995) recorded a relative growth rate of 0.0271 [ln (g g^{-1})] d^{-1} in nitrogen-poor sand with no added nitrogen, and a relative growth rate of 0.0405 [ln (g g^{-1})] d^{-1} with 17 g N m^{-2} yr^{-1}. Total and root biomass were reported by Gross et al. (1992) to increase by 0.5 and 0.12 mg d^{-1}, respectively, and root length to increase by nearly 3 cm d^{-1}. Dillman (1931 cited in King 1966) recorded a transpiration coefficient of 254 (ratio of water absorbed to aboveground dry matter produced) and a transpiration efficiency (grams of dry matter produced per 1000g of water applied) of 3.94.

Zgierska (1986) reported *P. capillare* to be a salt tolerant plant, thus enabling it to exploit specialized niches created on roadsides where salt is used.

(d) *Phenology—P. capillare* is a summer annual (Hattersley 1984; Baskin and Baskin 1986). Throughout most of its North American range, flowering occurs in July and August (McWilliams and Ludwig 1972; Stevens 1975), and seeds mature by early to mid-October (Baumgras 1943). Photoperiod is important for inducing reproduction. Vengris and Damon (1976) reported that in Massachusetts, USA, *P. capillare* seeded on May 1 emerged, on average, 26 d later, and formed seed heads and mature seeds, on average, 80 and 105 d after seeding, respectively. Development periods were reduced for later seeding dates. For instance, plants emerging in late August produced seed heads 35 d after emergence. Seedlings emerging in the field on Aug. 9 and receiving at least 70% natural light produced mature seeds by the end of the growing season. Although *P. capillare* is relatively shade tolerant, Vengris and Damon (1976) found that shading reduced growth. Under 76% shade, seedling emergence was delayed by 4 d, production of first heads by 6 d, and the production of the first mature seeds was delayed by 10 d compared with non-shaded control plants. Plant development was negatively affected under 51% shade, however, 30% shade did not significantly delay seedling emergence, head or seed production.

In general, field emergence of *P. capillare* takes place later in the season than most other crop weeds (K. Chandler, personal communications) but can occur throughout the growing season. In agricultural fields of Massachusetts, Vengris and Damon (1976) observed seedlings emerging no earlier than May 14. Miller (1987) reported peak and mean emergence dates of May 11 and May 20, respectively, for *P. capillare* in a Michigan old-field.

Brecke (1974) found that a 10-h photoperiod in a controlled environment resulted in the shortest interval to flowering (20 d) of five photoperiods (8 to 16 h) tested. In contrast, plants subjected to a 16-h photoperiod required, on average, 70 d to flower. However, dry matter accumulation was substantially greater for *P. capillare* plants exposed to the 16-hr photoperiod than for plants exposed to any of the four shorter photoperiods tested.

(e) *Mycorrhiza*—Field inoculation of *P. capillare* with the vesicular-arbuscular mycorrhizal fungus, *Glomus intraradices*, increased total biomass, shoot biomass, and total phosphorus uptake at low phosphorus levels (2.0 mg P L^{-1} in solution), but not at high phosphorus levels (5.0 mg P L^{-1} in solution) (Boerner 1992). A specimen of *Acaulospora delicata* Walker, Pfeiffer & Bloss (DAOM 211664) was found with *P. capillare* on Beausoleil Island, Ontario.

8. Reproduction

(a) *Floral biology—P. capillare* florets appear to function either in a chasmogamous or cleistogamous fashion (S. Darbyshire, unpublished observations). The genetic and/or environmental factors that control floret opening and exposure of anthers and stigmas for cross-pollination are not known. Terminal inflorescences produced early in the season on plants that are not under abiotic stress, appear to be more chasmogamous than axillary inflorescences, produced later in the season or inflorescences produced on plants under abiotic stress. Control and expression of facultative cleistogamy in grasses is complex and poorly understood (Philipson 1986).

