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The Biology of Canadian Weeds: 158. *Galega officinalis* L.

Stephen J. Darbyshire, Ardath Francis, Eden S.P. Bromfield, and Subbaiah Mechanda

Abstract: The biology of the weed goat's-rue, *Galega officinalis* (Fabaceae), is reviewed. Introduced to Canada in the late 19th Century as an ornamental, it has become established at scattered localities and is spreading locally in southern Ontario. The plant is considered a noxious weed and is legally regulated in many jurisdictions due to the production of toxic alkaloids and its invasive characteristics. Primarily a weed of pastures, grasslands and perennial crops, it also displaces native vegetation in areas where it becomes established. Originally endemic in the Black Sea region, it was spread by humans through Europe and eastward to Pakistan as a herbal medicine. More recently it has been introduced widely as a forage and ornamental plant. As a folk remedy it has been used primarily to treat diabetes in humans and to enhance milk production in both humans and livestock. The plant has also been used as a forage by limiting consumption to early growth stages and the quantity ingested. Effective control has been achieved with 2,4-D, dicamba, triclopyr, metsulfuron methyl and other herbicides. Goat's-rue forms a highly specific nitrogen-fixing symbiosis with the soil bacterium *Neorhizobium galegae* symbiovar *officinalis*. Successful establishment of Goat's rue in new regions depends on the co-introduction of plant and bacterium. The lack of long-distance dispersal adaptations, soil pH requirements and its symbiont dependency, reduces the ability of *G. officinalis* to spread into novel areas without anthropogenic activities. These constraints to establishment may facilitate management and eradication strategies.

Key words: *Galega officinalis*, goat's-rue, galéga officinal, common milkpea, *Neorhizobium galegae*, weed biology, noxious weed.

Résumé : Les auteurs passent en revue la biologie du galéga officinal (*Fabaceae*), mauvaise herbe introduite au Canada à la fin du 19^e siècle comme plante ornementale et qui, depuis, s'est établie à différents endroits. L'adventice se répand localement, dans le sud de l'Ontario. On considère l'espèce comme une mauvaise herbe nuisible et la loi la réglemente à de nombreux endroits, car elle produit des alcaloïdes toxiques en plus d'être envahissante. Adventice colonisant surtout les pâturages, les prairies et les cultures vivaces, le galéga officinal déloge la végétation indigène là où elle réussit à s'établir. À l'origine endémique en bordure de la mer Noire, l'être humain l'a essaimée partout en Europe et dans l'est, jusqu'au Pakistan, en raison de ses vertus médicinales. Plus récemment, la plante a été largement introduite comme plante fourragère ou ornementale. En herboristerie, on la conseille principalement pour traiter le diabète chez l'homme et accroître la production de lait chez l'être humain et le bétail. On s'en sert aussi comme fourrage, tout en en limitant la consommation aux jeunes plants ou en restreignant la quantité ingérée. Le 2,4-D, le dicamba, le triclopyr, le méthyle de metsulfuron et d'autres herbicides parviennent à la vaincre. Le galéga officinal fixe l'azote dans le sol en formant une symbiose avec la bactérie *Neorhizobium galegae* symbiovar *officinalis*. Pour que le galéga s'implante dans une nouvelle région, il faut introduire simultanément la plante et la bactérie. L'incapacité de se disperser sur de longues distances, la nécessité d'un pH particulier dans le sol et la dépendance sur le symbiote empêchent *G. officinalis* de se propager ailleurs sans l'intervention de l'être humain. Pareilles contraintes pourraient faciliter les stratégies de lutte et d'éradication. [Traduit par la Rédaction]

Mots-clés : *Galega officinalis*, goat's-rue, galéga officinal, rue des chèvres, *Neorhizobium galegae*, biologie des mauvaises herbes, adventice nuisible.

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1. Species Name and Taxonomic Relationships

Galega officinalis L. — Synonyms: *Accorombona tricolor* (G. Don) Benth. ex Walp., *Callotropis tricolor* G. Don, *Galega bicolor* Boiss. & Hausskn. ex Regel, *Galega coroniloides* Freyn & Sint., *Galega patula* Steven, *Galega persica* Pers., *Galega vulgaris* Lam. Common names: goat's-rue, catgut, common milkpea, French honeysuckle, French-lilac, galega, goat's rue, goatsrue, Italian fitch, professor weed; galéga officinal, rue des chèvres, lilas d'Espagne (Darbyshire et al. 2000; Darbyshire 2003). European and Mediterranean Plant Protection Organization Code: GAGOF. Fabaceae (Leguminosae); legume family; Fabacées (Legumineuses).

The genus *Galega* is an Old World group of herbaceous plants with 5–6 species. Two species are of economic importance, *G. officinalis* L. and *G. orientalis* Lam. The former is usually considered a weed, but is also used as a medicinal plant or forage and the latter is used as a livestock forage plant. Classification of the tribes in Fabaceae (Leguminosae) has been controversial and circumscribed in many ways (Polhill 1981, 1994; Endo and Ohashi 1997; Wojciechowski et al. 2000, 2004; Doyle and Luchow 2003).

2. Description and Account of Variation

(a) Species description

The following description is based on the literature (Stebler and Schröter 1889; Lubbock 1892; Knuth 1908; Gams 1924; Ball 1968; Gorshkova 1971; Polhill 1981; Kirkbride et al. 2003; Lasseigne 2003) and supplemented with observations of Canadian populations. Measurements are given as the usual range with extremes in parentheses. Many of the characteristics described are illustrated in Figs. 1–3.

A perennial herbaceous plant from a stout caudex (root crown). Tap root long, fleshy, whitish, with fibrous rootlets; rhizomes absent. Stems hollow, 40–150 (–200) cm tall, more or less erect or sprawling, branched, glabrous to sparsely pubescent, slightly ribbed. Leaves alternate, petiolate, (3–) 8–30 (–40) cm long, more or less glabrous to sparsely hairy, once pinnate; stipules herbaceous, 0.5–1.6 cm long, broadly lanceolate to sagittate with (1–) 2–4 (–6) basal teeth or acute lobes; leaflets (9–) 11–19 (–21), sessile (or rarely a petiolule to 0.5 mm), in opposite pairs (except the terminal one), (7–) 15–50 × 4–17 mm, lanceolate to narrowly ovate, sometimes sparsely pubescent on the margins and (or) veins of the lower surface, apices acute to obtuse, often emarginate, and usually mucronate. Inflorescences on long peduncles, elongate, 8–27 (–30) cm long (including peduncle), axillary, densely to loosely flowered racemes; pedicels filiform, about as long as or shorter than the calyx, with a subtending lanceolate bract 5–7 mm long; calyx of fused sepals with 5 linear subequal teeth about as long as the tube, 4–6 mm long, glabrous or puberulent on teeth; corollas papilionaceous; petals 5 (lower two fused

into a keel), (7–) 10–15 mm long, white, bluish, lilac to reddish purple, the banner (standard or vexillum) oblan-ceolate to obovate, more or less reflexed, the wings (alae) slightly shorter than to about as long as the keel, narrowly obovate, clawed (i.e., with a basal process or auricle), the keel (carina) broad and rounded, not auriculate. Stamens 10, monadelphous (the upper filament fused basally but partly free distally), included in the keel; anthers dimorphic (Endo and Ohashi 1997). Ovaries enclosed in the staminal sheath. Style filiform, curved upwards, with a small capitate stigma protruding beyond the anthers. Fruits elongate, 2-valved, cylindrical pods, (20–) 20–45 (–50) × 2–3 mm, glabrous, striate, erect to spreading at maturity, shallowly torulose (slightly constricted between the seeds), tardily dehiscent along sutures. Seeds (1–) 2–6 (–9), in one series, 2.5–4.5 × 1–2.5 mm, narrowly ellipsoid to somewhat reniform (slightly constricted at the hilum), greyish to yellowish-brown, dull. Seed coat microscopically rugose, with a thin layer of wax (Pandey and Jha 1988). The fruits and seeds of *G. officinalis* are described in detail and illustrated by Kirkbride et al. (2003).

Cotyledons are obovate-oblong, about 18–27 × 5–8 mm, smooth, entire. The first leaf of a seedling consists of one leaflet, the second leaf has a pair of leaflets, and the third leaf consists of a pair of leaflets and a terminal leaflet (Fig. 3C).

Details of root, stem and leaf anatomy were studied in populations from Turkey by Özbucak et al. (2005) who provide detailed descriptions and illustrations.

In their phylogenetic analysis of some Fabaceae tribes related to *Galega*, Endo and Ohashi (1997) reviewed various character states reported in the literature for *Galega* and provided unique observations on pollen grains and embryos of *G. officinalis* and *G. orientalis*.

