The biology of Canadian weeds. 121. *Galium mollugo* L.

D. Mersereau and A. DiTommaso[1]

Department of Crop and Soil Sciences, Cornell University, Ithaca, NY, USA 14853.
Received 14 September 2001, accepted 18 December 2002.

Mersereau, D. and DiTommaso, A. 2003. **The biology of Canadian weeds. 121. *Galium mollugo* L.** Can. J. Plant Sci. **83**: 453–466. *Galium mollugo* L. (smooth bedstraw) is a long-lived perennial broadleaved plant that reproduces both vegetatively and by seed. *Galium mollugo* can be a strong competitor in long-lived forage crops such as bird's-foot trefoil (*Lotus corniculatus* L.), timothy (*Phleum pratense* L.), and orchard grass (*Dactylis glomerata* L.), as well as in short-lived forage crops such as red clover (*Trifolium pratense* L.) and yellow sweet-clover [*Melilotus officinalis* (L.) Lam.]. It is also a problem weed in spruce plantations and re-vegetation areas. Livestock typically avoid this species, allowing it to become well-established in pastures where it outcompetes more favourable species. Moreover, *G. mollugo* is viewed as a successful invasive species because of its ability to colonize and proliferate in areas such as established meadows where most invasive species do not thrive. In natural meadow communities, *G. mollugo* is often a dominant species that is capable of colonizing areas left vacant by the death and/or displacement of other species. Under favourable conditions, *G. mollugo* growth and clonal expansion can increase rapidly. *Galium mollugo* is generally tolerant to herbicides such as 2,4-D, MCPA, 2,4-DB, and dicamba.

Key words: Smooth bedstraw, GALMO, *Galium mollugo,* Rubiaceae, weed biology, pastures

Mersereau, D. et DiTommaso, A. 2003. **Biologie des mauvaises herbes au Canada. 121. *Gaium mollugo* L.** Can. J. Plant Sci. **83**: 453–466. *Gallium mollugo* L. (gaillet mollugine) est une dicotylédone vivace longévive qui se reproduit autant de manière végétative que par le biais de semences. Il arrive que le gaillet parte férocement à la conquête de cultures fourragères longévives comme le lotier corniculé (*Lotum corniculatus* L.), la fléole (*Phleum pratense* L.) et le dactyle pelotonné (*Dactylis glomerata* L) mais aussi de cultures fourragères de courte durée tels le trèfle rouge (*Trifolium pratense* L.) et le mélilot (*Melilotus officinalis* (L.) Lam.). Cette adventice s'avère problématique dans les peuplements d'épinettes et les zones reboisées. Comme le bétail l'évite naturellement, le gaillet s'implante bien dans les pâturages, où il surpasse les espèces plus intéressantes. On qualifie le gaillet mollugine d'envahisseur efficace, car il réussit à coloniser des endroits où la plupart des espèces envahissantes ne parviennent pas à s'implanter, tels les prés biens établis, et à y proliférer. Dans les prairies naturelles, *G. mollugo* fait souvent partie des espèces dominantes capables de coloniser les emplacements que la destruction ou le déplacement d'autres espèces laissent vacants. Quand les conditions sont favorables, l'espèce s'étend rapidement par une vive croissance et par reproduction clonale. Le gaillet mollugine tolère généralement les herbicides comme le 2,4-D, le MCPA, le 2,4-DB et le dicamba.

Mots clés: Gaillet mollugine, GALMO, *Gallium mollugo*, Rubiacées, biologie des mauvaises herbes, pâturages

1. Name

Galium mollugo L. – **smooth bedstraw** or **gaillet mollugine** (Darbyshire et al. 2000), white bedstraw (Scoggan 1979; Crompton et al. 1988; Crowder et al. 1996; Qian and Klinka 1998; Hinds 2000), baby's breath (Hinds 2000; Crompton et al. 1988; United States Department of Agriculture – Natural Resources Conservation Service 2001), cleavers (Roland and Zinck 1998); wild madder (Hinds 2000), caillelait (Hinds 2000), gaillet (Crompton et al. 1988), gratte-cul (Crompton et al. 1988), gratteron (Crompton et al. 1988), rable (Hinds 2000). Rubiaceae, Madder family, Rubiacées. Bayer Code GALMO (Darbyshire et al. 2000).

2. Description and Account of Variation

(a) *Physical Description* – The following description is based on information from Alex (1992), United States Department of Agriculture – Agricultural Research Service (1971), Gleason and Cronquist (1991), Gray (1970), Grime et al. (1981), Kinne (1955), Korsmo (1935, 1954), Lawson (1976), Michalková (1993), Muenscher (1980), Parakh and Schreiber (1960) and Scoggan (1979) and observations by the authors. *Galium mollugo* is a long-lived perennial broadleaved plant that reproduce both vegetatively and by seed. Seedlings are totally glabrous with oblong cotyledons 8–11 mm long and 3.5–4.5 mm wide, oblong true leaves 6.0–7.0 mm long and 3.0–4.0 mm wide, with the second set of true leaves having rigid tips (Fig. 1f). Individual plants are 25–120 cm tall with a strong, much branched taproot that is 3.5–4.5 mm in diameter and can attain a depth of 50 cm. Woody rhizomes are branching and articulate, 1.0–3.5 mm in diameter, and spread horizontally producing new stems and roots at their nodes (Fig. 1a). The root system is dense and characteristically reddish-orange in colour while the rhizomes are yellow to orange. Most rhizomes are found in the top 5 cm of soil. Stems emerge from a crown-like clump that can attain a diameter of 20–60 cm. The stems are slender and soft, smooth to slightly pubescent, and angular with four or five longitudinal ribs, 1.0–3.5 mm in diameter, mostly unbranched in the lower part, but with two

[1]*To whom correspondence should be addressed (e-mail: ad97@cornell.edu)*

or sometimes four opposite branches arising from each node higher up on the stem (Fig. 1c). Internode lengths of plants in Ithaca, NY, ranged from 3.5 to 11.0 cm, with the longest internodes in the middle of the stem. Individual stems are 30–120 cm long. Stems are at first erect but soon become matted and climb over adjacent vegetation. Both roots and stem bases contain secondary vascular tissue. Leaves are bright green, oblanceolate or obovate or linear, 1–3 cm long and 0.20–0.35 cm wide, arranged in whorls, 7–12 (mostly 8) in each verticil on the main stems and 5–8 (mostly 6) in each verticil on the branches, entire, flat, or with slightly recurved margins, with one vein and are mucronate (i.e., having rigidly-pointed tips) (Fig. 1c). Leaf margins may be antrorsely scabrous (i.e., hairs pointing forward) with hairs mostly 0.06–0.10 mm long. Flowers are bisexual, white to greenish white in colour, with four stamens and two styles connected at the base. Stamens are free, sessile at the corolla with filaments straight, 0.3–0.4 mm long, and glabrous. Anthers are straight, oblong, black-brown, connective thread-shaped, dark reddish-brown, and 0.30–0.35 mm long. Styles are terminal, central, bipartite, half-globose, and glabrous and 0.20–0.25 mm long. The inflorescence is a loosely branching, almost leafless, many-flowered panicle (composed of cymes), with branches 5–15 cm long, the lowermost being the longest. Branches and pedicels are mostly wide spreading (Fig. 1d). The calyx is slightly dentate and has reduced lobes. The corolla is wheel-like, with a flat limb, 2–5 mm across, and contains four oblong mucronate petals. The ovary is inferior, brown-green with white spots, glabrous, and the body of the ovule is fully inverted, so that the micropyle is basal, adjoining the funiculus. The fruit is a schizocarp 1.0–2.0 mm thick, splitting into two carpels, each containing one seed (Fig. 1e). Seeds are kidney-shaped to globular, glabrous, wrinkled, and brown or dark brown in colour. Seeds in Europe have been found to average 1.0–1.5 mm in length, 0.50–1.25 mm in width, and have a mean weight of 0.4–0.6 mg.

The diploid number of chromosomes ($2n = 22$) has been reported in the United States (Batra 1984) and Canada (Gleason and Cronquist 1991) as well as in Europe (Michalková 1991; Natali and Jeanmonod 1992). Gleason and Cronquist (1991) indicate that individuals with $2n = 44, 66, 88$ have also been reported, though they do not specify where.

(b) *Distinguishing morphological features* – There are over 30 species of *Galium* in Canada and the northern United States according to Canadian national and provincial floras (Budd and Best 1964; Rousseau 1974; Scoggan 1979; Moss 1983; Catling et al. 1985; Morton and Venn 1990; Gleason and Cronquist 1991; Rouleau and Lamoureux 1992; Qian and Klinka 1998; Roland and Zinck 1998; Hinds 2000). Fifteen of these species are commonly found in the same regions where *G. mollugo* occurs. The fifteen *Galium* species can be identified using the key in Key 1, which has been adapted from Moss (1983) and Gleason and Cronquist (1991).

Galium mollugo can be distinguished from all other *Galium* species in Canada based on the following combination of characteristics: it is a rhizomatous perennial with leaves in whorls of 5–8 (12), which are mucronate and less than 3 cm long with one prominent vein, whose corolla is white or greenish white, ovary and fruit are smooth or slightly roughened and glabrous (see Section 2a for a more complete description of the species).

The annual *Galium aparine* L. (catchweed bedstraw or cleavers) is common in most of the same geographic locations as *G. mollugo* and is a better-known *Galium* species. Accounts for *G. aparine* and *G. spurium* L. have been presented in a previous Biology of Canadian Weeds account (Malik and Vanden Born 1988). *Galium aparine* can be distinguished from *G. mollugo* by the presence of bristles on stems, leaf tips and fruit. The stems and leaf tips of *G. mollugo* are smooth to slightly pubescent and the fruit is glabrous and wrinkled. *Galium spurium* is almost indistinguishable from *G. aparine*, and is frequently misidentified as such (Malik and Vanden Born 1988). The most obvious differences between these two species are their fruit size, flower size, and flower colour. *Galium aparine* flowers are larger (2 mm in diameter) and white, whereas flowers of *G. spurium* are 1.0–1.5 mm in diameter and greenish-yellow in colour (Moore 1975). The fruit of *G. aparine* is typically 2.8–4.0 mm long, but fruits of *G. spurium* are 1.5–2.8 mm long (Moss 1983).

Galium verum L. (true bedstraw or lady's bedstraw) can hybridize with *G. mollugo* and the two species can often be found growing in the same communities. The species can be confused because both have a perennial habit and strong creeping base. However, stems on *G. verum* are thinner and firmer, so tend to stand more erect than those of *G. mollugo* (Alex 1992). *Galium verum* also has a bright yellow corolla with inflorescences of dense panicles. The panicles in *G. mollugo* are looser, almost leafless, and support white flowers.