(b) *Seed production and dispersal—P. capillare* is a prolific seed producer, with a maximum seed output as high as 56 400 seeds per plant under non-competitive conditions (Stevens 1932). Gross et al. (1992) reported that *P. capillare* seeds collected from Michigan, USA, field populations had a mean seed mass of 0.15 mg. Shipley and Parent (1991) found the mean weight of *P. capillare* seeds from eastern Canadian populations to be 0.29 mg.

The seeds of *P. capillare* consist of the mature caryopsis securely enclosed by the indurate (hardened) floral bracts, the lemma and palea. These seeds are small (about 1–2 × 0.5–1 mm), unadorned and, in themselves, have no specialized dispersal mechanisms. There is, however, a dual mode of local and distance dispersal similar to that described for *Agrostis hyemalis* (Walt.) Britton, Sterns & Poggenb. by Rabinowitz and Rapp (1979).

Some seeds fall directly from the plant, in situ, but the mature inflorescence of *P. capillare* forms a voluminous spherical frame (King 1966) and also acts as a tumble-weed in dispersing seeds (Behrendt and Hanf 1979; Dore and McNeill 1980). In the Kansas dust storms of 1936, *P. capillare* seeds were prevalent in the drifts formed from windblown soil (King 1966). As the seeds mature the tissues of the inflorescence and the culm internode below the inflorescence become senescent and brittle. Tissues in the culm internodes disintegrate with age so that the mature culm becomes hollow (Figs. 5 and 6). In *P. capillare* there is extensive disintegration of medial tissues in the lower part of the culm internode below the inflorescence so that the supporting walls become thin and the central hollow region represents more than half the total culm diameter (Fig. 5). Other species in the complex that do not shed their inflorescences have a smaller central hollow (usually less than one third the culm diameter) and tend to have more extensive development of sclerenchyma tissues with thicker cell walls (Fig. 6). Before the seed fully matures the senescence and disintegration of culm tissues in *P. capillare* has progressed to the point where the main support for the inflorescence is the flag leaf sheath (S. Darbyshire, unpublished observations).

The sterile spikelet bracts (glumes and sterile lemma) are deciduous, but fall later than the seed (mature floret). Although the seeds shatter freely from the sterile bracts, a certain amount of force is required to shake them from these loosely enfolding bracts (S. Darbyshire, unpublished observations). Once the culm has fractured and the inflorescence drifts and rolls free in the wind, seeds are distributed widely. In both *P. capillare* and *P. gattingeri*, the primary abscission zone in seed shattering is above the glumes and below the fertile floret with a secondary zone below the glumes. In *P. tuckermanii*, however, the sterile bracts are shed with the fertile floret as the "seed".

Viable seeds of *P. capillare* have been retrieved from mud attached to shoes in London, Ontario (P. Cavers, unpublished observations). In laboratory tests, 12 to 100% of *P. capillare* seeds floated for over 1 h in still water and 4 to 50% remained afloat after 15 min in agitated water in a shaker (P. Cavers, unpublished observations). Viable seeds of *P. capillare* were found distributed throughout irrigation water in Yakima Valley, Washington (Kelley and Bruns 1975). Because *P. capillare* frequently grows on open emergent shorelines, water transport of seeds is inevitable.

Another significant means of dispersal of *P. capillare* seeds is as a contaminant of small crop seeds (Salisbury 1964; Wax et al. 1981). Seeds also may be dispersed by livestock. Muenscher (1955) reported that *P. capillare* seeds retained viability after passing through the digestive tracts of horses, cattle, swine and sheep. Post-dispersal seed predation by mammals and arthropods is reported for *P. dichotomiflorum* (Marino et al. 1997), and thus the seeds of *P. capillare* may be dispersed by these animals or birds as well.