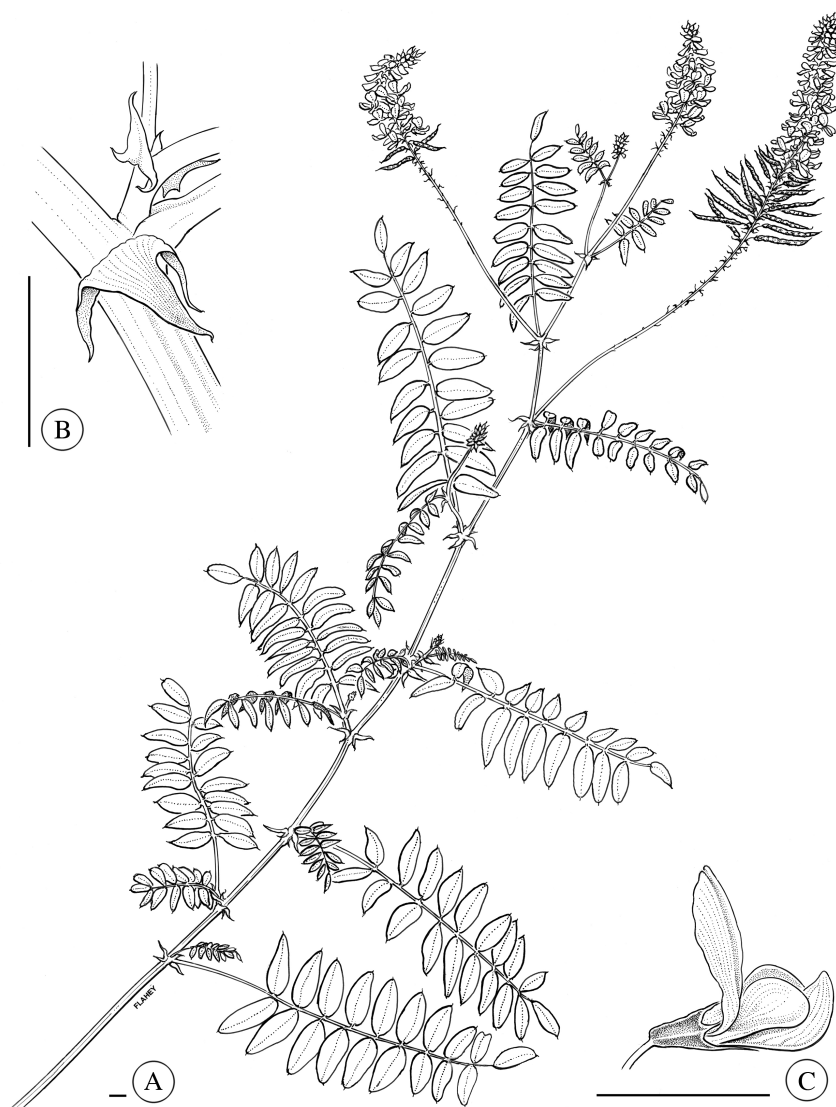
In Canada, Gervais (1979) reported a chromosome count of $2n = 16$ from an introduced population at Quebec City. Counts, $n = 8$ (Kreuter 1930; Senn 1938; Ruíz de Clavijo Jiménez 1990) and $2n = 16$ (Tschechow 1930; Polhill 1981; Izmailow 1990) have been reported for Eurasian plants.

The entire chloroplast genome of *G. officinalis* was sequenced and characterized by Du et al. (2021). They reported it to be 125 086 base pairs in length, with a GC content of 34.18% and containing 112 genes.

(b) Distinguishing features

The gross morphology and habitus of *Galega officinalis* are illustrated in Figs. 1 and 2. The similar species, *G. orientalis*, which is often cultivated as a forage (Varis 1986; Fairey et al. 2000; Raig et al. 2001), occupies cooler temperate habitats which partly overlap those of *G. officinalis* in Eurasia (Baležentienė 2011), however, it is not known to occur outside of cultivation in North America. This species differs from *G. officinalis* in: horizontal rhizomes present (versus rhizomes lacking); reflexed mature pods (versus erect or spreading fruits)

Fig. 1. Goat's-rue, *Galega officinalis*. (A) Upper stem with inflorescences and immature fruits; (B) stipules; (C) flower. Scales bars = 1 cm.



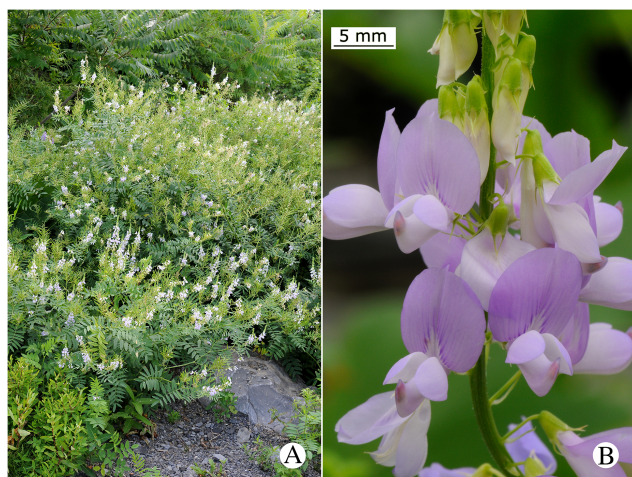
which are pubescent (versus glabrous); oval to orbicular stipules (versus deltoid to sagittate); distinctly pubescent calyx (versus glabrous or sparsely pubescent); calyx teeth shorter than the tube (versus about as long as the tube); and, the somewhat larger, more broadly ovate leaflets ($30\text{--}60 \times 10\text{--}25$, versus $7\text{--}50 \times 4\text{--}17$ mm in *G. officinalis*). The seeds of *G. orientalis* tend to be more yellowish and lustrous.

The two *Galega* species can also be readily distinguished by differences in DNA nucleotide sequences at several nuclear and chloroplast loci. Particularly useful genes include the Nod-factor receptor 5 (*nfr5*) and nodulation receptor kinase (*NORK*) (Österman et al. 2011; S. Mechanda, (unpublished data); Appendix A).

The genus *Astragalus* is closely related and usually placed in the tribe Galegeae. With more than 2000 species, it is one of the largest angiosperm genera making

morphological generalizations difficult. Species of *Galega* differ from *Astragalus* species in the following ways: the primary lateral veins of the leaflets extend to the leaflet margins (craspedodromous venation), while in *Astragalus* the primary lateral veins join each other and do not reach the leaflet margin (camptodromous venation) (Figs. 3D, 3E); the stamens are more or less monadelphous (versus usually didelphous); and, the pods have prominent oblique veins (versus transverse veins). In a vegetative state *G. officinalis* can be confused with cicer milk-vetch (*Astragalus cicer* L.), but the latter species has long rhizomes. In a reproductive state the yellowish flowers and rounded pods easily distinguish *A. cicer*. Weedy species of *Vicia* and *Lathyrus* in Canada are readily distinguished as climbing plants with tendrils present in place of the terminal leaflet. Crown vetch [*Securigera varia* (L.) Lassen, = *Coronilla varia* L.] may also be confused with *G. officinalis*, but the

Fig. 2. Goat's-rue, *Galega officinalis*. (A) Dense population at a disturbed site along the Ottawa River; (B) flowers. [Colour online.]



former has smaller flowers that are usually pink in colour in a globose umbel rather than a raceme, and the leaflets are smaller and broadly rounded at the tips without a mucro. Alfalfa (*Medicago sativa* L.) is also somewhat similar in growth habit, but in this species the pods are coiled, curled or falcate (rather than terete), the seeds are much smaller, and the leaves have only 3 leaflets. In central to western North America, the species might be confused with the native wild licorice (*Glycyrrhiza lepidota* Pursh), but the latter has solid (not hollow) stems, white to yellowish flowers with a strap-like standard and bur-like seed pods with hooked bristles.

In a survey by [Lersten and Horner \(2007\)](#), leaflets of *G. officinalis* were found to have calcium oxalate crystals in prisms along the vascular bundles, whereas crystals were lacking in the majority of examined species in the tribe Galegeae, including *Astragalus* spp. and *Oxytropis* spp. [Peters et al. \(2010\)](#) suggested that the absence of forisomes (spindle-shaped crystalline P-proteins that regulate phloem transport in the sieve tubes) in *G. officinalis* and some related species, might be related to the similarly unusual presence of calcium oxalate crystals in those species, both suggesting an unusual mechanism of calcium management in the leaves.

(c) Intraspecific variation

Variation within *G. officinalis* can be found in the flower colour, which ranges from bluish-purple to white, and in the number and shapes of leaflets in the leaves (see Section 1). Garden cultivars have been bred to intensify colour differences and nurseries offer plants with large white or deep purple racemes. An unusual sport with a simple leaf (not pinnate) has been described from Essex, UK ([Mullin 1983](#)).

In Turkey, six naturally occurring populations from the Middle Black Sea region differed significantly in number of flowers, flower nitrogen levels, above-ground

biomass, flower biomass, leaf width, leaf length, root biomass, and reproductive effort, suggesting the importance of genotype as well as local environmental conditions on phenotypic plasticity ([Özbucak et al. 2005](#)).