(c) *Intraspecific variation* – A highly polymorphic taxon, *G. mollugo* is usually considered as a species aggregate (Ehrendorfer et al. 1976) with numerous specific and subspecific segregates. Many of these segregate taxa are controversial (Ehrendorfer et al. 1976) and no clear consensus is found in the taxonomic literature (Stephen J. Darbyshire, personal communication, Agriculture and Agri-Food Canada - Eastern Cereal and Oilseed Research Centre, Ottawa, ON). Some of the synonyms attributed to this plant include *G. mollugo* var. *latifolium* Leers, *G. elatum* Thuill. [*G. mollugo* var. *elatum* (Thuill.) DC., *G. mollugo* subsp. *elatum* (Thuill.) Syme], *G. flaccidum* Salisb., *G. insubricum* Gaudin [*G. mollugo* subsp. *insubricum* (Gaudin) Arcang.], *G. pruense* C. Koch, and *G. tyrolense* Willd.[*G. mollugo* subsp. *tyrolense* (Willd.) Hayek] (Ehrendorfer et al. 1976; Kerguélen 1993; Michalková 1993).

Plants with more erect inflorescences and larger flowers are sometimes recognized as a distinct taxon, *G. album* Mill. (e.g., Ehrendorfer et al. 1976; Michalková 1993). Some authors do not distinguish this entity from *G. mollugo* at any taxonomic level (Boivin 1966; Hinds 2000), while others consider it at subspecific ranking of *G. mollugo* subsp. *erectum* Syme (Scoggan 1979) or *G. mollugo* var. *erectum* Asch. (Catling et al. 1985; Roland and Zinck 1998). Hinds (1986) initially recognized this entity at a subspecific level, however demoted it as a taxon and simply listed it as a synonym of *G. mollugo* in later work (Hinds 2000).

Key 1. Key for separation of the 15 species of *Galium* found in Canada and the Northern United States and which occur in regions occupied by *G. mollugo*

A. Fruit smooth to granular, with rounded to small sharp projections, but without hairs or bristles
  B. Stems erect or nearly so
    C. Principal leaves 3-nerved, in whorls of 4; flowers white .... *G. boreale*
    C. Principal leaves 1-nerved, in whorls of 5 or more; flowers white, greenish or yellow
      D. Leaves flat or slightly revolute; flowers white or greenish .... *G. mollugo*
      D. Leaves strongly revolute; flowers bright yellow .... *G. verum*
  B. Stems weak and ± matted, ascending or reclining or scrambling
    E. Leaves sharply pointed, the main ones in whorls of (5-)6 .... *G. asprellum*
    E. Leaves blunt or rounded to almost pointed, mostly in whorls of 4–6
      F. Corollas 2-4 mm wide, mostly 4-lobed, the lobes longer than wide
        G. Cymes repeatedly branched, bearing 5-many flowers; nodes glabrous .... *G. palustre*
        G. Cymes once or twice branched, bearing 2-4 flowers; nodes pubescent
          H. Leaves ascending or loosely spreading, usually 2.5–6 mm wide; mature fruit 2–2.8 mm .... *G. obtusum*
          H. Leaves ± recurved or reflexed when mature, mostly 1.0–2.5 mm wide; mature fruit 1–1.8 mm .... *G. labradoricum*
      F. Corollas less than 2 mm wide, mostly 3-lobed, the lobes about as wide as or wider than long
          I. Pedicels flexuous, curved at the tip, (6)8–20 mm long, densely minutely roughly hairy with hairs hooked backwards; leaves mostly in whorls of 4; flowers solitary (or 2) on peduncles; peduncles flexible .... *G. trifidum*
          I. Pedicels stiff, not curved at the tip, 3–8 mm long, glabrous; leaves mostly in whorls 4–6 (usually at least some 5-6 leaves); flowers mostly 2–3 on each peduncle; peduncles stiff .... *G. tinctorium*

A. Fruit bristly or hairy
  J. Main leaves in whorls of 4; stems erect or ascending, not roughly hairy.
    K. Flowers (and fruits), mostly sessile or subsessile, lateral on inflorescence branches
      L. Leaves oval or elliptic, widest near the middle, apex obtuse .... *G. circaezans*
      L. Leaves lanceolate, widest below the middle, acute or acuminate. .... *G. lanceolatum*
    K. Flowers (and fruits) all on stalks, terminal on inflorescence branches
        M. Leaves broadly obovate to broadly ovate-elliptic, margins glabrous; inflorescence diffuse, few flowered; pedicels (4)5–15 mm long; hairs of fruit hooked .... *G. kamtschaticum*
        M. Leaves lance-linear; margins ciliate; inflorescence dense, many flowered; pedicels 1-4 mm long; hairs of the fruit not hooked .... *G. boreale*
  J. Main leaves in whorls of 6 or 8; stems prostrate or ascending; roughly hairy with hairs -hooked backwards
          N. Perennial; stems glabrous or slightly pubescent; flowers 2–3 mm wide; leaves roughly hairy on the margins with hairs directed towards the tip, other hairs hooked backwards on the midvein beneath .... *G. triflorum*
          N. Annual; stems roughly hairy; flowers 1–2 mm wide; leaves roughly hairy with hairs hooked backwards on the margins and often the midvein beneath
            O. Stem nodes glabrous to slightly pubescent; flowers 1.0–1.5 mm wide, greenish yellow; fruits 1.5–2.8 mm long (excluding spines) .... *G. spurium*
            O. Stem nodes usually covered with tangled or matted, woolly hairs; flowers 2 mm wide, white; fruits mostly 2.8–4.0 mm long (excluding spines) .... *G. aparine*

Natali and Jeanmonod (1992) examined differences in pollen shape and structure of these plants on the Mediterranean island of Corsica and assigned them species rank (i.e., *G. album* Mill.). In Europe, Michalková (1993) also identified *G. album* as a separate species from *G. mollugo*, distinguishing between the two by using a number of characteristics including inflorescence length, corolla diameter and leaf size. She found that *G. album* inflorescence lengths range from 6.2–10.5 cm, corollas are 2.9–3.8 mm in diameter, and leaves are 1.2–2.0 cm long and 0.15–0.30 cm wide. In contrast, *G. mollugo* inflorescence lengths range from 10.6 to 12.7 cm, corollas are 2.0–5.0 mm in diameter, and leaves are 1.0–3.0 cm long and 0.20–0.35 cm wide.

The high degree of variability in *G. mollugo*, which has been the cause of this taxonomic controversy among European researchers, is evident in North America and Asia as well (Lawson 1976; Muenscher 1980). Plants with more erect inflorescences and wider corollas have been reported in Prince Edward Island (Catling et al. 1985), New Brunswick (Hinds 1986), Nova Scotia (Roland and Zinck 1998), and eastern Québec (Scoggan 1979). In reviewing 162 dried specimens of *G. mollugo* from the southeastern United States, Lawson (1976) found a high level of variability in terms of size, shape, and pubescence of leaves and of abundance and size of flowers. Even specimens collected from the same site showed important stem and flower size variations. Hara (1983) reported leaf size variation in Japanese populations.

There does not appear to be any consistent difference in morphological characteristics between the species in North America and Europe. European descriptions of the species (Korsmo 1935; Korsmo 1954; Michalková 1993) are consistent with their North American counterparts (Kinne 1955; Lawson 1976; Gleason and Cronquist 1991; Alex 1992; and based on the collections of eight Canadian herbaria: WIN, UBC, CAN, MT, DAO, SASK, UNB, and NFLD), in terms of pubescence, abundance and size of flowers, and shape, length, width, and pubescence of leaves, although there are significant degrees of intracontinental variability both in Europe and North America.

(d) *Illustrations* – Figure 1 includes line drawings/images of *Galium mollugo* (a) base of stem rooting at nodes, (b) aboveground growth form, (c) leaf arrangement, (d) inflorescence, (e) fruit, and (f) seedling.

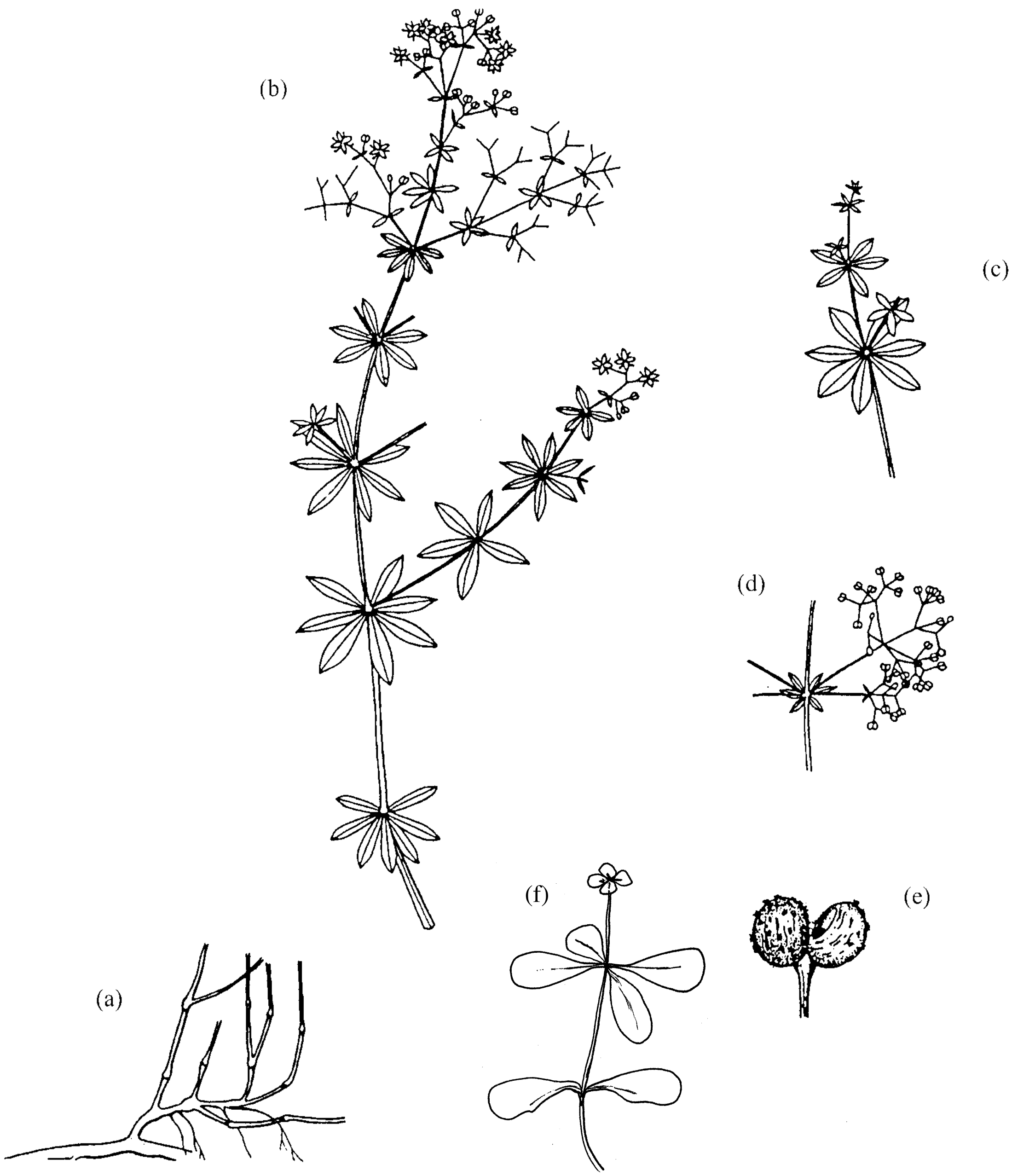

Fig. 1. *Galium mollugo* (a) base of stem rooting at nodes × 1, (b) aboveground growth form × 0.5, (c) leaf arrangement × 1, (d) inflorescence × 1, (e) fruit × 8 and (f) seedling × 2. Fig. 1(a) to (e) reprinted with permission from Michalková (1993), Preslia **65**: 201–207. Fig. 1(f) by Laurie Hanley, Cornell University, Ithaca, NY.