(c) *Seed banks, seed viability and germination* —It is well known that seeds of *P. capillare* remain viable in the soil for long periods in a variety of environments (Pipal 1916; Prince and Hodgdon 1946; Livingston and Allessio 1968; Van der Valk and Davis 1979). Viable seeds were found in soil from 47-yr-old white (*Pinus strobus* L.) and red

(*P. resinosa* Ait.) pine plantations (Prince and Hodgdon 1946). Unger et al. (1999) found large numbers of *P. capillare* seeds in various crops in Texas, particularly in association with sorghum. Brecke (1974) reported a 95, 84, and 52% emergence for *P. capillare* seeds planted at depths of 0, 1.3, and 2.5 cm. No emergence was recorded for seeds planted at depths of 5.1 and 7.6 cm.

Freshly mature seeds are dormant (Brecke 1974; Baskin and Baskin 1986). Baskin and Baskin (1986) observed that all seeds were dormant at maturity in early October in Tennessee, USA. This dormancy was broken after burial throughout winter, but was again induced in ungerminated seeds during spring and summer. In late spring, seeds developed a light requirement for germination and by late summer 63–100% of seeds did not germinate under dark or light conditions. Thus, most seeds that do not germinate in the spring likely persist as dormant propagules in soil until the following season. Brecke (1974) found that *P. capillare* seeds collected in autumn in Central New York State had lost all dormancy after 5 months dry-storage in the dark at room temperature. Seeds of *P. capillare* from eastern Canada stored at room temperature for 6–8 mo did not show significant dormancy when planted in soil in a greenhouse, unlike those of other related *Panicum* species (S. Darbyshire, unpublished observations). Baskin and Baskin (1986) concluded that light is required for germination in *P. capillare* and that most seeds on the soil surface germinate under April day/night temperatures of 20/10°C in Tennessee. When Cross (1931) subjected seeds to a constant temperature of 20°C, less than 3% of seeds germinated, but when alternating temperatures of 20 and 30°C were used, germination increased to 91% on paper blotters and 39% on soil. Maximum germination generally occurs at temperatures of 25°C or higher (Rivera and Peters 1971; Vengris and Damon 1976; Baskin and Baskin 1986; Smith 1986). Brecke (1974) reported that alternating temperatures of 10/30°C were more important in triggering germination of *P. capillare* seeds than either storage temperatures (ranging from –15° to 22°C) or the number of weeks of storage (4 to 40 wk). Martin (1943) found that removing seed coats, either partially or wholly, from freshly harvested seeds increased germination. Removal of the lemma and palea resulted in greater than 90% germination of *P. capillare* seeds (Brecke 1974). However, simply causing a break in the seed covering without removing any of the exterior coating from seeds resulted in substantially lower germination (43%). Shipley and Parent (1991) reported 87% germination of 9-mo-old *P. capillare* seeds collected in Eastern Canada following a 30-d experimental period at day/night temperatures of 30/20°C under a natural 15-h photoperiod in a phytotron. Seeds required a minimum of 4 days to germinate and the maximum germination during any one 24-h period was 19%.

Variability in emergence of *P. capillare* under field conditions appears to be linked to temperature. Under simulated May day/night temperatures of 24/14°C, *P. capillare* seeds had a high rate of germination and a greater total percent germination compared with its congener *P. dichotomiflorum*. This difference was not observed under simulated July day/night temperatures of 30/20°C (Smith 1986). Non-dormant seeds germinated at percentages ranging from 76 to 100% under a variety of thermoperiods (15/6, 20/10, 25/15, 30/15, and 35/20°C) in the light (Baskin and Baskin 1986).