Genetic variability was assessed by [Wang et al. \(2012\)](#) in 35 populations of *G. officinalis* from Europe and Russia using inter-simple sequence repeat (ISSR) and sequence-related amplified polymorphism (SRAP) DNA markers. Considerable variation was detected between the sampled populations. Ten ISSR primers produced a total of 100 bands which were an average of 77% polymorphic (expected heterozygosity = 0.292). Seven SRAP primers produced 88 bands which were an average of 67% polymorphic (expected heterozygosity = 0.257). Similarly, high levels of variability have also been found in morphological characteristics ([Wang et al. 2008](#)).

(d) Illustrations

The whole mature plant of *Galega officinalis* is illustrated in [Fig. 1](#), along with details of a stipule and flower. A dense population at a disturbed site along the Ottawa River (Ontario, Canada) ([Fig. 2](#)) shows the competitive nature of the goat's-rue symbiosis in a disturbed habitat. Morphological details of a stipule, seeds, seedling and leaf venation are illustrated in [Fig. 3](#). Other illustrations of *G. officinalis* may be found in [Stebler and Schröter \(1889\)](#), [Vasey \(1893\)](#), [Step \(1896\)](#), [Gams \(1924\)](#), [Gorshkova \(1971\)](#), [Barneby \(1989\)](#), [Eckel \(2004\)](#), [CFIA \(2012\)](#) and [CABI \(2019\)](#). An accurate colour plate of morphological characteristics was published in *Flora von Deutschland, Österreich und der Schweiz*, and there are several copies available at different Internet websites ([Thomé 1905](#)).

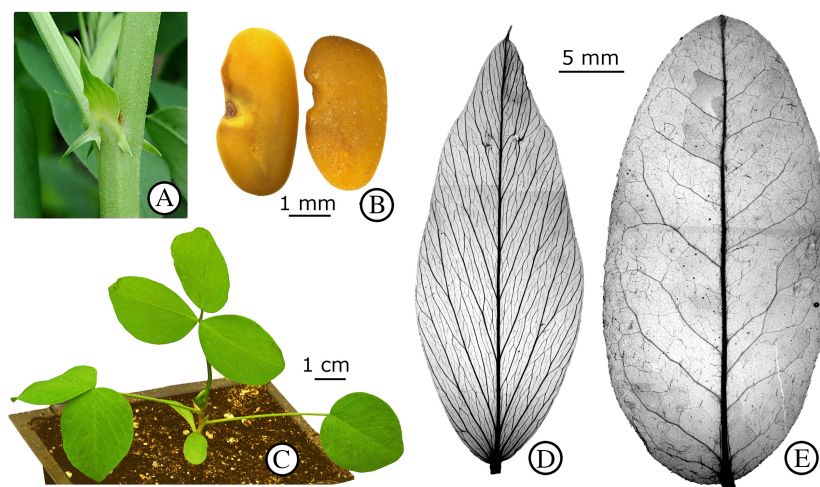
3. Economic Importance and Environmental Impact

(a) Detrimental

While *Galega officinalis* has a long history of economic uses in Europe, it is considered a noxious weed in most areas where it has been introduced. As a weed, it can form dense thickets and monocultures in pastures and meadows, reduce yields of better forage plants, contaminate pedigree seed crops, cause toxic injury to livestock, and can compete with and crowd out native flora ([Evans et al. 1997](#); [Wiersema and León 1999](#); [Guitart et al. 2010](#); [Fraiture 2014](#); [Oregon Department of Agriculture 2015](#); [CABI 2019](#)). Its weediness and toxicity has been considered a particular problem in the United States, Argentina, Chile and New Zealand ([Holm et al. 1991](#)).

In the United States, where it was introduced as a trial forage plant, medicinal plant, and ornamental, the plant has escaped and become weedy, particularly in Utah ([Evans 1984](#)) and sporadically in other states (see Section 6). It has been reported as infesting irrigated pastures, roadways, ditch banks, fence lines, wet areas and alfalfa crops ([Evans 1984](#); [Patterson 1992, 1993](#)). The species is not only subject to U.S. federal legislation but has also been targeted in state programs for prohibition or eradication (see Section 3c). In Great Britain,

Fig. 3. Goat's-rue, *Galega officinalis*. (A) Stipule; (B) seeds; (C) seedling showing narrowly ovate cotyledons and first three true leaves, the later with one, two and three leaflets, respectively; (D) Craspedodromous leaflet venation of *G. officinalis*; (E) Camptodromous leaflet venation of *Astragalus cicer*. [Colour online.]



G. officinalis is among alien plants listed as persistent, weedy, garden escapes (Salisbury 1961). It is listed as a noxious invasive weed in eastern France with a moderately negative economic impact on local biodiversity and agriculture (EPPO 2008). In Argentina the plant is considered a weed in pastures and vegetable crops where it can be a host to insects that attack crops (Liljeström and Rabinovich 2004). In Chile, where it was introduced as a forage in 1872, it has become a weed of pastures and crops (Oehrens and González 1975; Ellison and Barreto 2004), including vineyards (Longone et al. 2011).

A major concern is the potential for poisoning of livestock due to the toxic properties of alkaloids (Williams 1978, 1980; DiTomaso 1994), including guanidine, galegine (isoamylene guanidine), hydroxygalegine and galuteolin (Barger and White 1923a, 1923b; Pufahl and Schreiber 1961). Galegine is synthesized in seedlings, leaves, flowers and fruit with highest levels occurring in the seed and the levels in plants increasing through the flowering, fruiting and seed maturation stages (Reuter 1962; Oldham 2009; Oldham et al. 2011). However, because of the bitter alkaloids, mature plants are generally unpalatable to livestock (Tingey 1971; Williams 1978, 1980), and intoxication is largely restricted to times of drought or under other conditions which limit the availability of alternative forage, such as when contaminated fodder has been fed to animals (Durieux 1968; Williams 1978; Puyt et al. 1980; Poulet-Wolgust et al. 2012; Fraiture 2014). Poisoning generally occurs when the plant is at flowering or fruiting stages (Parton and Bruere 2002; De Otazúa et al. 2009), with young plants being much less toxic. Similarly, mature seed was more toxic to sheep than semi-mature seed in feeding trials by Keeler et al. (1986).

Observed clinical manifestations after consumption of *G. officinalis* include dyspnea, anoxia, foaming nasal discharge, vomiting, pulmonary congestion, edema and hydrothorax lesions (Keeler et al. 1988; Lasseigne 2003; Roch et al. 2007). Mortality can occur 24 h or less after ingestion (Durieux 1968; Puyt et al. 1981). Clinical signs were observed at 0.8 g *G. officinalis* per kg of sheep body weight, and mortality was observed at 10 g *G. officinalis* per kg of sheep body weight (Keeler et al. 1986, 1988). Mortality was observed in sheep fed approximately 0.7% of body weight of *G. officinalis* dry matter by De Otazúa et al. (2009), depending on individual plant toxin levels and animal sensitivity. Dried aerial parts fed to rats at a rate of 5 g·kg⁻¹ did not result in any mortalities or any clinical signs of toxicity although there was evidence that significant liver and lung alterations had occurred suggesting these organs are the target of *G. officinalis* toxicosis (Rasekh et al. 2008). In German tests, alcoholic extracts from seeds and leaves were poisonous to mice, the average lethal dose of galegine sulphate amounting to 77.5 mg·kg⁻¹ body weight (Köhler 1969). Susceptibility of animals to experimental poisoning has shown considerable variation and the reasons for this remain unclear (Keeler et al. 1988).

Confirmed reports of livestock poisoning by *G. officinalis* are relatively rare. Most cases have been reported from southern and central France, where such reports go back to the late 19th Century (Faliu et al. 1981, 1985). Sheep are the primary victims of poisoning, and mortality rates from 10%–50% have been reported (Faliu et al. 1981; Puyt et al. 1981; Gresham and Booth 1991; Guitart et al. 2010). Severe outbreaks with numerous deaths following consumption of contaminated fodder have been reported in sheep (Durieux 1968; Puyt et al. 1980, 1981; Bézard et al. 2002; Poulet-Wolgust et al. 2012; Fraiture 2014), goats

(Lasseigne 2003) and cattle (Roch et al. 2007). In the United Kingdom, a number of sheep died with symptoms of goat's-rue poisoning when put to graze in a newly-seeded pasture adjacent to an embankment infested with *G. officinalis* (Gresham and Booth 1991). Poisoning in sheep has also been reported from New Zealand (West 1982). In Canada and the United States, toxicity of the plant has been of little significance to date, because of its limited and scattered distribution (Burrows and Tyrl 2013).