3. Economic Importance

(a) *Detrimental* – Unlike *G. aparine* and *G. spurium*, which infest row crops and for which annual yield and economic losses can be calculated easily, economic losses due to *G. mollugo* infestations are more difficult to quantify because this species is typically found in mixed forage pastures with highly variable soils and topography. Hence, the value of the livestock is often the only economically measurable end product in such systems (Batra 1984). However, *G. mollugo* can be a strong competitor in long-lived forage crops, such as bird's-foot trefoil (*Lotus corniculatus* L.) (Kinne 1955; Parakh and Schreiber 1960), timothy (*Phleum pratense* L.) and orchard grass (*Dactylis glomerata* L.), as well as in short-lived forage crops, such as red clover (*Trifolium pratense* L.) and yellow sweet-clover (*Melilotus officinalis* (L.) Lam.) (H. McClelland, personal communication, MAPAQ, Buckingham, QC). It is also a problem weed in spruce plantations and re-vegetation areas. In pasture areas of eastern Canada and the Northeastern United States, between 10 and 80% of the land area may become infested by *G. mollugo* (see Section 10). In timothy (*Phleum pratense* L.) fields in New Brunswick, competition with *G.*

mollugo has been observed to eliminate 80–90% of the grass sward (Doohan 1981). As dairy farms continue to be consolidated in Eastern Ontario and southern Québec and land is converted to less-intensively managed pastures or to long-term hayfields, spread of the species has and will continue to occur, since *G. mollugo* thrives in these environments. The species is spreading at an increased rate in Ontario, Québec (H. McClelland, personal communication), New Brunswick (McCully 2000) and Prince Edward Island (C. Lacroix, personal communication, University of Prince Edward Island, Charlottetown, PEI), and was listed as one of the leading weed problems in New Brunswick in 2000 (McCully 2000).

Livestock typically avoid this species, such that it becomes firmly established and highly competitive in pasture areas, displacing more palatable forage crops (Parakh and Schreiber 1960; J. Ivany, personal communication, Agriculture and Agri-Food Canada, Crops and Livestock Research Centre, Charlottetown, PEI). In addition, *G. mollugo* contains anthraquinone compounds, which have systemic toxicity to mammals and may result in skin irritation or sensitization (Batra 1984).

Galium mollugo has also been found to be a host or secondary food source for various European plant pests, including pear aphids [*Dysaphis reaumuri* (Mordv.) and *D. pyri* (Boy.)], cherry aphids *Myzus cerasi* (F.), and various species of the genus *Formica* L., which transmit the trematode *Dicrocoelium lanceatum* Rud. to grazing livestock (Kolesova 1974; Grigorov 1977; Paraschivescu 1978; Rakauskas 1984).

(b) *Beneficial — Galium mollugo* has been used to curdle milk (Kinne 1955) and has served as an ornamental, particularly in rock gardens (Bailey 1947). The pollen of *G. mollugo* flowers also serves as a food source for a variety of beneficial non-phytophagous insects (Batra 1984). Tansley and Adamson (1925) reported that it was a food source for wild rabbits.

Anthraquinones found in this species (Heide and Leistner 1983) are used as purgatives and in the manufacture of vat dyes (Wilson and Marron 1978). Moreover, its roots contain high levels of pigments (Schulte et al. 1984) that are applied to seeds to make them distasteful to birds (Batra 1984). Bedstraw species, including *G. mollugo*, also contain mollugin (Schildknecht et al. 1976), flavonoids (Borisov 1974), coumarins, phenolic acids, and iridoid glucosides (Corrigan et al. 1978; Uesato et al. 1986). Some of these compounds have allelopathic, fungistatic, or repellent effects, and may also be used to flavour food or wine (Batra 1984).

(c) *Legislation – Galium mollugo* is not listed in the 1986 version of the Canada Seeds Act (Anonymous 2000), nor in any provincial noxious weed statutes but it has been informally categorized as a "minor invasive alien" weed of natural areas (White et al. 1993). This species is not listed as a federal or state noxious weed in the United States (United States Department of Agriculture - Animal and Plant Health Inspection Service 2000; National Plant Board 2000).

4. Geographical Distribution

Galium mollugo is found in many parts of Canada and the United States, as well as throughout Europe, western and parts of eastern Asia, and northern Africa (Korsmo 1935; Morita 1975; Holm et al. 1979;Hara 1983). It has been found as far south as New Zealand (Holm et al. 1979; Batra 1984) and as far north as Norway, where it is a common weed of cultivated land (Kinne 1955).

In Canada, the species is found in Newfoundland, Nova Scotia, Prince Edward Island, New Brunswick, Québec, Ontario, British Columbia and, just in the past decade, in Alberta (Gray 1970; Scoggan 1979; and based on provincial flora publications referenced in Section 2B and specimens from eight Canadian herbaria: WIN, UBC, CAN, DAO, MT, SASK, UNB, NFLD) (Fig. 2). In the United States, it is found throughout much of the eastern and western parts of the country, extending as far south as the state of Georgia (Fig. 3). The Canadian and U.S. distributions of *Galium mollugo* are shown in Figs. 2 and 3, respectively.

5. Habitat

(a) *Climatic requirements – Galium mollugo* prefers moist and cool temperate habitats both in Europe and North America (Psarski et al. 1971; Batra 1984; Hundt and Velve 1992), but has been found to tolerate drought in Tioga County, NY (Kinne 1955). The species has been found in diverse climates, including mountainous regions of the Pyrenees in southern France and northern Spain at altitudes of 350–1000 m above sea level, mean annual rainfall of 1200 mm, and mean annual temperatures of 12°C (Psarski et al. 1971; Onaindia and Amezaga 2000) and in central New York, USA, at elevations of 420 m, mean annual rainfall of 841 mm, and temperatures of 8.5°C (Mellinger and McNaughton 1975).

Specimens in the collections of various Canadian herbaria have also been gathered from diverse habitats. Specimens have been collected from Petit-Saguenay, Québec (DAO collection) where the mean annual rainfall is 712 mm and at Port-aux-Basques, Newfoundland (NFLD collection) where the mean annual rainfall is 1193 mm. Mean annual temperature at collection sites also shows a range of diversity, from 2.5°C at Petit-Saguenay (DAO collection) to 12.9°C at Upsalquitch Lake, New Brunswick (UNB collection). Specimens have been collected at altitudes of over 1170 m (Jasper National Park, AB, ALTA collection) and under 10 m (Bathhurst, NB; UNB collection). (Climate data obtained from Meteorological Service of Canada 2002).

(b) *Substratum – Galium mollugo* shows a marked ability to grow on a variety of soil types and under varying soil conditions. Collectors of Canadian herbarium specimens report finding the species in sandy, gravelly, and rocky soils as well as in clay soils, and under dry, well-drained, moist, wet, and marshy conditions (herbaria specimen label information: DAO; CAN; UNB; MT; WIN collections). *Galium mollugo* is primarily found in the Southeastern part of Canada where Podzolic and, to a lesser extent, Luvizolic soils are most common (Agriculture and Agri-food Canada - Research Branch 2001). *Galium mollugo* thrives in cal-

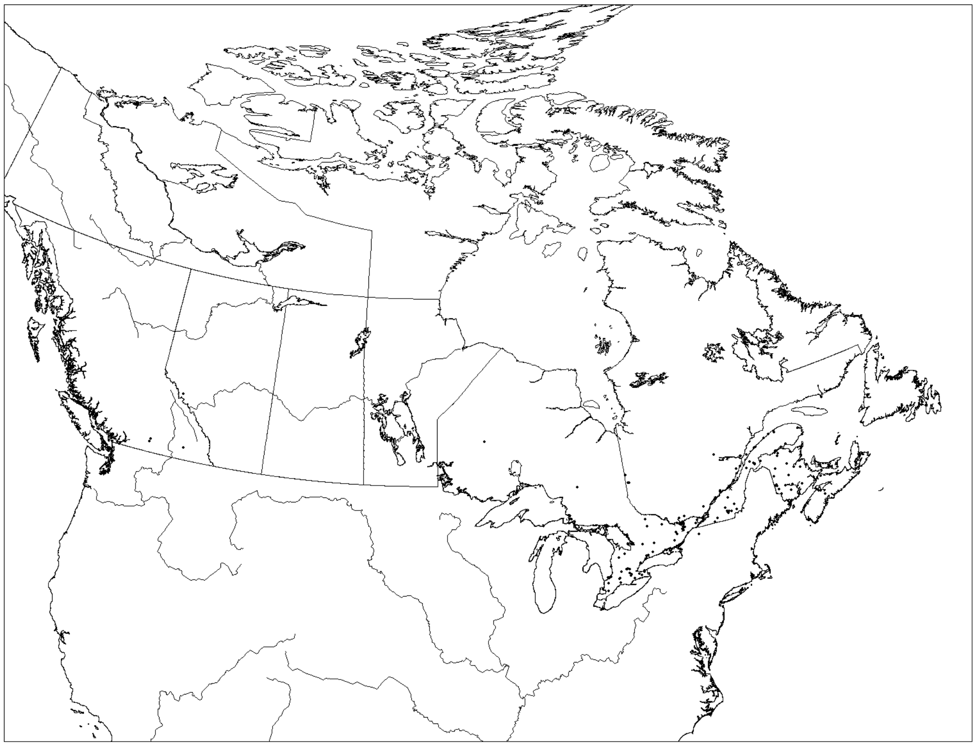

Fig. 2. The distribution of *Galium mollugo* in Canada. This map is based on herbarium specimens from WIN, UBC, CAN, MT, DAO, SASK, UNB, and NFLD collections [see Holmgren (2001) for detailed addresses].

careous and nitrogen-rich soils (Tansley and Adamson 1926; Booth 1974; Batra 1984) and is frequently found growing in thin layers of soil over limestone (herbaria specimen label information: CAN; DAO collections). Mellinger and McNaughton (1975) found *G. mollugo* growing in Onondaga County, NY on a Honeoye-Lima soil, a gray-brown, podzolic silt-loam, which was deep, well drained, and calcareous. Michalková (1993) found the species commonly growing in Central Europe on eutrophic and mesophytic soils. Steele (1955) classified *G. mollugo* as a calciole species being most successful on calcium-rich neutral soils, but with a considerable range of tolerance of pH and calcium levels. Steele (1955) also found *G. mollugo* growing in England on more acid soils with lower calcium concentrations and on neutral soils low in calcium. Similarly, Hundt and Velve (1992) reported the growth of *G. mollugo* on Norwegian soils with a pH of 4.5. Muenscher (1980) noted that in the northeastern United States the species was often found growing on gravelly or sandy loam soils. Many specimens have also been collected in Canada from sandy river beds or meadows or along gravelly railroad tracks and roadsides (herbaria specimen label information: UBC; DAO; CAN; UNB; NFLD; MT; SASK collections).