Methods employed successfully to break dormancy have included removal of seed coats, stratification, scarification and the use of anaesthetic substances. Data collected at the University of Western Ontario, in London, Ontario, over a number of years revealed that scarification increased germination by approximately 30% and gibberellic acid (0.1%) by 70–95% (P. Cavers, unpublished observations). Moreover, seeds stored outdoors in water or soil for at least 4 wk had greater than 90% germination. Brecke (1974) reported that 24-h exposure to a 500-ppm gibberellic acid solution resulted in a 30% increase in germination compared with controls, but that a 30-d exposure of seeds to indoleacetic acid (IAA) at concentrations ranging from 0.1 to 10 ppm had no effect on germination. Taylorson (1989) found that the anaesthetic substances benzyl alcohol, n-pentanol, n-propanol, n-butanol, ethanol, and diethyl ether stimulated germination of dormant *P. capillare* seeds, whereas methanol and 2-propanol did not. In contrast to seeds of *Amaranthus retroflexus* L. (redroot pigweed), seeds of *P. capillare* did not require the far-red absorbing form of phytochrome (P_{fr}) for these effects to occur (i.e. broadband red irradiation had no effect on germination responses by *P. capillare*). Germination of *P. capillare* caryopses induced by solutions of ethanol and ethyl ether was prevented by application of a pressure >1 MPa during the period of exposure to the anaesthetic (Hendricks and Taylorson 1980). This reversal by pressure of the effect of ethanol on germination indicated that cell membrane expansion might be involved in the germination process.

Sulphuric acid, mechanical scarification, 0.2% KNO_3, 0.1% NH_4HPO_4, and soil leachates promoted germination (i.e., total germination of 50–100%) of 4–5 mo-old seeds (Rivera and Peters 1971). Exposure to 97% sulphuric acid for 10 min resulted in a 41% germination of *P. capillare*, but germination dropped to 3 and 0% following exposure periods of 20 and 30 min, respectively (Brecke 1974). Very little germination occurred when seeds were exposed to sulphuric acid concentrations of 10, 20, 30, or 75% for either 10, 20, or 30 min. Germination of 2 mo-old *P. capillare* seeds exhibited a temperature and photoperiodic response, especially when KNO_3 was used as a moistening agent. However, exposure to dry heat, and exposure to freezing temperatures did not increase germination appreciably (i.e., less than 25% germination). Brecke (1974) also found that washing *P. capillare* seeds in running tap water for up to 96 h had no effect on germination.

As is characteristic of the genus *Panicum* (Hitchcock and Chase 1910) and most other related genera in the tribe Paniceae (Johnson and Watson 1983), there is a "germination flap" at the base of the indurate fertile lemma of *P. capillare*. A semicircular line of lighter tissue is visible near the base of the mature lemma. It outlines an area over the underlying embryo. This line marks the weaker tissues of an abscission zone along which the lemma ruptures, allowing the expanding radicle to emerge as if pushing back a flap or trap door. The expanding coleoptile of the shoot grows in the opposite direction and emerges from between the apex of the lemma and palea.

(d) *Vegetative reproduction—P. capillare* does not reproduce by any vegetative means.

9. Hybrids

No hybrids have been reported involving *P. capillare*.

10. Population Dynamics

P. capillare appears to be a relatively poor competitor. Kroh and Stephenson (1980) determined relative competitive ability and ranked four weedy species as follows: *Amaranthus retroflexus* L. > *Chenopodium album* L. > *Setaria viridis* (L.) P. Beauv. > *P. capillare* L. *S. viridis* is also a C_4 NADP-ME grass (see section 5a), but in a survey of weeds in Essex and Kent Counties in Ontario, Hamill et al. (1983) found *P. capillare* in 8.2% of fields surveyed, with an "overall relative abundance" value of 4.1, whereas *S. viridis* was found in 42.6% of fields with a relative abundance of 18.1. Kroh and Stephenson (1980) also found *P. capillare* to be more susceptible to interspecific competition than to intraspecific competition. Although tillering is common, shading greatly reduces the numbers of tillers and panicles produced (Vengris and Damon 1976). This factor, along with the relatively late emergence of *P. capillare* may contribute to its poor competitive ability (Vengris and Damon 1976; T. Miller personal communications).

According to Zgierska (1986), a late emergence time may favour *P. capillare* as a pioneer species in man-made environments such as snow dumps. Strong sunlight, heavy trampling and high salt concentrations, especially in the spring when the snow melts are characteristic of these sites. The ability to germinate in late season as well as a tolerance for salt enables *P. capillare* to exploit this specialized niche.