(b) Beneficial

As a folk remedy, *G. officinalis* has been used for centuries in Europe for a variety of purposes. It has been suggested that it was a plant known to Dioscorides and Pliny the Elder, although it has not been unambiguously identified in their works. Traditional uses include as a poison antidote, mild astringent, vermifuge, plague treatment, anti-convulsive, anti-inflammatory compress, pot or salad herb, egg production stimulant for hens, and galactagogue to increase lactation (Gerard 1597; Culpeper 1650; Loudon 1849; Rasekh et al. 2008). Actual and potential medicinal uses of various secondary metabolites of *G. officinalis* were reported by Karakaş et al. (2016a, 2016b), Nagalievska et al. (2018) and Atanasov et al. (2019). The common practice of using the plant in livestock feed to increase milk production led to the ancient common name galega (see, for example, Gerard 1597) and to the Linnaean generic name *Galega*, from the Greek “gala” for milk. Extracts have also been used to treat reproductive disorders and enhance reproduction in goats and sheep (Viegi et al. 2003). As a fodder containing phytoestrogens (see Section 7c), it appears to promote the estrogenic receptors and increase both the length of lactation and milk volume in ewes (González-Andrés et al. 2004; Tabares et al. 2014). A similar effect has also been reported for cows (Hanelt 2001; Witters 2001; González-Andrés et al. 2004) and rabbits (Pałka et al. 2019).

Used in traditional herbal medicine, and now widely available on the Internet as a herbal remedy, there is doubt concerning the safety of extracts of *G. officinalis* as a galactagogue or hypoglycaemic for human use (Duke et al. 2002; Zuppa et al. 2010; Zecca et al. 2016). Secondary metabolite production has been shown to vary greatly with abiotic stress, indicating that appropriate dosage levels may be difficult to determine in crude plant preparations (Karakaş and Bozat 2020).

Extracts of *G. officinalis* have been shown to have a significant impact on glucose transport (Neef et al. 1996), although physiological actions are poorly known. In Bulgaria (where *G. officinalis* is endemic) and Chile (where it is introduced), the aerial parts of the plant have been traditionally used as a hypoglycemic and diuretic (Muñoz et al. 1981; Lemus et al. 1999; Kiselova et al. 2006; Atanasov et al. 2019). A concoction derived from this species had been used in mediaeval Europe to treat

symptoms including frequent urination, a symptom of diabetes (Witters 2001). Such practices led to studies early in the 20th Century of potentially useful compounds in the species to treat type 2 diabetes focusing on guanidine and galegine. Subsequently, various new anti-hyperglycaemic compounds were synthesized, including the much less toxic dimethylbiguanide, also known as Metformin or Glucophage (Bailey et al. 1996; Witters 2001; Bailey and Day 2004; Howlett and Bailey 2007). Metformin was introduced into clinical practice in Europe as a treatment for hyperglycemia in the late 1950s (Bailey and Day 2004; Goetz 2007; Goetz and Le Jeune 2008). The drug was introduced to Canada in 1972 and to the United States in 1995 (Bailey et al. 1996; Dowling et al. 2011) and has been prescribed world-wide (Hadden 2005; Mentreddy 2007; Dowling et al. 2011). Metformin has also been studied in the treatment of obesity (Campbell and Howlett 1995; Witters 2001) and polycystic ovary syndrome, as well as showing antiviral and anticancer activity (Dowling et al. 2011). Galegine in *G. officinalis* has been found to cause weight reduction in mice (Palit et al. 1999; Mooney et al. 2008), but, as with guanidine, subsequent studies have synthesized more effective analogues (Coxon et al. 2009).

In addition to the alkaloids, some of the 48 detected phenolic compounds may contribute to the hypoglycemic activity observed in *G. officinalis* (Barchuk et al. 2017). Experiments on rats with induced hyperglycemia showed that blood glucose concentration was significantly reduced when treated with saponins, tannins and glycosides extracted from *G. officinalis* (Luka and Omoniwa 2012).

Galega officinalis has reportedly been used medicinally in hand and foot baths, and to improve skin healing through antibacterial and antifungal activity (Pundarikakshudu et al. 2001; Özbucak et al. 2005; Ertürk 2010; Karakaş et al. 2012). A widely used biguanide compound, chlorhexidine, is a useful germicide and disinfectant (Hadden 2005). Anti-microbiological properties of *G. officinalis* have been investigated in Turkey, where extracts of leaves and shoots have been found to be effective against bacteria and to a lesser extent against fungi (Özbucak et al. 2005; Karakaş et al. 2012, 2016a, 2016b). Extracts from the plant were found to be inhibitory on both gram-positive and gram-negative bacteria; and, significant tumour inhibition (98% with aqueous extract) was obtained in assays with *Agrobacterium tumefaciens*-induced potato disk tumors (Karakaş et al. 2012).

An aqueous extract of compounds from *G. officinalis* was found to have an anti-coagulation effect (Atanasov 1994; Atanasov and Spasov 2000). The fraction inhibiting platelet aggregation contained 19%–23% protein and about 74% polysaccharides, with the high biological activity being attributed to its protein component (Atanasov et al. 2003).

Aqueous extracts (1:4 weight to volume) of *G. officinalis* were tested on the dagger nematode *Xiphinema index* in

Chile for nematicidal activity (Insunza et al. 2001). Extracts of leaves and flowers killed 100% of the nematodes after 24 h exposure, while root extracts killed 91.7% of the nematodes.

In Europe *G. officinalis* has been cultivated as forage and green manure (Whyte et al. 1953; Ball 1968; Uphof 1968; Hanelt 2001) as well as for soil amelioration (Našinec and Němcová 1990). Cultivars have been developed that are adapted to acid soils (see Section 5b) and cold climates (Našinec and Němcová 1990). It has been used as a forage crop in Switzerland (Stebler and Schröter 1889), Italy (Peiretti and Gai 2006; Peiretti 2009), Spain (González-Andrés et al. 2004), Finland (Laakso et al. 1990), and China (Xu et al. 2010). As a crop, it is highly productive and might be improved with modern breeding techniques designed to reduce toxicity (Našinec and Němcová 1990). Forage and cutting for fodder are currently best done prior to flowering when alkaloid and phenolic content is low and plants are most palatable and nutritious (Stebler and Schröter 1889; Parton and Bruere 2002; De Otazúa et al. 2009; Oldham et al. 2011; Section 7c).

In Europe and Russia, *G. officinalis* has been investigated for potential bioremediation of hydrocarbon contaminated soils (Našinec and Němcová 1990; Lyubun and Tychinin 2007).

Pollen of *G. officinalis* has been a valuable source of food for bee colonies in several areas. It has been grown as bee forage in southern Europe, Germany and Switzerland (Whyte et al. 1953; Hanelt 2001). In Ankara province of north-central Turkey, it was among the top preferred plant species of bumblebees (Apidae: Hymenoptera) (Aytakin et al. 2002). Pollen of *G. officinalis* has been identified as a component in honey from a few sites in Chile (Montenegro et al. 2004; Montenegro et al. 2010), in one small district (Maniwatu) in New Zealand (Moar 1985), and in Italy (Mercuri and Porrini 1991; Canini et al. 2009).

Various other uses of *G. officinalis* have been reported. The leaves have been cooked like spinach (Gerard 1597) and plant extracts have been used as a substitute for rennet in the manufacture of curdled milk products (Facciola 1990). An extract claimed to inhibit tyrosinase activity in the production of melanin has been promoted as a skin whitener (Lee et al. 2012) and skin conditioner products containing “galega officinalis extract” (Chemical Abstracts Service registry number 84650-07-7) are available for sale.

In Europe, *G. officinalis* has been used as a garden ornamental plant for centuries (Gerard 1597; Loudon 1849; Stebler and Schröter 1889; Step 1896; Hedrick 1919; Gams 1924; Hellyer 1955; Salisbury 1961; Polunin 1969) and horticultural trade may have been a significant pathway in its establishment to other countries prior to widespread soil quarantine regulations (see Section 6). Various cultivars have been previously imported for North American gardens (Macoun 1908; Bailey and

Bailey 1976), although regulations now prevent such trade.

(c) Legislation

In Canada, *G. officinalis* is listed as a class 2 primary noxious weed under the Weed Seeds Order (CFIA 2018; Canada Gazette Vol. 150, No. 10 — May 18, 2016) where tolerance levels are set for contamination in traded seed commodities. Its import is also regulated under the Plant Protection Act (CFIA 2018). It is, however, not listed on any provincial weed legislation.

In the United States, it is listed on the U.S. Plant Protection Act and Federal Seed Act (USDA-APHIS 2020). It is also considered a noxious or quarantine weed under State regulations in Alabama, California, Florida, Massachusetts, Minnesota, North Carolina, Nevada, Oregon, Pennsylvania, South Carolina, Vermont and Washington (USDA-NRCS 2020). In 1981 a program was established by the United States Department of Agriculture providing funding for the eradication of goat's-rue. In Cache County, Utah, the population size was reduced by as much as 95%, but the species has not yet been eliminated (Westbrooks 1993; Evans et al. 1997).