Galium mollugo does not grow well in saline soils. Bakker et al. (1985) found that the relative dry weight of greenhouse-grown *G. mollugo* plants watered with 50% Hoagland solution plus 5 g L^{-1} NaCl was 14.4% of the dry weight of plants watered with the nutrient solution alone. When 10 g L^{-1} NaCl was added to the nutrient solution, the relative dry weight of plants was only 2.3% of that for plants watered with the nutrient solution only. Similarly, Bakker et al. (1985) reported low germination levels for *G. mollugo* seeds sown in trays across a range of soil salinity concentrations (0–35 g L^{-1} NaCl). Bakker et al. (1985) also conducted a field experiment in an abandoned Dutch salt marsh, where soil salinity in the top 0–1 cm ranged from 0 to 3 g L^{-1} NaCl, and found that none of the seedlings emerging in plots with higher salinities survived the first year.

(c) *Communities in which the species occurs – Galium mollugo* is commonly found growing along roadsides, in pastures and natural meadows of varying age (Gray 1970; United States Department of Agriculture – Agricultural Research Service 1971; Mellinger and McNaughton 1975), and on dry hills and along hedgerows (Korsmo 1954). Montgomery (1957) found it a very common weed and sometimes the dominant vegetation along river flats. Montgomery (1957) also noted that it was common along roadsides and was invading cultivated fields in Southwestern Ontario. In New Brunswick, where it has been increasing steadily in the past 10–15 yr, it is found mostly along roadsides and in neglected fields (K. McCully,

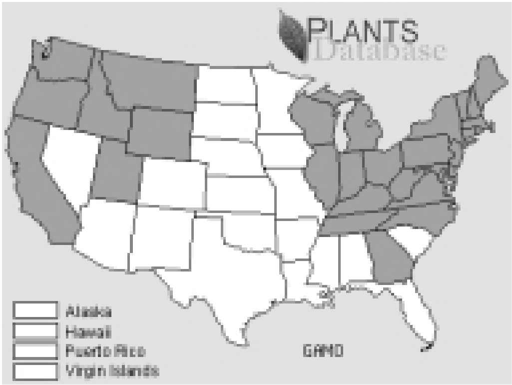

Fig. 3. Distribution (shaded areas) of *Galium mollugo* in the United States. Map reprinted with permission by USDA, NRCS, National Plant Data Center.

personal communication, New Brunswick Department of Agriculture, Fisheries, and Aquaculture, Fredericton, NB). In Prince Edward Island, it is likewise found in small patches in fields with frequent rotations, increasingly large patches in long-term pastures, and as extensive, rapidly spreading infestations along roadsides and in waste areas (J. Ivany, personal communication). It is a weed in lawns, orchards, vineyards, forest edges, and river flats (Batra 1984; Alex 1992) and is frequently found growing in the same locations as *G. verum* (Batra 1984) In Canada, *G. mollugo* has commonly been found growing in old fields in association with *Echium vulgare* L., *Rudbeckia hirta* L., *Agrostis* spp., *Solidago* spp. and *Setaria* spp., along marshy roadside edges with *Carex cryptolepis* Mackenzie and *C. vulpinoidea* Michx., in damp roadside thickets with *Echinocystis lobata* (Michx.) T. & G., and along deciduous forest edges dominated by *Quercus rubra* L., *Thuja* spp., *Salix* spp., *Alnus* spp., and *Acer saccharum* Marsh (herbarium specimen label information: CAN; UNB; DAO; WIN; MT collections). *Galium mollugo* commonly inhabits Canadian and U.S. fields of bird's-foot trefoil (*L. corniculatus*), timothy *(P. pratense*), and orchard grass (*D. glomerata*) (Kinne 1955; herbaria specimen label information: UBC; DAO collections), as well as red clover (*T. pratense*) and yellow sweet-clover (*M. officinalis*) (H. McClelland, personal communication; herbaria specimen label information: CAN collection). *Galium mollugo* was one of the most common species in Polish meadow-pasture communities, which included species such as *Festuca rubra* L., *Poa pratensis* L., *Dactylis glomerata* L., *Vicia cracca* L., *Trifolium repens* L., *Veronica chamaedrys* L. and *Stellaria graminea* L. (Grzegorczyk and Alberski 1999). Hundt and Velve (1992) have described in detail the *G. mollugo-Geranium sylvaticum* L. and *G. mollugo Leucanthemum vulgare* L. meadow communities in southern Norway. Onaindia and Amezaga (2000) found the species growing in mountainous woodlands of Spain that were dominated by *Quercus rubra* L. and other tree species such as *Fagus sylvatica* L., *Fraxinus excelsior* L. and *Castanea sativa* Miller.

6. History

Galium mollugo is thought to be indigenous to Eurasia (United States Department of Agriculture – Agricultural Research Service 1971) and was introduced into North America from Europe as an ornamental (Kinne 1955). The earliest specimen in Canada was collected by Mr. Fowler in Richibucto, New Brunswick, on 5 July 1873 (CAN collection). Specimens were next collected in Northumberland Co., Nova Scotia, on 1 August 1883 (CAN collection) and in a cultivated field in St. John's, Newfoundland, on 4 August 1894 (CAN collection). The first Ontario specimen was collected in a Toronto cemetery by W. Scott on 20 June 1898, and the first Québec specimen was found along the edge of a field in Rawdon, Québec in 1915 (DAO collection). The first collections in British Columbia, presumably of plants from a separate introduction, were in 1930 (DAO collection). Notes from labels of early specimens indicate that the species was introduced from Europe and describe the suitability of the species as a ground cover or decorative garden plant. However, even as early as 1902, *G. mollugo* was seen as a potential problem weed. In 1902, H. Tripp noted in a letter attached to an Ontario specimen that the species had probably been introduced to the field from which it was collected via contaminated seed, and that based on the size of the clumps already forming in the two-year old field, it was a species that could spread very rapidly and become a pest to farmers (letter to John Dearness, DAO collection).

Specimens collected in Alberta in 1994 (by Anne Holcroft Weerstra, ALTA collection) confirm the presence of the species along a roadside and railway bed in Jasper National Park, even though provincial and national floras do not yet list this species for Alberta (Scoggan 1979; Moss 1983; Gleason and Cronquist 1991).

7. Growth and Development

(a) *Morphology* – In North America, *Galium mollugo* plants can attain a height of up to 120 cm and, due to the large number and the decumbent nature of stems, vigorous mature plants can extend over an area 1 m or more in diameter, often smothering adjacent plants (Kinne 1955). Rhizomes are important carbohydrate stores that allow robust shoots to emerge in spring and tolerate clipping during the growing season (Kinne 1955). In Wyoming County, NY, the fibrous root system was often found entangled with the roots of nearby leguminous crops; Kinne (1955) suggested that the plant might be taking advantage of the nitrogen-fixing ability of these crops; however, further research needs to be carried out to determine whether or not this is the case.

Galium mollugo is an amphistomatous species (i.e., it contains stomata on both sides of leaves), with most being on the abaxial surface (Korsmo 1954). Kelly and Beerling (1995) found that in England the species had a total abaxial and adaxial stomatal density of 210 stomata mm^{-2}, a density that is typical of herbs growing along forest margins.

(b) *Perennation* – Kinne (1955) found that in western NY *Galium mollugo* overwintered via its woody stems, rhizomes and seeds. He also found that older plants with root crowns

20 cm and over in diameter could overwinter successfully and produce new shoots in the spring (Kinne 1955).

(c) *Physiological data* – Bedstraw species, including *G. mollugo,* contain mollugin (Schildknecht et al. 1976), flavonoids (Borisov 1974), coumarins, phenolic acids, and iridoid glucosides (Iavarone et al. 1983; Uesato et al. 1986). Some of these compounds are known to have allelopathic, fungistatic, or repellent effects (Batra 1984). The presence of these chemical compounds in *G. mollugo* has stimulated much research on methodologies for growing cell cultures as well as biochemical pathway and protein synthesis sequencing (Wilson and Marron 1978; Schulte et al. 1984; Mousdale et al. 1985; Fidgeon and Wilson 1987). *Galium mollugo* has also been used in bioassays assessing the effects of glyphosate on the shikimic pathway (Amrhein et al. 1980). Glyphosate was found to block the synthesis of anthraquinones in cell cultures and to cause a toxic buildup of shikimate. Recently, extracts from this plant were evaluated for their anti-cancer and anti-malarial activities and for their ability to inhibit HIV–1 reverse transcriptase, but initial results showed no activity (Grzybek et al. 1997).

Bakker et al. (1985) found the growth of *G. mollugo* to be suppressed under low-light conditions. Plants grown at 38 and 13% of full light under greenhouse conditions had 48 and 15% of the total dry biomass, respectively, compared with plants grown in full light. This preference for high light environments may explain why the species is most frequently found in open areas. In situations where *G. mollugo* must compete with neighbours for available light, its ability to grow over them is of competitive advantage.

Mellinger and McNaughton (1975) measured the aboveground productivity of *G. mollugo* on adjacent abandoned hayfields of different age in central New York State. On a field that had been abandoned for 36 yr, the productivity rate was 0.518 g^{-2} d^{-1}, whereas on an adjacent field that was abandoned for only 5 yr, the productivity rate was 0.092 g^{-2} d^{-1}. The authors suggested that changes in productivity rate may have been due to soil nutrient fluctuations that occurred through succession, including gradual enrichment of K, as well as increases in P, Mg, and Ca as shrubs invaded the fields. Productivity increased even though nitrate was depleted and pH had declined, suggesting that these factors were not significant enough to offset other benefits of succession. Köhler et al. (2001) found that *G. mollugo* shoot and root biomass were significantly more reduced in P-limited soils than in N-limited soils. They also speculated that when infected by well-established P-fixing mycorrhizal fungi, this species would be less impacted in P-limited soils.