Populations of *P. capillare* increased in a mixed community of eight species subject to disturbance by tillage prior to sowing to a depth of 10 cm (Wilson and Tilman 1995). Without nutrient addition, growth rates of *P. capillare* were not affected by competition but with added nitrogen neighbouring plants suppressed its growth. The root:shoot ratio was greater in the presence of neighbours (Wilson and Tilman 1995).

11. Response to Herbicides and Other Chemicals

Good control (90–100% control under ideal conditions) of *P. capillare* is achieved in corn by the following soil-applied grass herbicides: flufenacet/metribuzin (0.57–1.0 kg a.i. ha^{-1}), metolachlor (1.14–1.6 kg a.i. ha^{-1}), EPTC (3.4–4.4 kg a.i. ha^{-1}), and dimethenamid (1.0–1.25 kg a.i. ha^{-1}) as well as a variety of tank mixes (Anonymous 2002). Isoxaflutole (105 g a.i. ha^{-1}) or metolachlor/atrazine (2.2–2.9 kg a.i. ha^{-1}) may also be used as more general herbicides, controlling broadleaf weeds as well. Postemergent grass herbicides with 90–100% efficacy in corn include metolachlor (1.14–1.6 a.i. kg ha^{-1}), dimethanamid (1.0–1.25 kg a.i. ha^{-1}), nicosulphuron (25 g a.i. ha^{-1}), and nicosulphuron/rimsulphuron (25 g a.i. ha^{-1}). A variety of tank mixes are also effective against *P. capillare* (Anonymous 2002). Nicosulphuron/rimsulphuron (25 g a.i. ha^{-1}) or linuron (1.1–2.25 kg a.i. ha^{-1}) may be used as a directed post-emergence spray. The sulphonylurea herbicide, DPX–79406, a 1:1 mixture of nicosulphuron and rimsulphuron controlled *P. capillare* seedlings with up to eight leaves, at doses as low as 3.1 g ha^{-1} and reduced dry weight by 94% (Swanton et al. 1996). Some corn varieties are sensitive to imazethapyr, but Wicks et al. (1997) found that imazethapyr was effective against *P. capillare* in conjunction with imidazolinone-resistant and -tolerant corn hybrids. Imazethapyr, glufosinate ammonium or glyphosate may be used to control *P.* capillare in the corresponding herbicide tolerant corn hybrids (Anonymous 2002).

A similar selection of herbicides is effective in soybean crops. In addition trifluralin (0.6–1.1 kg a.i. ha^{-1}) is recommended as a soil-applied grass herbicide, and the general broadleaf/grass soil-applied herbicides metolachlor/metribuzin (1.48–2.25 kg a.i. ha^{-1}), flumetsulam/metolachlor (2.2 kg a.i. ha^{-1}), imazethapyr (75–100 g a.i. ha^{-1}), and imazethapyr/pendimethalin (1.2 kg a.i. ha^{-1}) provide good control of *P. capillare* in soybeans (Anonymous 2002). Post-emergence options in soybeans include quite a range of chemicals not available in corn (Anonymous 2002): quizalofop-p-ethyl (36–72 g a.i. ha^{-1}), fenoxaprop-p-ethyl (54 g a.i. ha^{-1}), diclofop-methyl (1.0 kg a.i. ha^{-1}), sethoxydim (0.15–0.2 kg a.i. ha^{-1}), clethodim (30 - 90 g a.i. ha^{-1}), fluazifop-p-butyl (75–250 g a.i. ha^{-1}), and imazamox (25 g a.i. ha^{-1}). Soil-applied trifluralin (0.4–0.5 kg a.i. ha^{-1}) is the only recommended herbicide for control of *P. capillare* in winter cereals in Ontario (Anonymous 2002).

Wicks et al. (1995) found control of *P. capillare* ranged between 31 and 71% following applications of glyphosate plus 2,4-D plus atrazine at rates of 0.6, 0.8 and 1.7 kg ha^{-1}, respectively. Since *P. capillare* is a relatively late-emerging weed, the effectiveness of herbicides may be reduced if residues are degraded prior to the initiation of growth (Anderson 1985).