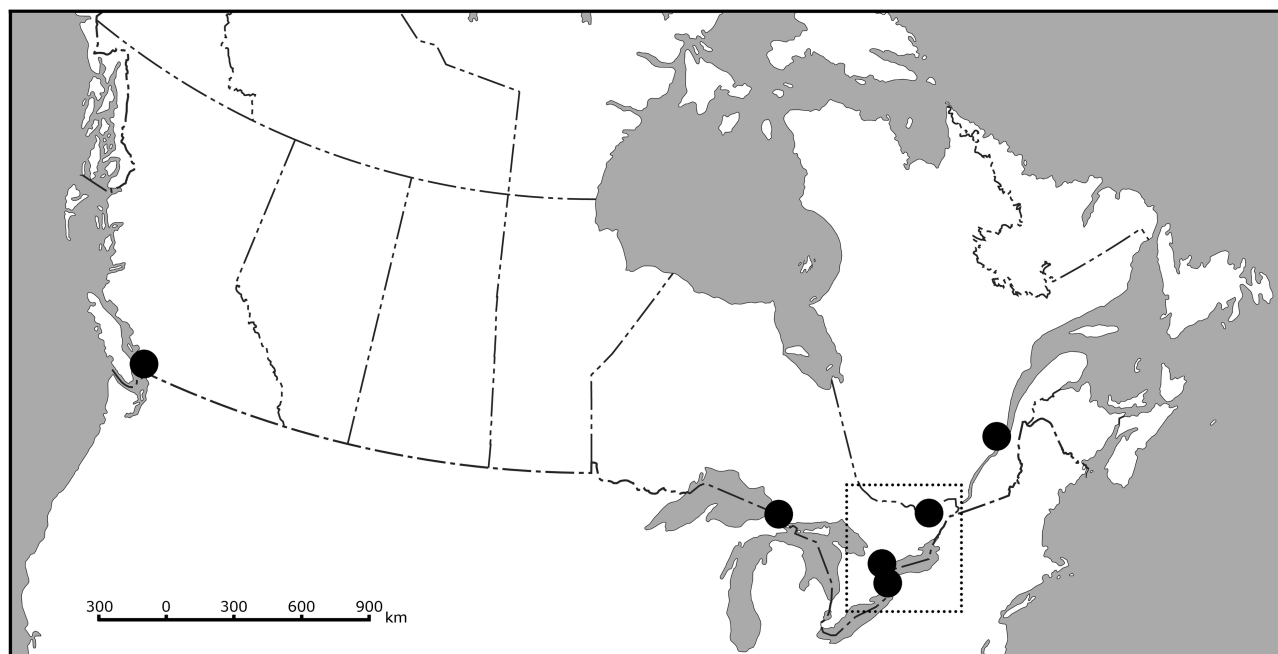
In New Zealand, *G. officinalis* is a regionally regulated weed. To reduce the occurrence and impact in the Hawke's Bay region, *G. officinalis* has been designated as a “total control” pest where land occupiers must destroy all plants before the production of mature seed (Hawke's Bay Regional Council 2004). In the Auckland region it has been designated a “surveillance pest plant”, where it is banned from sale, propagation, distribution and exhibition (Auckland Council 2020).

4. Geographical Distribution

The native range of *G. officinalis* is centred around the Black Sea region (Österman et al. 2011) extending from southeastern Europe through the Caucasus to western Asia, and is now extensively naturalized in western and northern Europe and eastwards to Pakistan (Gams 1924; Clapham et al. 1987; Ball 1968; Varis 1986; CABI 2019). It is reported as a native plant in Algeria and Morocco, but this status is uncertain (CABI 2019). The species has been introduced to Argentina, Chile, Ecuador (CABI 2019; Jørgensen and León-Yanez 1999), New Zealand (Webb et al. 1988), China (Xu et al. 2010) and at scattered locations in North America (CABI 2019). It was reported to have been introduced to the island of Mauritius prior to 1837 (Bojer 1837).

In Canada, *G. officinalis* has been recorded as a naturalized plant at sites in the provinces of Quebec, Ontario and British Columbia (herbarium specimen records plotted in Fig. 4). All known sites are at disturbed, urban or semi-rural places. In Quebec, it is known from one site at Quebec City (Gervais 1979). In Ontario, it has become established in several areas including around Ottawa, Toronto, Sault Ste. Marie, St. Catharines and the

Fig. 4. Distribution of goat's-rue, *Galega officinalis*, in Canada based on data from herbarium specimens (DAO, QFA, TRT and UBC). Plots near Niagara, Ottawa and Toronto (indicated with a box) represent multiple known locations. Outline map based on Coastline and Boundaries of Canada map, Atlas of Canada, 6th edition, Natural Resources of Canada.



Niagara region. In British Columbia, it has been collected at one site in Vancouver, but, in spite of the large population documented to have persisted for more than 25 yr, [Klinkenberg \(2020\)](#) considered it “A non-established species not considered to be part of the BC flora.”

In the United States, the species is currently established or naturalized in California, Colorado, Connecticut, Massachusetts, Maryland, Maine, Nebraska, New York, Oklahoma, Oregon, Pennsylvania, Utah and Washington ([Kartesz 2015](#); [USDA-NRCS 2020](#); [Calflora 2020](#)). In Utah and Pennsylvania, where the species is well established and spreading, control measures have reduced its presence ([Oldham and Ransom 2011](#); [Pennsylvania Department of Agriculture 2011](#)). Originally reported from New York City area in 1948 ([Ahles 1951](#)), it was considered rare in the state until recently reported in the Niagara region ([Eckel 2004](#)). In Michigan, it was collected from a well-established stand in a marsh in 1985 ([Reznicek et al. 2011](#)). In Oregon, where the species was thought to have been eradicated following a brief appearance in 2007, it remained a target invasive species subject to the state’s Early Detection and Rapid Response (EDDR) program, and a later reassessment ([Oregon Department of Agriculture 2015](#)) noted that new sites had been located around Portland.

Originally distributed in southeastern Europe, its introduction westward, before or during the medieval period, expanded the range throughout the southern part of the continent and into northwest Africa ([Roskov et al. 2006](#)). In recent times populations have continued

to spread locally, such as in the United Kingdom ([Biological Records Centre 2014b](#)), eastern France ([EPO 2008](#)) and the Czech Republic ([Moravcová et al. 2010](#)).

5. Habitat

(a) Climatic requirements

It is reported that *Galega officinalis* has a low winter-hardiness ([Whyte et al. 1953](#)) which should tend to restrict its spread into and within colder climate zones. In Canada, the species has naturalized in continental climate zones in eastern Canada between 43° and 47° N latitude, and was found at 49° in the Pacific maritime zone of British Columbia. This suggests that it can tolerate an annual minimum temperature of at least –35 °C, which would include most of the important agricultural production areas in southern Canada.

In the United States, the plant has spread widely in Utah in a mid-latitude desert zone ([Evans 1984](#)). In greenhouse studies in that state, growth of *G. officinalis* was favoured by a long photoperiod for flowering (16–18 h), daily temperatures of 26–29 °C and was poorly adapted to large diurnal temperature fluctuations ([Patterson 1992, 1993](#)). Growth increased with elevated daytime temperatures from 15 to 29 °C but declined at 36 °C ([Patterson 1993](#)). In Pennsylvania it is established ([Pennsylvania Department of Agriculture 2011](#)) in a mid-latitude temperate climate. In Oregon and Washington, the plant grows in a Pacific climate zone similar to southern British Columbia.

Using observed growth responses of *G. officinalis* to temperature and diurnal fluctuations, [Patterson \(1993\)](#) generated a model to predict growth rates at various locations in the United States based on day/night temperature normals from May to September. His model predicts that optimal growth would be achieved in areas with a daytime average of 23 °C or greater and a diurnal change of 7 °C or less, geographically corresponding largely to areas in the southeastern United States. Since this model was formulated from observations of plants reared from surface-sterilized seed established in growth chambers, it is not clear whether effectively nodulating symbionts (see Section 7e) were present or whether their presence would affect growth responses and alter the model predictions.

In Europe, *G. officinalis* is widespread along river valleys, such as the Rhine, Danube, Thaya and Volga ([Gams 1924](#)). Further east, near the Black and Caspian Seas, as in northern Turkey ([Özbucak et al. 2005](#)), southern Russia, Ukraine and the Caucasus ([Dzyubenko and Dzyubenko 2003](#)), it is found in temperate to mild temperate lowland and sub-montane areas. It is rare in the Mediterranean climate of south-west Turkey ([Bennett et al. 1998](#)). It is rare in the United Kingdom outside of central and southeastern England ([Biological Records Centre 2014b](#)) and in Switzerland it is naturalized in temperate areas on low-lying lands sheltered from extreme cold ([Stebler and Schröter 1889](#)). In Spain, it has been successfully grown in regions with an average annual rainfall 440 mm and average daily maximum and minimum temperatures of 18.8 °C and 6.1 °C ([González-Andrés et al. 2004](#)). Through much of Italy it commonly occurs in natural pastures mostly below 1000 m elevation ([Peiretti 2009](#)). It is cultivated in areas of northern Italy with high precipitation in April, May and October and little rainfall in summer and winter with mean daily temperatures of 0.5 °C in January and 22 °C in July ([Peiretti and Gai 2006](#)). In Argentina, plants are found in areas which are humid and warm with an annual precipitation of 950 mm and maximum daily summer temperature of 22 °C ([Ansín 2001](#)). In tropical Ecuador, it is found only at 2500–3500 m asl. (metres above sea level) in the Andes ([Jørgensen and León-Yanez 1999](#)).