High water tables negatively affect *G. mollugo* growth and development. Justin and Armstrong (1987) conducted experiments in which flats of this species were kept under flooded conditions for 1 mo (i.e., water level maintained at 10–20 mm above the soil surface). In flooded flats, *G. mollugo* had a maximum rooting depth and root length of 30 mm and 180 mm, respectively, compared with a maximum rooting depth of 37 mm and maximum root length of 264 mm in a well-drained soil. The ratio of fresh shoot weight for plants in flooded soil to that of plants in the well-drained soil was 0.4. Moreover, fractional root porosity and redox potential did not increase in response to flooding. There was secondary root growth under flooded conditions, but the secondary cortex was narrow and was of low porosity, indicating an inability by *G. mollugo* plants to adapt to flood conditions through aerenchyma formation.

(d) *Phenology* – In London, Ontario, seeds typically mature in September (P. Cavers, personal communication, University of Western Ontario, London, ON) and Roberts (1986) also found that seeds collected in September in the United Kingdom were mature. Kinne (1955) collected mature seeds in late July in central New York.

Seedlings typically emerge in the spring following the year in which they are produced in London, Ontario; few if any emerge in the fall that they mature in London or in central New York (P. Cavers, personal communication; A. DiTommaso, unpublished data). However in field experiments in the United Kingdom, Roberts (1986) found that many seedlings emerged in the fall from newly matured seeds (41% of seeds sown), though in the subsequent year, the largest number of additional seedlings emerged during the January-April period. An initial fall flush of seedling emergence was unusual in this study; of the 70 species examined, only one had a higher number of seedlings in the fall of sowing than *G. mollugo*. Since seeds appear to emerge in different seasons in the United Kingdom and in North America, further investigation into the effect of temperature and other factors on seed dormancy are required.

Plants that overwinter resume growth in early April, and flower in mid-June to August in Eastern Canada (Alex 1992; H. McClelland, personal communication) and in the northeastern United States (Muenscher 1980). When mowed in late June following flowering, secondary flowering typically takes place in August in New York (Kinne 1955) and in late September in Wales (Chater 1977). Leafy offshoots are produced from the rhizomes in late summer or fall (Gleason and Cronquist 1991) with plant growth continuing late into the fall (Kinne 1955; Alex 1992).

(e) Mycorrhiza – In pot experiments using soil collected from a calcareous grassland in Switzerland, Köhler et al. (2001) found that *G. mollugo* seedlings were infected by arbuscular mycorrhizal fungi within the first three weeks of growth. Although the identification of fungi infecting *G. mollugo* was not determined, it was speculated that these fungi might have improved the effects of limited P on *G. mollugo* growth (see Section 7C for details of the study).

8. Reproduction

(a) *Floral biology* – Flowers are bisexual (Korsmo 1954). Both cells of the ovary are usually fertile, but one is sometimes aborted (Armitage 1909). Flowers are fragrant and are visited by beetles, flies, ants, wasps, and short- or long-tongued bees (Batra 1984). Among the pollinating species Batra (1984) collected from the flowers of *G. mollugo* plants in New York and Vermont were: *Cantharis* sp., *Paravilla* spp., *Pollenia rudis* (F.) *Anthalia* spp., *Rhamphomyia* spp., *Cheilosia pallipes*

Loew, *Bombus pennsylvanicus* (De Geer), *Hylaeus ellipticus* Kirby, and *Dialictus* nr. *cressoni* (Robertson).

(b) *Seed Production and dispersal* – *Galium mollugo* produces two seeds per fruit (Korsmo 1935). The fruits dehisce passively when ripe (Korsmo 1954). Kinne (1955) determined that one of 18 stems from a single plant produced 2283 seeds and he was able to harvest 30 kg ha^{-1} of *G. mollugo* seeds from a field in Tioga County, New York.

Birds, water and contaminated crop seeds have been found to be the primary agents of seed dispersal in Europe and the United States (Korsmo 1935; Kinne 1955). Plants growing on sloped roadsides that are impractical to mow often set seeds, which are then carried to nearby fields by birds and/or water (Kinne 1955). In infested fields of bird's-foot trefoil (*Lotus corniculatus*) in Canada and the United States, seed contamination commonly occurs during harvest because the two species produce seeds at the same time of year and because seeds of both species are of similar size and difficult to separate (Kinne 1955; Tasse 2000). Contamination of bird's-foot trefoil seeds contributes to the entry of this weed into non-contaminated fields (Kinne 1955). This has been particularly problematic in Ontario, where contamination is resulting in the spread of *G. mollugo* from farm to farm and has prompted warnings to farmers by the Ontario Ministry of Agriculture, Food, and Rural Affairs (Tasse 2000).

The lack of adhesive structures such as hooks or bristles on *G. mollugo* seeds suggests that attachment to animal fur is not an important mode of dispersal. However, Fischer et al. (1996) found that some seeds of the species were transported by sheep in the UK and speculated that those seeds produced at heights of 61–80 cm were optimally-placed to come into contact with sheep fleeces and that the wrinkled surface of the seed was sufficient for attachment to wool.

(c) *Seed banks, seed viability and germination* – There are no data available on seed banks or seed viability of this species in Canada. Research in the United Kingdom has shown that *G. mollugo* seeds possess little or no innate dormancy and generally do not persist in soil for more than 1 yr (Roberts 1986; Grime et al. 1981). Roberts (1986) reported that 42% of seeds germinated during the first flush and another 17% by the end of the first year. Less than 1% of seeds germinated after the first year, with few viable seeds remaining. Onaindia and Amezaga (2000) found this species to have a transient seed bank lasting only until the spring in Spain, with all viable seeds germinating at that time.

Germination levels of *G. mollugo* seeds vary under different storage conditions. In the United Kingdom, Grime et al. (1981) reported that 70 and 98% of seeds germinated within 3 and 12 mo, respectively, of being dry-stored at 5°C. In Sweden, Kolk (1962) found that the initial high viability of hand and machine-collected seeds stored dry in an unheated location was preserved over 20–22 mo, but that samples stored for 32–34 mo decreased substantially in viability and germinability. *Galium mollugo* seeds collected near London, Ontario, over 7 different years and stored at room temperature for 8 wk prior to the start of experiments had greater germination after 3 wk in light (72%) [25/10°C day/night temperatures and 14-h photoperiod] than in the dark (54%) (Unpublished student data, University of Western Ontario, London, ON).

Roberts (1986) conducted a multi-year field germination study in the United Kingdom. He found that in spite of fluctuating moisture and temperature conditions during the years of the study, germination and emergence levels for *G. mollugo* were relatively consistent. Alternating temperatures, however, have been shown to influence germination levels under laboratory conditions. Grime et al. (1981) found very little germination (~1%) of fresh seeds 30 d after exposure to day/night temperatures of 20/15°C and a 15-h photoperiod. However, freshly collected seeds near London, ON, that were exposed to day/night temperatures of 25/10°C and a 14-h photoperiod had up to 80% germination after 35 d (unpublished student data, University of Western Ontario, London, ON). In the Netherlands, Bakker et al. (1985) found that dry-stored seeds were most successful in germinating at a constant 20°C (70% after 28 d), but that germination totals were slightly lower at 10°C (65%) and were below 10% at 30°C. Similarly, Kolk (1962) found that fresh seeds germinated best at 21°C and that the germination percentages were markedly reduced by lower as well as higher constant temperatures.

A constant temperature of 20°C resulted in greater germination (70%) of dry stored *G. mollugo* seeds after 28 d than a fluctuating 25/15°C temperature regime (50%) (Bakker et al. 1985). This effect was more pronounced at lower temperatures, where a fluctuating 15/5°C temperature regime resulted in 10% of seeds germinating as compared with 65% of seeds germinating at a constant 10°C.

Seed germination in *G. mollugo* is also suppressed under conditions of high salinity. Bakker et al. (1985) conducted greenhouse experiments in which dry-stored seeds were sown and watered with a 50% Hoagland nutrient solution and the addition of a range of NaCl concentrations from 0 to 35 g L^{-1}. *Galium mollugo* had 93% germination when no NaCl was added; however, germination dropped to 13% at a NaCl concentration of 5 g L^{-1}. No germination occurred at salt concentrations at or above 25 g L^{-1}.

Silvertown and Dickie (1981) studied seedling mortality among nine species in a British chalk grassland. They found that while seedling mortality in the first year exceeded 80% for most species, *G. mollugo* experienced a seedling mortality of only 67%, which was among the lowest in the group of species studied. The species had a half-life of 0.83 yr; this was the amount of time that elapsed before the seedlings of the species experienced 50% mortality. This was the longest half-life among the species studied.

(d) *Vegetative reproduction* – *Galium mollugo* reproduces vegetatively, primarily by rhizomes that produce new roots and shoots at each node (Kinne 1955). See also Sections 2(a) and 10.

9. Hybrids

Introgressive hybridization between *G. mollugo* and *G. verum* can result in aggressive weedy plants with variable intermediate morphological characteristics (Batra 1984).

These hybrids have been found in regions of Central Europe where the two species overlap (Lawson 1976). Batra (1984) reported finding hybrid populations in Plitivice, Yugoslavia and Lake Placid, NY. Hybrids have also been identified in Slovakia where they occur in disturbed habitats ranging from lowlands to submontane zones (Michalková 1993). Armitage (1909) identified three distinct forms of *Galium* hybrids growing with their parental lines in Herefordshire, England. Armitage (1909) noted that Hybrid A most nearly resembled *G. verum*, Hybrid C most nearly resembled *G. mollugo*, and Hybrid B possessed intermediate traits. Hybrid A had obscure stem angles, linear leaf shape, inrolled leaf margins, leaf lengths of 22 mm, pointed leaf apices, and lemon yellow coloured corollas. Hybrid C had winged stem angles, oblanceolate leaves, flat leaf margins, leaf lengths of 15 mm, stiffly pointed leaf apices, and cream coloured corollas. Hybrid B had obscure stem angles, lanceolate leaves, slightly rolled leaf margins, leaf lengths of 14 mm, pointed leaf apices, and buff-cream coloured corollas.