Control of *P. capillare* growing within perennial cool season grass crops (C_3 photosynthetic pathway) was achieved by applications of MSMA (monosodium methanearsonate) at rates of 3.36–6.72 kg ha^{-1} (Morrow and Canode 1982). Control at 3.36 kg ha^{-1} was 58% with a further reduction at 4.48 kg ha^{-1}, but there was no further reduction seen at higher rates.

Although some triazine herbicides are currently recommended for control of *P. capillare* (Anonymous 2002), resistant strains have been found in Ontario since 1981 when they were identified from Grenville and Grey counties (Stephenson et al. 1990). In the early 1980s, triazine-resistant biotypes of *P. capillare* were found along railway beds in most northeastern states from New York to Michigan (Parochetti et al. 1982). A triazine-resistant biotype was also reported from a cornfield near Holstein, Ontario (Bandeen et al. 1982). By 1990, the distribution of triazine resistant *P. capillare* had expanded to include Norfolk, Prescott and Wellington counties.

Robinson and Greene (1976) measured the relative translocation of the herbicides simazine and atrazine from roots to shoots of 2–4 leaf *P. capillare* seedlings. In comparison to crabgrass [*Digitaria sanguinalis* (L.) Scop.], *P. capillare* seedlings were able to translocate more of the herbicides to shoots and metabolize less product thus making it more susceptible to triazine herbicides. *P.capillare* is more susceptible to simazine than to atrazine. Both herbicides are

translocated to the shoots and susceptibility depends on the rate of their conversion to hydrophilic metabolites (Robinson and Greene 1976).

12. Response to Other Human Manipulations

Cultivation may provide control of *P. capillare*, and mowing or burning prior to production of seeds has been recommended (Runnels and Schaffner 1931). Frick et al. (1990) reported that *P. capillare* was more frequent in corn (maize) fields (especially continuous corn with no-till management) than in bean fields or in fields with conventional tillage. Different crops vary in their ability to compete with *P. capillare*. Wicks et al. (1995) found that among barley, oats, spring and winter wheat, wheat was the most competitive.

The application of nitrogen to native warm-season grasslands in areas such as the US great plains region has been found to increase the herbage production of *P. capillare* at the expense of some of the perennial grasses such as sideoats grama, *Bouteloua curtipendula* (Michx.) Torr. (Huffine and Elder 1960; Launchbaugh 1962; Berg 1995). This tendency was reduced during years of reduced moisture availability (Berg 1995).

13. Response to Herbivory, Disease and Higher Plant Parasites

Herbivory

(a) Mammals—*P. capillare* seeds may form an important constituent in the diets of the voles *Microtus pennsylvanicus* and *M. ochrogaser* (Zimmerman 1965).

(b) Insects—Kieckheffer and Lunden (1983) reported that four cereal aphid species, the greenbug, *Schizaphis graminum* Rondani, the English grain aphid, *Macrosiphum avenae* F., *Rhopalosiphum padi* L., and the corn leaf aphid, *R. maidis* Fitch, fed and reproduced on *P. capillare* seedlings or adult plants in the US northern plains. However, the preference for *P. capillare* was not as strong as for barley and some other grass species. Kroh and Beaver (1978) found that a variety of phytophagous insects occurring in Michigan preferred to feed on *Chenopodium album* L. when exposed to a mixture of plant species, including *C. album*, *Amaranthus retroflexus*, *Setaria viridis* (L.) Beauv. and *P. capillare*. This was consistent with the hypothesis proposed by Caswell et al. (1973) that C_4 grasses are a relatively poor food source for herbivores. Among the four plant species, the highest biomass of non-herbivores was collected from *P. capillare*, but no indication was given as to the identity of these species (Kroh and Beaver 1978). Larvae of the clouded skipper, *Lerema accius* (J. E. Smith), are reported to feed on *P. capillare* in the Washington, DC, area (Etheridge 1998).