(b) Substratum

In Canada, *G. officinalis* has been reported from clay soils and rocky landfill in the Ottawa area ([Reddoch and Reddoch 2000](#)). Analysis of soil samples from five sites harbouring *G. officinalis* populations in Ontario, showed a pH of 7.4–7.8 ([Bromfield et al. 2019](#)), 140–360 parts per million (ppm) potassium, 120–320 ppm magnesium, 10–37 ppm phosphorus, 1–34 ppm nitrate (NO₃-) and negligible amounts of nitrite (NO₂-); and, the carbon/nitrogen ratio ranged from 7.2–17.0% [Eden Bromfield, (unpublished data)].

In Cache County, Utah, *G. officinalis* is found in clay loam and loam soil pH 7.3–7.5 with 3.3–5.7% organic matter ([Oldham 2009](#)). In New York, it was growing at dumps covered with gritty soil with a high percentage of chert in the form of pebbles ([Ahles 1951](#)). In Switzerland, the plant was observed to satisfy its nutritive requirements from the subsoil, so that the quality of the topsoil was deemed of little importance; however, it grew best in deep humus soil where moisture was available to its deep taproots ([Stebler and Schröter 1889](#)). Naturalized populations in Spain have been found on solonchic soils (alfisol typic rhodoxeralf) of pH 7.7, and plants have been cultivated in experimental field plots on regosolic soil (entisol typic xerorthent) of pH 8.0 and solonchic soil (alfisol typic palexeralf) of pH 8.2 ([González-Andrés et al. 2004](#)). In the Black Sea region of Turkey, *G. officinalis* is a glycophyte usually found in weakly acidic to alkaline soils rich in nitrogen ([Özbucak et al. 2005](#)), but around the northern and eastern shores of the Black Sea, the plant is tolerant of saline soils ([Dzyubenko and Dzyubenko 2003](#)). Plants thrive in mesic habitats with deep soil in the Czech republic ([Kubešová et al. 2010](#)). Along the walls of the upper tidal Thames River in the United Kingdom, plants are commonly found in wasteland among boulders ([Francis and Hoggart 2012](#)), where the underlying soil is of alluvial deposits. In Argentina and central Chile, the plant has spread in rich and humid soils ([Whyte et al. 1953](#)).

In Canada, populations of *G. officinalis* were found at sites with soils above pH 7.0 ([Bromfield et al. 2019](#)) which is consistent with reports from the United States ([Oldham and Ransom 2009](#)) and Spain ([González-Andrés et al. 2004](#)) of plants growing in soils with pH ranges of 7.3–7.5 and 7.7–8.2, respectively. This suggests that the apparent adaptation of *G. officinalis* to soils above pH 7.0 may act in concert with the high level of specificity between host plant and symbiotic bacterium (see Section 7e) to limit the spread of the plant in new environments ([Bromfield et al. 2019](#)).

To assess the adaptation of *G. officinalis* as a fodder crop to saline soils in northeastern Europe, [Egamberdieva et al. \(2013\)](#) established a greenhouse experiment which involved inoculation of salt-stressed plants either with the symbiotic bacterium *Neorhizobium galegae* symbiovar *officinalis* (see Section 7e) alone, or co-inoculation with two growth-promoting bacteria, *Pseudomonas extremorientalis* and *P. trivialis*. Increasing salt concentrations decreased the ability of *N. galegae* alone to colonize the roots, whereas co-inoculation significantly alleviated the effects of salt stress, increasing nodulation and the nitrogen content of the shoots and, to a lesser extent, the roots.

(c) Communities in which the species occurs

In Canada, *G. officinalis* has naturalized along riverbanks, ditches, channels and other waterways and sometimes along roadsides, abandoned fields or landfill

sites, usually not far from waterways (herbarium specimen label data). It can form dense patches (Fig. 2) in communities which are usually open or partly shaded and consist primarily of introduced grasses and herbaceous plants.

In the United States, *G. officinalis* has also been found mostly near waterways. In Utah, it spread from the forage testing fields into natural seepage areas, ditch-banks, marshes, irrigated pastures, high line canals and drainage systems (Tingey 1971; Evans 1984; Patterson 1992; Welsh et al. 1993). In Philadelphia, it was first detected along roadsides and floodplains in and around the Morris Arboretum (Stokes 1964; Klugh 1998), but has subsequently spread to other parts of Pennsylvania (Pennsylvania Department of Agriculture 2011). In New York, *G. officinalis* was first seen along river banks in Bronx County, with such plants as *Lotus corniculatus* L., *Coriandrum sativum* L., *Diplotaxis* sp., *Artemisia annua* L. and *Matricaria inodora* L. (Ahles 1951).

In its native range, the species occurs in a variety of habitats. In Turkey, it is found on mountain sides, roadsides, edge of lakes, beside fields and streams and in scrub woodlands at low elevations between 5–550 m asl (Davis 1970; Özbucak et al. 2005). In the former USSR (including the southern Russian Federation, southern Ukraine, Georgia, Azerbaijan, Armenia and western Kazakhstan) it occurs on riverbanks and in river valleys, meadows, scrub, beech woods, roadsides and ravines (Gorshkova 1971). It is among pioneer flora in disturbed sites in the western Caucasus, generally present at lower latitudes than *G. orientalis* (Andronov et al. 2003) and is among native species of closed communities along shoals of western Caucasian rivers at elevations ranging from 70–80 m asl., where occurrence was relatively low, to 800–900 m asl., where occurrence was considerably greater (Akotov and Akatova 2010). In the Italian Alps, *G. officinalis* is found in grazed natural pastures (Peiretti 2009) at elevations of 260–523 m asl. (Siniscalco et al. 2011). In Tuscany, it occurs primarily in wetlands and is common in pastures, along with hemp-agrimony (*Eupatorium cannabinum* L.) and field horsetail (*Equisetum arvense* L.), less frequent along canals and watercourses dominated by galingale (*Cyperus longus* L.) and rare in deciduous oak-dominated woods and inland swamps dominated by devil's beggarticks (*Bidens frondosa* L.) and climbing nightshade (*Solanum dulcamara* L.) (Giallonardo et al. 2011). In New Zealand it is found mostly along waterways and in wetlands (Webb et al. 1988; Parton and Bruere 2002).

6. History

Introduced to Canada in the late 19th Century as an ornamental, *Galega officinalis* was cultivated in Ottawa as early as 1897 (Macoun 1908) and herbarium records show that the species continued to be grown in gardens through the first half of the 20th Century. Established populations of plants found in the Ottawa area since

1973 have probably originated as garden escapes (Macoun 1908). Populations at other sites in Ontario (Toronto, 1964; St. Catherines, 1974; Sault Ste. Marie, 2007) may also have arisen as garden escapes rather than through cultivation as forage. Herbarium specimens at Université Laval (QFA) indicate the plant was cultivated at Ste.-Anne-de-la-Pocatière (1940) and at Sainte-Foy (1960–1975), and was found established in Quebec City as early as 1974. A herbarium specimen at the University of British Columbia (UBC) documents the garden cultivation of *G. officinalis* in Vancouver, BC, as early as 1964 and a well-established population along the Fraser River in Vancouver has been known since 1998. While escape from ornamental or forage cultivation seems the most likely introduction pathway, it likely has also spread through association with transportation systems as an unintentional hitchhiker.

In the United States, *G. officinalis* was imported in small quantities as a trial green forage soiling crop at several localities in the late 19th and early 20th centuries, but was not adopted for agricultural use (Piper 1916; Evans 1984). Material imported from France was trialed for forage in Garden City, Kansas, in 1892, but the crop was destroyed by grasshoppers (J.A. Sewall in Vasey 1893). At the Utah Agricultural Experimental Station in Cache Valley County trials assessing its value as a forage crop were conducted from 1891–1893 until it was determined that the plant was unpalatable and toxic and the fields were subsequently abandoned (Tingey 1971). By the 1980s the plant had spread from the trial plots and become weedy over an area of about 155 km² (Evans 1984). A specimen at the New York Botanical Garden (NY 505379) documents *G. officinalis* cultivation in San Francisco, California, as early as 1927. In Pennsylvania, the seeds were among those of traditional medicinal plants sown experimentally near the Morris Arboretum in the 1950s where the plant became naturalized along floodplains and riverbanks (Stokes 1964). The species also became naturalized at scattered temperate and tropical montane locations elsewhere in the Americas (Barneby 1989; see Section 4).