10. Population Dynamics

Under favourable conditions, growth and clonal expansion can occur rapidly (Kinne 1955). Moreover, *G. mollugo* is considered an effective invasive species because of its ability to colonize and proliferate in areas such as established meadows, where most invaders do not thrive (Tansley and Adamson 1925; Buchwald 1996). For instance, in a 4-ha bird's-foot trefoil pasture in Lodi, NY, *G. mollugo* density increased from a few scattered clumps of plants to more than 17 clumps m^{-2} in less than 10 yr (Kinne 1955). In pasture areas of eastern Canada, infestation levels within individual fields of 5–10% of the land area are common; however, infestations of up to 75% have been found in pastures of the St. John River Valley of New Brunswick and the Gatineau Valley of Ontario and Québec (H. McClelland, personal communication). In minimally managed New England pastures, *G. mollugo* has been reported to infest 80% of the land area within some fields, although 10% infestations are most common (Batra 1984). On sloped rights-of-way, where mowing is difficult, plants are able to form dense, uniform stands (Kinne 1955). In natural meadow communities, *G. mollugo* is often a dominant species (Jans and Schulz 1998) that is capable of colonizing areas that have been left vacant by the death of other species (Sustar 1988; Leskosek 1996). *Galium mollugo* competes effectively in bird's-foot trefoil, timothy and orchard grass fields because tillage operations are not performed for several years (Kinne 1955). Livestock prefer grasses and legumes over *G. mollugo* plants, thereby allowing this weed to mature and set seed in most pastures (Kinne 1955). In contrast, the weed does not compete effectively with vigorous fast-growing stands of alfalfa (*Medicago sativa* L.), since rotation cycles for alfalfa are generally short and include adequate tillage to reduce *G. mollugo* growth and spread (Kinne 1955).

11. Response to Herbicides and Other Chemicals

As a result of the perennial habit and extensive underground carbohydrate storage system of this species, treatment of *G. mollugo* using contact herbicides only causes top-kill and typically does not prevent new growth (Parakh and Schreiber 1960). Therefore, systemic herbicides are most effective for suppressing this weed. The auxin-type herbicide 2,4,5-TP has been used to control *G. mollugo* in pastures and grass hayfields (Hahn 1992); however, use of this herbicide was banned in both Canada and the United States in 1985 (Compliance Monitoring Staff – U.S. Office of Pesticides and Toxic Substances 1990; E. Chabot, personal communication, Pest Management Information Service). In Columbia County, NY, Hahn (1988) found that glyphosate had limited activity against this weed at rates of up to 4.5 kg a.i. ha^{-1}, when applied to *G. mollugo* in July after mowing, with 7–10 cm of regrowth. McCully et al. (1989) in Kings County, NB, reported that glyphosate applied at 3 kg a.i. ha^{-1} provided 95% control when sprayed on actively growing 30 cm tall *G. mollugo* plants and suggested using this systemic herbicide for site preparation before planting a new crop. Doohan (1981) found glyphosate completely effective in eliminating *G. mollugo* in New Brunswick when applied at 4 kg a.i. ha^{-1} to plants 58 cm tall and in the bloom stage. However by late summer, *G. mollugo* was re-establishing in sprayed areas, apparently from seed.

Hahn (1988) conducted field experiments in New York State to assess the efficacy of several herbicides sprayed on *G. mollugo* in autumn and spring. He rated control on a 0 to 10 scale, where 1 = no effect and 10 = complete kill. Dicamba was found to be ineffective except when applied in the autumn at a rate of 2.2 kg a.i. ha^{-1}; the control rating at this rate was 6.8 (Hahn 1988). Picloram was effective (control rating = 7.0 when applied in spring and 9.3 when applied in autumn) at rates as low as 0.14 kg a.i. ha^{-1} (Hahn 1988). Triclopyr + 2,4-D provided acceptable rates of control when applied in spring at rates of 0.6 kg a.i. ha^{-1} and 1.1 kg a.i. ha^{-1} respectively (control rating = 7.8), or in autumn at 0.4 kg a.i. ha^{-1} and 0.8 kg a.i. ha^{-1}, respectively (control rating = 8.5).

Picloram + 2,4-D (applied at 0.51 kg a.i. ha^{-1} and 2.0 kg a.i. ha^{-1}, respectively), hexazinone (applied at 4.0 kg a.i. ha^{-1}) and triclopyr (applied at 1.8 kg a.i. ha^{-1}) were tested for control of *G. mollugo* in timothy (*Phleum pratense* L.) in New Brunswick (Doohan 1981). Both picloram + 2,4-D and triclopyr provided over 95% control in the year of and 1 yr following the trial, with no significant damage to the timothy. Hexazinone reduced *G. mollugo* stands by 88% in the year of spraying and 73% in the year following spraying. Hexazinone also reduced timothy stands by 37% in the year of spraying, however those stands recovered and were considerably larger and more vigorous than those in control plots in the following year.

McCully et al. (1991) tested the efficacy of several herbicides including mecoprop, triclopyr, fluroxypyr, and dicamba + mecoprop in controlling *G. mollugo* in hay in New Brunswick when applied either immediately after cutting or 2 wk after cutting. Three months after application, plots sprayed with triclopyr showed the greatest reductions in *G. mollugo*; however, control was significantly better when the herbicide was applied after 2 wk of re-growth (92% control) than when applied immediately after cutting (78.5% control).

In greenhouse pot trials, quinmerac applied at 1 kg a.i. ha^{-1} effectively killed all *G. mollugo* plants within 4 wk of spraying, as did fluroxypyr when applied at 0.2 kg a.i. ha^{-1} (Boatman and Bain 1992). In field experiments by Kleijn and Snoeijing (1997) in the Netherlands, fluroxypyr applied yearly for 3 yr at 0.1 kg a.i. ha^{-1} when plants were about 20 cm tall decreased the percentage of plots in which *G. mollugo* was present from 90% in the second year to 10% in the third year. Kinne (1955) found mecoprop to be ineffective against *G. mollugo* in a bird's-foot trefoil pasture in Seneca County, NY. However, Marrs et al. (1991) in a UK study reported reductions in biomass, coverage and flower production following exposure to mecoprop drift. This herbicide was also found to be effective when applied at a rate of 2.0 kg a.i. ha^{-1} to actively growing plants in a French meadow (Psarski et al. 1971). Two years following application, the frequency of *G. mollugo* was reduced to 0% from an initial frequency of 22% at the start of the trial (Psarski et al. 1971). In Kings County, NB, Doohan (1980) found that mecoprop reduced *G. mollugo* in timothy by 75–80% when applied in early July, but less than 30% when applied in mid-August. The Ontario Weed Committee (2000) reports an "intermediate response" by the species to mecoprop; where an intermediate response is defined as "killed less rapidly (than by a herbicide to which the species is susceptible) but controlled by higher rates or repeated applications." In Canada, *G. mollugo* has been found generally tolerant to applications of MCPA, 2,4-DB, 2,4-D, and dicamba (Doohan 1981; Ontario Weed Committee 2000). Jansson (1974) found in Sweden that *G. mollugo* plants tolerant or resistant to 2,4-D contained higher levels of vitamin K compared with susceptible plants and speculated that vitamin K was offsetting the effects of the herbicide.

12. Response to Other Human Manipulations

Galium mollugo does not tolerate tillage (Kinne 1955). Historically, recommendations for control of the species in Canada and the United States have included plowing highly infested fields, growing a cultivated crop, and then reseeding a forage crop (Muenscher 1980; Hahn 1992). This method can be successful but costly, particularly for animal producers (Hahn 1992; J. Ivany, personal communication). Although clipping is not effective in killing *G. mollugo*, it can prevent seed production (Kinne 1955; Muenscher 1980). Clipping a mixed stand of bird's-foot trefoil and *G. mollugo* in Seneca County, NY, to a height of 5 cm every 2 wk throughout the summer resulted in dwarfed plants of both species, but *G. mollugo* stand density was not affected (Kinne 1955).

13 Response to Herbivory, Disease, and Higher Plant Parasites

Herbivory

(a) and (b). *Mammals, birds and/or other vertebrates* – Kinne (1955) investigated grazing by sheep in Lodi, NY, as a means of control and found that only after all other species in a pasture had been consumed was grazing on *G. mollugo* observed. Geese will not consume the plant, even when no other food is available for extended periods of time (Kinne 1955). Cattle have been found to graze on young, tender plants, but avoid mature plants in hay both in Canada and the United States (Kinne 1955; McClelland, personal communication), in spite of the fact that nutritional analysis of *G. mollugo* plant samples collected near Florenceville, NB, in early July 1992 showed that levels of several nutrient quality parameters are comparable to those of common forage crops (Sample Analysis Report, NB Department of Agriculture 1992). For instance, the level of crude protein in *G. mollugo* samples was 13.1% of dry matter, acid detergent fiber = 37.0%, total digestible nutrients = 56.6%, neutral detergent fiber = 45.2%, calcium = 1.3%, and phosphorus = 0.3%. Nutritional analysis of *G. mollugo* samples collected on another New Brunswick farm in August 1992 showed in vitro true digestibility and cell wall digestibility levels of 80.0 and 51.1%, respectively.

(c) *Insects* – Batra (1984) reported small natural populations of phytophagous insects on *G. mollugo* in North America and Europe. Many gall insects in Europe that use *G. mollugo* as a host plant are themselves parasitized by wasps, thereby maintaining their populations at low levels (Batra 1984). In Europe, natural insect populations were highest in unmown fields and in mown fields in late summer (Batra 1984). Not surprisingly, low populations of natural enemies are present in North America where *G. mollugo* is a relatively recent arrival (Batra 1984).

In their native Europe, Batra (1984) found the gall-forming Eurasian Cecidomylidae to be the most conspicuous, ubiquitous, damaging, and relatively host-specific of 145 insects studied on *G. mollugo*. Among the most effective Cecidomylidae were: (1) *Clinodiplosis auripes* (F.) Lw., which formed subterranean rhizome galls on plants, (2) *Contarinia molluginis* Rubs. and *Dasyneura galiicola* (F.) Lw., which produced galls on the apical meristem and terminal leaves of the plant, thus preventing elongation, (3) *Geocrypta galii* (H.) Lw., which produced spheroidal galls, resulting in stem necrosis and breakage, and (4) *Schizomyia galiorum* Keiffer, which galled the flower buds and prevented seed formation (Batra 1984). Rohfritsch (1987) found that *Geocrypta galii*-induced galls formed within 2 wk of attack and provided access to vascular tissue for the insect. Both larvae and adults of the Chrysomelid *Timarcha maritima* Perris were shown to feed on several *Galium* spp., including *G. mollugo* in France (Chevin 1992). Preliminary testing using a leaf-rolling eriophyid mite (identity not established because the taxonomy of European eriophyids is not clear) showed the mite to colonize *G. mollugo* successfully under a variety of conditions in Italy (S. L. Clement, personal communication, Washington State University). Moreover, the fly *Dasineura* sp., produced galls on *G. mollugo* but not *G. aparine* in side-by-side tests (S. L. Clement, personal communication). Pavlinec (1992) found *Sermylassa halensis* to attack and completely defoliate *G. mollugo* plants in Germany, whereas use of C*ecidophyes galii*, although not directly decreasing the vitality of plants, reduced the production of viable seeds by 30–40%. Batra (1984) also examined several species of mites that caused leaf and flower deformities on *G. mollugo*. However, because of efficacy and host-specificity difficulties these biological control agents were not evaluated further. Nonetheless, before biological control programs targeted at *G. mollugo* are established in North America, rigorous host specificity testing should take place given that two *Galium* species (*Galium buxifolium* Greene and *Galium californicum* ssp. s*ierrae* Demp. & Steb.) are listed as endangered in the United States (United States Fish and Wildlife Service 1999), although none is listed as endangered in Canada (COSEWIC 2000).