(c) Other invertebrates—*P. capillare* was reported to act as a host for the root-lesion nematode, *Pratylenchus penetrans* (Cobb) Filip. & Stek in the United States (Miller and Ahrens 1969). In Ireland, it was recorded as a host reservoir for root eelworm, *Heterodera schachtii* Schmidt, a pest of sugar beet (Gahan 1955). Bélair and Benoit (1996) reported that *P. capillare* was not a suitable host for the northern root-knot nematode, *Meloidogyne hapla* Chitwood in Québec. O'Bannon et al. (1984) reported that *P. capillare* was a poor host for the Columbia root-knot nematode, *Meloidogyne chitwoodi* Golden et al.

Diseases

(a) Fungi—In Canada, the Ustillaginales fungi *Puccinia emaculata* Schw. and *Sporisorium cenchri* (Lagerh.) Vánky (= *Sorosporium cenchri* Henn.) have been reported from *P. capillare* (Conners 1967; Ginns 1986). In addition to these species, a wider range of fungi has been reported on *P. capillare* in the United States (Farr et al. 1989), including the Oomycetes *Phytophthora cactorum* (Lebert & Cohn) J. Schröt., *Pythium debaryanum* auct., *P. graminicola* Subram. and *Sclerophthora macrospora* (Sacc.) Thirum., C. G. Shaw & Naras., the Ascomycete *Phyllachora graminis* (Pers.:Fr.) Nitschke, the Ustillaginales *Sorisporium destruens* (Schltdl.) Vánky and *Tilletia barclayana* (Bref.) Sacc. & Syd., the Basidiomycete *Thanatephorus cucumeris* (A. B. Frank) Donk, the Hyphomycetes *Bipolaris sorokiniana* (Sacc.) Shoemaker, *B. yamadai* (Shoemaker) Y. Nisik., *Dreschlera gigantea* (Heald & F. A. Wolf) Ito, *Fusarium acuminatum* Ellis & Everh., *F. equiseti* (Corda) Sacc., *F. oxysporum* Schltdl.:Fr., *F. poae* (peck) Wollenw., *F. sporotrichoides* Sherb., *Helminthosporium* sp. and *Microdochium bolleyi* (R. Sprague) de Hoog & Herm.-Nijhof., the Coelomycetes *Ascochyta graminicola* Sacc., *A. sorghi* Sacc., *Colletotrichum graminicola* (Ces.) G. W. Wilson, *Phoma terrestris* E. M. Hansen, *Phyllosticta owensii* R. Sprague, *Septoria arechavaletae* G. Winter, *S. tandilensis* R. Sprague, and the Deuteromycete *Rhizoctonia solani* Kühn.

(b) Bacteria—No information is available on the occurrence of bacteria on *P. capillare*.

(c) Viruses—Field sampling in Kansas revealed that *P. capillare* acts as a host for wheat streak mosaic virus, WSMV (Christian and Willis 1993). This virus is also found in Canada, and is spread by the wheat curl mite, *Eriophyes tulipae* Keifer (Slykhuis 1953). Using a bioassay procedure, *P. capillare* was identified as a potential host for bromegrass mosaic virus (BMV), a virus that causes severe disease in a variety of crops including corn (Ford et al. 1970). In New York State several strains of Barley yellow dwarf virus (BYDV), a phloem-limited luteovirus transmitted by several species of aphids, have been found on wild grasses including *P. capillare* (Power and Remold 1996).

Brunt et al. (1996) report that *P. capillare* is susceptible to a number of seed and vector transmitted viruses, including barley stripe mosaic hordeivirus (BSMV), foxtail mosaic potexvirus (FoMV), Johnsongrass mosaic potyvirus (JGMV), maize chlorotic mottle machlomovirus (MCMV), maize dwarf mosaic potyvirus (MDMV), sugarcane mosaic potyvirus (SCMV), and wheat American striate mosaic nucleorhabdovirus (WASMV). They also report that it is not susceptible to guinea grass mosaic potyvirus (GGMV). This is not an indication of natural host range, but only as a potential host.

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