The plant's introduction to northern and western Europe was probably driven by its medicinal attributes and galactagogue properties. Loudon (1849) states that its introduction to the United Kingdom occurred prior to 1598 at which time it was growing in John Gerard's physic garden (Gerard 1597). The English naturalist and physician William Turner did not mention the plant in his 1538 *Libellus de re herbaria novus*, however, after his medical studies in Italy (1540–1542) where he saw it naturalized, he mentioned its cultivation and medical properties in subsequent publications (Britten 1881; Chapman et al. 1995).

7. Growth and Development

(a) Morphology

The plant's strong taproot provides access to deep soil moisture under drought conditions and to nutrients in

the subsoil when growing in disturbed and nutrient-poor soils. The lax stem bases reduce the impact of mowing for fodder production or control. After cutting, axillary buds at the base of the stem quickly form a new set of stems. Lateral branches originating from buds in the axils of the radical leaves will develop into lateral branches in the first or second year (Stebler and Schröter 1889).

(b) Perennation

A long-lived perennial. Unless killed by frost, the large tap roots (see illustration in King County 2018) overwinter and sprout new stems from the caudex each spring.

(c) Physiology and biochemistry

An early nutritional analysis of *G. officinalis* as a fodder plant noted that prior to flowering, plants contained 78.7% organic matter, 17.1% nitrogen, 1.4% fat, and 34.4% fibre (Stebler and Schröter 1889). A more recent Italian study simulating forage production have shown a decline in nutritional quality and digestibility through the growth stages of rosette, shooting and budding, although some components were partially restored in the post-cut regrowth stage (Peiretti and Gai 2006; Peiretti 2009). Palmitic, linoleic and α -linolenic represented 82%–85% of the fatty acid content during the mid-season growth stage and in late-season regrowth. These percentages changed little during development; however, α -linolenic proportion was significantly higher at the regrowth stage. Organic matter, neutral detergent fibre, acid detergent fibre, lignin and gross energy increased during maturation, while crude protein, ether extract, ash and organic matter digestibility declined with plant maturation. Amino acid proportions did not vary significantly across growth stages, with only serine showing a significant change with development (highest at shooting and regrowth stages). In overall dry matter and chemical content, dry matter content increased from 111–157 g·kg⁻¹ during first growth stages, and to 180 g·kg⁻¹ at the regrowth stage; total nitrogen decreased from 31.6 g·kg⁻¹ to 20.2 g·kg⁻¹ (dry matter) from vegetative to budding stages, but increased to 33.5 g·kg⁻¹ during the regrowth stage; soluble nitrogen decreased during growth from 5.9 g·kg⁻¹ to 4.8 g·kg⁻¹ and then increased to 5.4 g·kg⁻¹ at regrowth. No significant changes were noted in water soluble carbohydrates (74–82 g·kg⁻¹) or pH (5.6–5.7). The fermentation and quality of ensiled *G. officinalis* fodder varied with harvest growth stage and post-harvest wilting time.

The free amino acid canavanine is present in seeds of the genus *Galega* (Turner and Harborne 1967), perhaps functioning as both an anti-herbivore defense and nitrogen source for the embryo.

The most toxic molecules in *G. officinalis* include the guanidine alkaloids galegine (dimethylallylguanidine), hydroxygalegin and peganine (= vasicine) (Schäfer and

Stein 1969). Galegine is found in increasing concentrations from the stem to leaves to the immature pod stage, with no storage in the roots and with some decrease at the ripe seed stage (Reuter 1962; Oldham et al. 2011). The quinazoline alkaloid, vasicine, was once believed to be responsible for the bitter taste avoided by animals, but later analysis suggested that the vasicine content (0.1%–0.35%) was too low to be responsible for reducing the fodder acceptability to livestock (Laakso et al. 1990).

In France, a rare norterpeneoid glucoside, dearabinosyl pneumonanthoside, and several phytoestrogens (flavonol triglycosides), were isolated from the vegetative parts of *G. officinalis* by Champavier et al. (1999, 2000). Flavonoids absorbing UV radiation, isorhamnetin, kaempferol and quercetin, were reported by Kay (1987) in the flowers of *G. officinalis*. Luka and Omoniwa (2012) identified alkaloids, flavonoids, saponins, tannins, cardiac glycosides, phenols, resins, terpenes and steroids from aqueous extracts of whole plants. A number of compounds extracted with methanol were identified by Fukunaga et al. (1987). In a study by Kiselova et al. (2006), aqueous extracts of *G. officinalis* had a total phenol content of 361.48 (\pm 1.30) μ M (quercetin equivalent), indicating a moderate antioxidant capacity.

In a comparative study of plants grown from seed and nodal explants, Karakaş et al. (2016a) found 25% less total phenolic content (methanol extract) present in explants than in plants grown from seed. Although the total phenolic content was lower, observed levels of apigenin, luteolin and chlorogenic acid were higher in explants (10 \times , 100 \times and 2 \times , respectively). Shymanska et al. (2020) found that phenolic compounds were at the highest concentrations in flower buds and flowers.

Galega officinalis is one of the Fabaceae species with an attenuated extended bundle sheath (EBS) system (paraveinal mesophyll), consisting of digitated cells positioned between the palisade and spongy mesophyll of the leaf. The EBS tissue cells mainly join the spongy mesophyll cells lying between the veins rather than bridging between all of the vein islets, as occurs in species with a continuous EBS system (Franceschi and Giaquinta 1983a, 1983b; Kevekordes et al. 1988). The species is somewhat anomalous in having two layers of bridging cells, but these do not appear to extend throughout the large interveinal regions of the leaf. These specialized cells may act as routes for phloem loading of photosynthesis assimilates (Franceschi and Giaquinta 1983a) or as an EBS recovery system for concentrated amino acid solutes in the transpiration stream (Canny 1988, 1990).

(d) Phenology

The embryo of *G. officinalis* develops entirely from the apical cell of the zygote, while the basal cell remains part of the suspensor enabling nutrients to reach the developing embryo (Souèges 1949; Packa 2001).

Leaflets of emerging leaves are initially folded along the midrib, and unfurl as they develop (Klugh 1998).

Cauline leaves develop alternately on each stem and flowering racemes emerge successively from leaf axils. Flowers and fruits develop acropetally along the racemes. In a laboratory experiment using different temperature regimes (Patterson 1992), the first flower buds appeared at an average 86, 46 and 40 d after seedling emergence at photoperiods of 14, 16 and 18 h, respectively, indicating a large variation in development times depending upon climate and light conditions. Fruits remain attached as they mature and dehisce (Stebler and Schröter 1889). At senescence, which may not occur until first-frost, pods dehisce along both sutures with the valves twisting to release the seeds (Kirkbride et al. 2003). The indeterminant development pattern results in plants bearing flowers and fruits at various stages of development throughout much of the growing season.

Plants in eastern Canadian populations are in flower by late June with fruits developing from early July into September; plant senescence commences in early fall and becomes complete with the first hard frost (herbarium specimen label data). In Pennsylvania, flowering was reported as beginning in June and continuing throughout the growing season (Klugh 1998) and although the upper parts of plants senesced in September, late-season new growth was sometimes observed at plant bases (Stokes 1964). In the Inter-mountain region of the western United States, the growing season was reported as late April to August (Barneby 1989) and from June to October in Washington State (King County 2018). Two fodder cuttings per season were obtained from plants grown for ensilage in Virginia (Piper 1916).

The flowering season for Europe as a whole was given as June to August by Polunin (1969) and in England, plants were reported to flower from July to August by Gerard (1597). In Switzerland, plants sown in early spring began flowering between the end of June and late July and, after cutting at the early flowering stage, quickly produced new stems from the base and began flowering again in late summer (Stebler and Schröter 1889). In Italy, plants sown in early spring were in full leaf by late June, began to shoot one week later, and began to bud two weeks later (Peiretti and Gai 2006).

Seedling relative growth rate as calculated in Czech trials (Moravcová et al. 2010) was $0.160 \text{ g g}^{-1} \text{ day}^{-1}$. In growth chamber trials (Patterson 1992, 1993), vegetative growth patterns (resource allocation) were significantly affected by variations in day and night temperatures. After 89 d plants attained maximum dry weight at day/night temperatures of 26/22 °C, while plants grown in regimes with greater day/night fluctuation (12–20 °C) or a higher day temperature (34 °C) were smaller. Root biomass, averaged over a period from 14 to 89 d after emergence, was highest at 26/14 °C, and least at 34/22 °C. In a comparison of the root weight ratio with that of alfalfa, *G. officinalis* tended to partition more biomass into roots than the latter at night temperatures of

18 °C or less, with a tendency for proportional root biomass to increase with decreasing night temperature. The greatest period of root growth was between 28 and 60 d after emergence. Given the response to temperature, photoperiod and moisture, Patterson (1992, 1993) predicted that *G. officinalis* could potentially flourish in large areas of North America, especially where conditions are suitable for alfalfa production.