(d) *Diseases – Galium mollugo* has been found to be infected by tobacco rattle tobravirus in Germany, although the degree of damage is unclear (Kegler et al. 1994).

(e) *Higher plant parasites – Cuscuta europaea* L. (dodder) has been found to parasitize *Galium* spp. in Yugoslavia (Batra 1984).

ACKNOWLEDGEMENTS

The authors would like to thank the curators of Canadian herbaria who generously loaned their specimens, particularly Paul Catling of Agriculture and Agri-Food Canada and Mike Shchepanek of the National Herbarium of Canada who provided large collections. We also express appreciation to Bob Dirig of Cornell University's Bailey Hortorium for coordinating loans and providing space and comparison specimens. We would also like to thank Russ Hahn and David Clements for reviewing an earlier draft of the manuscript, Stephen Darbyshire for his constructive comments on the taxonomy of this species and key for the genus, Laurie Hanley for the seedling line drawing, Johannes Lehmann for his help with German translation, and H. McClelland, K. McCully, P. Cavers, C. Lacroix, S.L. Clement, and J. Ivany for valuable information on the species.

Agriculture and Agri-Food Canada - Research Branch. 2001. Soils of Canada. [Online]. Available: http://sis.agr.gc.ca/cansis/publications/health/frontin.html [5 June 2001].

Alex, J. F. 1992. Ontario weeds. Descriptions, illustrations and keys to their identification. Publ. 505. Ontario Ministry of Agriculture and Food, Toronto, ON. 304 pp.

Amrhein, N., Deus, B., Gehrke, P. and Steinrucken, H. C. 1980. The site of the inhibition of the shikimate pathway by glyphosate. II. Interference of glyphosate with chorismate formation in vivo and in vitro. Plant Physiol. **66**: 830–834.

Anonymous. 2000. Seeds Act, Canada. [Online] Available: http://laws.justice.gc.ca/en/S-8/index.html [15 May 2002].

Armitage, E. 1909. Hybrids between *Galium verum* & *G. mollugo*. New Phytol. **8**: 351–353.

Bailey, L. H. 1947. The standard cyclopedia of horticulture: a discussion, for the amateur, and the professional and commercial grower. Rev. and enl. ed. MacMillan, New York, NY. 3639 pp.

Bakker, J. P., Dijkstra, M. and Russchen, P. T. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. New Phytol. **101**: 291–308.

Batra, S. W. T. 1984. Phytophages and pollinators of *Galium* (Rubiaceae) in Eurasia and North America. Environ. Entomol. **13**: 1113–1124.

Boatman, N. D. and Bain, A. B. 1992. Evaluation of quinmerac and fluroxypyr against hedgerow flora and uncommon arable weeds. Tests Agrochem Cultiv. **13**: 42–43.

Boivin, B. 1966. Énumération des plantes du Canada. Le Naturalist Canadien. **93**: 371–437.

Booth, E. M. 1974. Additional plant records for County Carlow. Ir. Nat. J. **18**: 91.

Borisov, M. I. 1974. Flavonoids of *Galium mollugo*. Rastit. Resur. **10**: 66–71.

Buchwald, R. 1996. Basicline purple moorgrass meadows (*Molinietum caeruleae*) and their adjacent vegetation in the Alb-Wutach region (Southwestern Germany). Tuexenia. 179–225. [In German, English abstract.]

Budd, A. C. and Best, K. F. 1964. Wild plants of the Canadian prairies. Dept. of Agriculture, Research Branch, Ottawa, ON. 519 pp.

Catling, P.M., Erskine, D. S. and MacLaren, R. B. 1985. The plants of Prince Edward Island: with new nomenclatural changes, and corrections and deletions. Publication 1798. Research Branch, Agriculture Canada, Ottawa, ON. 270 pp.

Chater, A. O. 1977. *Galium mollugo* hedge bedstraw in Ceredigion Wales. Nature in Wales **15**: 142–143.

Chevin, H. 1992. Contribution à la biologie des Timarcha (Col. *Chrysomelidae*). VI. *Timarcha maritima* Perris. L'Entomologiste **48**: 133–140.

Compliance Monitoring Staff – U.S. Office of Pesticides and Toxic Substances. 1990. Suspended, cancelled and restricted pesticides. 5th ed. EPA, Washington, DC.

Corrigan, D., Timoney, R. F. and Donnelly, D. M. 1978. Iridoids and alkanes in 12 species of *Galium* and *Asperula*. Phytochemistry **17**: 1131–1134.

COSEWIC. 2000. Canadian species at risk, November 2000. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON. 24 pp.

Crompton, C. W., McNeill, J., Stahevitch, A. E., Wojtas, W. A. 1988. Preliminary inventory of Canadian weeds. Technical Bulletin 1988-9E. Research Branch, Agriculture Canada, Ottawa, ON. 292 pp.

Crowder, A., Topping, K. E. J. and Topping, J. C. 1996. Plants of the Kingston region: 1996. Fowler Herbarium, Department of Biology, Queen's University, Kingston, ON. 123 pp.

Darbyshire, S.J., Favreau, M. and Murray, M. 2000. Common and scientific names of weeds in Canada. Publication 1397/B, Agriculture and Agri-Food Canada, Ottawa, ON. 132 pp.

Doohan, D. J. 1981. Demonstration of control of smooth bedstraw (*Galium mollugo* L.) in timothy. NBDARD Adpt. Res. Rpt. 3: 251–253.

Doohan D. J. 1980. Control of smooth bedstraw in grassland. NBDARD Adpt. Res. Rpt. **2**: 148–150.

Ehrendorfer, F., Krendl, F. and Puff, C. 1976. *Galium* L. Pages 14–36 *in* T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb, eds. Flora Euopaea. Volume 4. Plantaginaceae to Compositae (and Rubiaceae). Cambridge University Press, Cambridge, UK.

Fidgeon, C. and Wilson, G. 1987. Growth regulation of *Galium mollugo* L. cell suspensions by alpha-naphthalene acetic acid. J. Exp. Bot. **38**: 1491–1500.

Fischer, S. F., Poschlod, P. and Beinlich, B. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. J. Appl. Ecol. **33**: 1206–1222.

Gleason, H. A. and Cronquist, A. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. New York Botanical Garden, New York, NY. 910 pp.

Gray, A. 1970. Gray's manual of botany; a handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada. 8th ed. D.Van Nostrand Co, New York, NY. 1632 pp.

Grigorov, S. 1977. Study on aphids of the genus *Dysaphis* C.B. (Homoptera, Aphididae) on pear. Gradinar. Lozar. Nauka. **14**: 22–28. [In Bulgarian, English abstract.]

Grime, J. P., Mason, G., Curtis, A. V., Rodman, J. and Band, S. R. 1981. A comparative study of germination characteristics in a local flora. J. Ecol. **69**: 1017–1059.

Grzegorczyk, S. and Alberski, J. 1999. The presence of forbs in meadow-pasture plant communities of the Olsztyn Lakeland. Folia Universitatis Agriculturae Stetinensis, Agricultura. **75**:103–106. [In Polish, English abstract.]

Grzybek, J., Wongpanich, V., Mata-Greenwood, E., Angerhofer, C. K., Pezzuto, J. M. and Cordell, G. A. 1997. Biological evaluation of selected plants from Poland. Int. J. Pharmacogn. **35**: 1–5.

Hahn, R. R. 1988. Smooth bedstraw control in pastures and hayfields. Annual Meeting of the Northeastern Weed Science Society **42**: 35–36.

Hahn, R. R. 1992. Smooth bedstraw control provides opportunity to improve hayfields. What's Cropping Up? **2**: 4.

Hara, H. 1983. Comments on East Asiatic plants 11. J. Jpn. Bot. **58**: 33–38.

Heide, L. and Leistner, E. 1983. Enzyme activities in extracts of anthraquinone-containing cells of *Galium mollugo*. Phytochemistry **22**: 659–662.

Hinds, H. R. 1986. Flora of New Brunswick: a manual for the identification of the vascular plants of New Brunswick. Dept. of Biology, University of New Brunswick, Fredericton, NB. 460 pp.

Hinds, H. R. 2000. Flora of New Brunswick: a manual for the identification of the vascular plants of New Brunswick. 2nd ed. Dept. of Biology, University of New Brunswick, Fredericton, NB. 699 pp.

Holm, L., Pancho, J. V., Herberger, J. P. and Plucknett, D. L. 1979. Geographical Atlas of World Weeds. John Wiley & Sons, New York, NY. 391 pp.

Holmgren, P. K. 2001. Index Herbariorum. [Online] Available: http://www.nybg.org/bsci/ih/ih.html [28 April 2001].

Hundt, R. and Velve, O. 1992. Untersuchungen an Arrhenatheretalia-Gesellschaften in Südnorwegen unter soziologischen, ökologischen, pflanzengeographischen und syntaxonomischen Aspekten. Flora **186**: 393–424. [In German, English summary.]

Iavarone, C., Sen, A., Trogolo, C. and Villa, S. 1983. Mollugoside, an iridoid glucoside from *Galium mollugo*. Phytochemistry **22**: 175–178.

Jans, M. and Schulz, H. 1998. Persistence of herbs in sown landscape turf at various locations. Rasen-Turf-Gazon. **29**: 8–21. [In German, English abstract.]

Jansson, O. 1974. Phylloquinone (vitamin K1) levels in leaves of plant species differing in susceptibility to 2,4-dichlorophenoxyacetic acid. Physiol Plant. **31**: 323–325.

Justin, S. H. F. W. and Armstrong, W. 1987. Anatomical characteristics of roots and plant response to soil flooding. New Phytol. **106**: 465–495.

Kegler, H., Fuchs, E., Knapp, H. D. and Ehrig, F. 1994. Investigations on the evidence of plant pathogenic viruses in the nature reserve of the island Vilm. Arch.Phytopathol. Plant Prot. **29**: 211–216. [In German, English abstract.]

Kelly, C. K. and Beerling, D. J. 1995. Plant life form, stomatal density and taxonomic relatedness: a reanalysis of Salisbury (1927). Funct. Ecol. **9**: 422–431.

Kerguélen, M. 1993. Index synonymique de la flore de France. Muséum National d'Histoire Naturelle, Secrétariat Faune-Flore, Paris. 196 pp.

Kinne, E. A. 1955. Preliminary studies of the control of smooth bedstraw (*Galium mollugo* L.) in bird's-foot trefoil (*Lotus corniculatus* L). M.Sc. Thesis, Cornell University, Ithaca, NY. 75 pp.

Kleijn, D. and Snoeijing, G. I. J. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. J. Appl. Ecol. **34**: 1413–1425.

Köhler, B., Ryser, P., Güsewell, S. and Gigon, A. 2001. Nutrient availability and limitation in traditionally mown and in abandoned limestone grasslands: a bioassay experiment. Plant and Soil **230**: 323–332.

Kolesova, D. A. 1974. Pear aphids of the genus *Dysaphis* C.B. (Homoptera, Aphididae) – two-host species. Entomol. Obozr. **53**: 38–53. [In Russian, English abstract.]

Kolk, H. 1962. Viability and dormancy of dry-stored weed seeds: Studies in several species occurring frequently in Swedish grassland seed lots. Växtodling **18**: 35–38.

Korsmo, E. 1935. Weed seeds: 34 coloured plates of seeds and parts of infructescences of 306 different species of weeds in cultivated ground, with corresponding text and an index of plant names in 11 languages. Gyldendal norsk forlag, Oslo, Norway. 175 pp.

Korsmo, E. 1954. Anatomy of weeds: Anatomical description of 95 weed species with 2050 original drawings. Grondahl and Sons, Oslo, Norway. 413 pp.

Lawson, C. A. 1976. The genus *Galium* (Rubiaceae) in the southeastern United States. PhD Thesis, University of Oklahoma, Norman, OK. 216 pp.

Leskosek, M. 1996. Can we prevent the invasion of weeds in intensively used meadows? Novi izzivi v poljedelstvu . '96 Zbornik simpozija, Ljubljana, Slovenia, 9–10 decembra 1996: 329–336. [In Slovenian, English abstract.]

Malik, N. and Vanden Born, W. H. 1988. The biology of Canadian Weeds 86. *Galium aparine* L. and *Galium spurium* L. Can J. Plant Sci. **68**: 481–499.

Marrs, R. H., Frost, A. J. and Plant, R. A. 1991. Effect of mecoprop drift on some plant species of conservation interest when grown in standardized mixtures in microcosms. Environ. Pollut. **73**: 25–42.

McCully, K. V., LeBlanc, S. J. and Hanscomb, D. O. 1989. Bedstraw control in timothy hay fields. Adpt. Res. Rpt. 10: 112–115

McCully, K. V., Mann, M. A. and Hanscomb, D. O. 1991. Smooth bedstraw control in New Brunswick hayfields. NBDA Adpt. Res. Rpt. **13**: 331–334.

McCully, K. 2000. Report to the Expert Committee on Weeds: New Brunswick. [Online] Available: http//www.cwss-scm.ca/pdf/ecw2000proceedings.pdf [20 March 2003].

Mellinger, M. V. and McNaughton, S. J. 1975. Structure and function of successional vascular plant communities in central New York. Ecol. Monogr. **45**: 161–182.

Meteorological Service of Canada. 2002. Canadian climate normals. [Online] Available: http://www.msc-smc.ec.gc.ca/climate/climate_normals/index_e.cfm [2 March 2002].

Michalková, E. 1991. Results of the study of the chromosome numbers of *Galium-Mollugo* agg. in Slovakia. Biologia **46**: 799–810.

Michalková, E. 1993. *Galium mollugo* agg. (Rubiaceae) in Slovakia. Preslia **65**: 201–207.

Montgomery, F. H. 1957. The introduced plants of Ontario growing outside of cultivation (Part II). Royal Canadian Institute Transactions (Toronto) 32: 3–35.

Moore, R. J. 1975. The *Galium aparine* complex in Canada. Can. J. Bot. **53**: 877–893.

Morita, H. 1975. *Galium-mollugo* naturalized in Hokkaido Japan. Acta. Phytotaxon. Geobot. **26**: 188.

Morton, J. K. and Venn, J. M. 1990. A checklist of the flora of Ontario vascular plants. Department of Biology, University of Waterloo, Waterloo, ON. 218 pp.

Moss, E. H. 1983. Flora of Alberta. 2nd ed. Rev. by J. G. Packer. University of Toronto Press, Toronto, ON. 687 pp.

Mousdale, D. M. A., Fidgeon, C. and Wilson, G. 1985. Auxin content and growth patterns in auxin-dependent and auxin-autotrophic plant cell and tissue cultures. Biol. Plant. **27**: 257–264.

Muenscher, W. C. 1980. Weeds. 2nd ed. Cornell University Press, Ithaca, NY. 586 pp.

Natali, A. and Jeanmonod, D. 1992. La présence du *Galium mollugo* L. s.str. en Corse. Candollea **47**: 311–318.

National Plant Board. 2000. Regulated noxious weeds: State list. [Online] Available: http://www.aphis.usda.gov/npb/statenw.html [6 February 2001].

Onaindia, M. and Amezaga, I. 2000. Seasonal variation in the seed banks of native woodland and coniferous plantations in northern Spain. For. Ecol. Manag. **126**: 163–172.

Ontario Weed Committee. 2000. Guide to weed control 2000. Ministry of Agriculture, Food and Rural Affairs, Pub. 75, Toronto, ON. 274 pp.

Parakh, J. S. and Schreiber, M. M. 1960. Control of bedstraw (*Galium mollugo*) with alpha-phenoxypropionic acid derivatives. Weeds **8**: 94–106.

Paraschivescu, D. 1978. Dynamics of formicids (Hym., Formicidae) in tetany in some meadows with dicrocelioza in Romania. Trav. Mus. Hist. Nat. 'Grigore Antipa'. **19**: 321–323.

Pavlinec, M. 1992. The significance of phytophagous insects on *Galium aparine* (Rubiaceae) and other *Galium* species. Mitteilungen der Deutschen Gesellschaft fur Allgemeine und Angewandte Entomologie **8**: 169–173.

Psarski, P., Jarry, A., Peres, G., Diris, J. and Duthen, G. 1971. L'envahissement des prairies naturelles des Hautes-Pyrénées par le gaillet lisse (*Galium mollugo*) et le problème de leur amélioration. La Défense des Végétaux **149**: 171–175.

Qian, H. and Klinka, K. 1998. Plants of British Columbia: Scientific and common names of vascular plants, bryophytes, and lichens. UBC Press, Vancouver, BC. 534 pp.

Rakauskas, R. P. 1984. Biology and ecology of cherry aphids *Myzus-Cerasi* in the Lithuanian- SSR USSR. Liet. Tsr. Mokslu. Akad. Darb. Ser. C Biol. Mokslai: 80–87. [In Russian, English abstract.]

Roberts, H. A. 1986. Seed persistence in soil and seasonal emergence in plant species from different habitats. J. Appl. Ecol. **23**: 639–656.

Rohfritsch, O. 1987. Different food supply strategies in midge induced plant galls. Pages 195–200 *in* V. Labeyrie, G. Fabres, and D. Lachaise, eds. Series Entomologica. Vol 41. Insects-plants. 6th International Symposium, Pau, France, 1986. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Roland, A. E. and Zinck, M. 1998. Roland's flora of Nova Scotia. Rev. ed. Nimbus Publishing and Nova Scotia Museum, Halifax, NS. 2 vols., 1297 pp.

Rouleau, E. and Lamoureux, G. 1992. Atlas of the vascular plants of the island of Newfoundland and of the islands of Saint-Pierre-et-Miquelon. Fleurbec, Saint-Henri-de-Lévis, QC. 777 pp.

Rousseau, C. 1974. Géographie floristique du Québec-Labrador : distribution des principales espèces vasculaires. Les Presses de l'Université Laval, Québec. 798 pp.

Schildknecht, H., Straub, F. and Scheidel, V. 1976. Mollugin a new pigment from rhizomes of *Galium mollugo*. Justus Liebigs Ann. Chem. **7–8**: 1295–1306.

Schulte, U., El Shagi, H. and Zenk, M. H. 1984. Optimization of 19 Rubiaceae species in cell culture for the production of anthraquinones. Plant Cell Rep. **3**: 51–54.

Scoggan, H. J. 1979. Flora of Canada. Part 4. National Museums of Canada, Ottawa, ON.

Silvertown, J. W. and Dickie, J. B. 1981. Seedling survivorship in natural populations of 9 perennial chalk grassland plants. New Phytol. **88**: 555–558.

Steele, B. 1955. Soil pH and base status as factors in the distribution of calcicoles. J. Ecol. **43**: 120–132.

Sustar, F. 1988. Effect of fertilization and greensward use on some weed species in certain areas in Slovenia. Fragm. Herbol. Jugosl. **17**: 159–167.

Tansley, A. G. and Adamson, R. S. 1925. Studies of the vegetation of the English Chalk. III. The chalk grasslands of the Hampshire-Sussex border. J. Ecol. **13**: 177–223.

Tansley, A. G. and Adamson, R. S. 1926. Studies of the vegetation of the English Chalk. IV. A preliminary survey of the chalk grasslands of the Sussex Downs. J. Ecol. **14**: 1–32.

Tasse, D. 2000. Weed control: be on the lookout for "smooth bedstraw." [Online] Available: http://www.gov.on.ca/OMAFRA/english/crops/facts/info_bedstraw.htm [3 May 2001].

Uesato, S., Miyauchi, M., Itoh, H. and Inouye, H. 1986. Biosynthesis of iridoid glucosides in *Galium mollugo*, *Galium spurium* var. *echinospermon* and *Deutzia crenata*. Intermediacy of deoxyloganic acid, loganin and iridodial glucoside. Phytochemistry **25**: 2515–2521.

United States Department of Agriculture–Agricultural Research Service. 1971. Common weeds of the United States. Dover Publications, Inc., New York, NY. 463 pp.

United States Department of Agriculture–Animal and Plant Health Inspection Service. 2000. Federal noxious weed list as of 09/08/2000. [Online] Available: http://www.aphis.usda.gov/ppq/weeds/noxwdsa.html [9 November 2000].

United States Department of Agriculture–Natural Resources Conservation Service. 2001. Plants database. [Online] Available: http://plants.usda.gov/ [10 November 2000].

United States Fish and Wildlife Service. 1999. Endangered and threatened wildlife and plants: 50 CFR 17.11 and 17.12. Department of the Interior, US Fish and Wildlife Service, Washington, DC. 57 pp.

White D. J., Haber, E. and Keddy, C. 1993. Invasive plants of natural habitats in Canada: an integrated review of wetland and upland species and legislation governing their control. Canadian Wildlife Service, Ottawa, ON. 121 pp

Wilson, G. and Marron, P. 1978. Growth and anthraquinone biosynthesis by *Galium-mollugo* cells in batch and chemostat culture. J Exp. Bot. **29**: 837–852.