(e) Mycorrhizal and bacterial symbioses

Mycorrhiza are fungi that form a symbiotic associations with plant roots and facilitate the uptake of nutrients (Bolan 1991). Mycorrhizal relationships of *Galega* species have not been well studied, although Palta et al. (2016) reported that roots of *G. officinalis* were colonized by mycorrhizal fungi and Püschel et al. (2011) reported that the growth of *G. orientalis* responded positively to soil inoculation with mycorrhizae.

Like most of the Fabaceae, species of *Galega* form a symbiotic association with soil bacteria (rhizobia) which stimulate the formation of swellings called nodules on the roots of the plant and convert atmospheric nitrogen (N_2) into forms of ammonia (NH_3) that are used by the host plant. In exchange, the bacteria receive energy in the form of fixed carbon from the plant host (Proctor and Moustafa 1962, 1963).

The two most studied species of *Galega*, *G. officinalis* and *G. orientalis*, form a highly specific symbiotic association only with the bacterial species *Neorhizobium galegae* which consists of two distinct symbiotic varieties (symbiovars): *orientalis* and *officinalis*. Both of these symbiovars form nodules on the two plant species but fix nitrogen only on their respective *Galega* host species (Lindström et al. 1983; Lipsanen and Lindström 1988; Lindström 1989; Kajjalainen and Lindström 1989; Räsänen et al. 1991; Mousavi et al. 2014; Österman et al. 2014; Karasev et al. 2019). The mechanisms controlling the specific interaction between *Galega* plants and their respective bacterial symbiont are poorly understood (Franche et al. 2009; Österman et al. 2011). Genome sequencing of several strains of *N. galegae* indicated few differences between the symbiovars *officinalis* and *orientalis*, although a single symbiosis related gene was found to be specific for symbiovar *orientalis*; the function of this gene remains to be determined (Österman et al. 2014, 2015).

In New Zealand, Liu et al. (2012) identified 2 strains of *N. galegae* isolated from root nodules of *G. officinalis*. Phylogenetic analyses of four housekeeping (16S rRNA, *atpD*, *glnIII*, and *recA*) and two symbiosis gene (*nodC* and *nifH*) sequences indicated that 50 bacterial isolates from root-nodules of *G. officinalis* plants at five Canadian sites were identical to strains of *N. galegae* symbiovar *officinalis* originating either from Europe or the Caucasus (Bromfield et al. 2019). Moreover, plant tests with *G. officinalis* indicated that soils collected from four Canadian sites without a history of agriculture or

presence of *G. officinalis* were deficient in symbiotic bacteria capable of eliciting nodules on this plant. In this connection, it is noteworthy that strains of the species, *N. galegae*, were not represented in culture collections of rhizobia isolated from diverse sites across Canada (Prévost and Bromfield 2003). Collectively, these data suggest that anthropogenic activities are responsible for the co-introduction of *G. officinalis* and its specific bacterial symbiont (*N. galegae* symbiovar *officinalis*) into Canada from the Old World.

Although *G. officinalis* can grow and reproduce under cultivation without its effective bacterial symbiont (González-Andrés et al. 2004), establishment and persistence in natural vegetation communities is highly unlikely. Cultivation trials in Estonia showed biomass production of the related *G. orientalis* was increased by 80% when plants were inoculated with the appropriate bacterial symbiont, but by only 35% when fertilized with supplemental nitrogen in the absence of symbionts (Raig et al. 2001). At sites in Spain, where *G. officinalis* and its symbiont, *N. galegae*, are naturalized, 5.9×10^4 infective bacterial cells per gram of soil were found (González-Andrés et al. 2004).

The establishment of *G. officinalis* populations in Canada outside of cultivation requires the co-introduction of both the plant host and its symbiotic bacterium. This is most likely accomplished through human transport of soil containing both seeds and bacteria (Bromfield et al. 2019).

8. Reproduction

(a) Floral biology

The flowers, like those of all Fabaceae, are hermaphrodite, however, plants are not able to self-pollinate as enclosed plants do not produce fruits (Fruwirth 1906). Details of floral anatomy and the pollination mechanism are described by Knuth (1908). Plants are pollinated by bees which are attracted to the reddish-yellow pollen grains (Knuth 1908) and nectar is not produced (Knuth 1908; Rodríguez-Riaño et al. 1999). Flowers possess a monadelphous androecium in which the lower part of the filaments are fused to form a tube of ten stamens surrounding the ovary. The stigma protrudes beyond the staminal tube and the anthers dehisce before the flower opens (Knuth 1908).

This species was determined to be a preferred plant species for bumblebees in Turkey (Aytekin et al. 2002) and *G. officinalis* pollen has been identified in honey from Chile (Montenegro et al. 2004; Montenegro et al. 2010), New Zealand (Moar 1985) and Italy (Mercuri and Porrini 1991; Canini et al. 2009). The plant has been deliberately grown as a bee forage in Switzerland (Hanelt 2001). The plant was listed as being economically important for honey production by Wiersema and León (1999), but is only significant as a pollen source for sustaining colonies and not honey production itself.

(b) Seed production and dispersal

Goat's-rue is a prolific seed producer. Plants collected in Canada averaged seven racemes per stem, with about 25 flowers per raceme, and 4–6 seeds per pod (approximately 1000 seeds per stem), and an average seed weight of 6.07 mg (S.J. Darbyshire, (unpublished data)). From cultivated plants in Switzerland, Stebler and Schröter (1889) estimated an average seed weight of 7.32 mg. In Pennsylvania, Klugh (1998) reported 20–50 flowers per raceme, producing pods with up to nine seeds. In Utah, Oldham and Ransom (2009) observed seed production ranging from 174–1230 seeds per stem (depending on stem density), while Evans (1984) reported of up to 25 000 seeds per plant averaging six per pod. In the Czech Republic, the average seed weight was reported as 6.56 mg, with 1652 seeds per stem (Moravcová et al. 2010).

Seeds initially fall close to the plant. An experiment to measure speed of seed fall showed a very low capacity for wind dispersal (Moravcová et al. 2010). The spread of the species along waterways or in wetlands (see Section 5c), suggests that water is the main natural dispersal mechanism for seeds (Faliu et al. 1985), individually, in pods, or perhaps occasionally whole plants. In Utah, seeds spread primarily through irrigation systems were subsequently found in nearly all fields downstream of the original infestation (Evans 1984; Keeler et al. 1986). Irrigation channels were also reported to be the main dispersal pathway in Chile (Oehrens and González 1975). This suggests that, although the seeds are not buoyant and have been observed to sink quickly (Klugh 1998; Moravcová et al. 2010), they could be carried in stages by fast-moving water which follows the opening of sluice gates or sudden flooding. Moravcová et al. (2010) reported that some of the seeds in an experimental test remained floating for up to 24 min before sinking. Although seeds do not float for long, they may still approach neutral buoyancy when submerged and be readily transported by moving water.

Seeds of plants not growing near flowing water are likely to remain near the plant, which, together with regrowth from, and expansion of the caudex, may account for the scattered and localized patterns in which many colonies continue to be found in North America.

Soil transport from sites with established *G. officinalis* populations appears to have contributed to seed dispersal over short to medium distances. In Canada, movement of contaminated soil by excavators and vehicles is believed to have led to the spread of the species in the Ottawa area away from original garden plantings or other locations. In Pennsylvania, dredging equipment at a lake led to dispersal of seed in the sediments, as well as transport of aggregate construction material (Pennsylvania Department of Agriculture 2011). In New York, the species was found where ballast had been dumped (Ahles 1951). In the United Kingdom, plants growing along a roadside in Essex were apparently the

source of seed transferred via construction equipment to an embankment which was then converted to pasture for sheep (Gresham and Booth 1991; see Section 3a). Seed can be dispersed by farm equipment or as commodity contaminants (Patterson 1992), but there is little evidence that these are important factors. The plant is not common in arable crops (Evans 1984), with the exception of alfalfa (Patterson 1993) where mowing is usually done before the plants are mature and contamination of alfalfa seed can be prevented by sieving because of the different seed sizes (Tingey 1971). The likelihood of animal dispersal is speculative, however, in a laboratory experiment in the Czech Republic, 51% of seeds scattered over a wild boar pelt remained embedded in the fur following agitation (Moravcová et al. 2010). Mature seeds, which are the most toxic part of the plant, could possibly be eaten by livestock and passed in feces.

The absence of *N. galegae* in native soils has been implicated in the slow spread of *G. officinalis* in both Canada (Bromfield et al. 2019) and New Zealand (Proctor 1963). The co-dispersal of *G. officinalis* seed with the bacterial symbiont would seem most effectively accomplished through soil transport either by water or human actions. Apart from deliberate soil inoculation, the intentional spread of the plant and its symbiont can be achieved by transplanting from gardens where *N. galegae* is already present or by illegally importing soil containing the bacterium. Inadvertent co-dispersal may occur through the movement of soil or construction aggregate, or on contaminated vehicles from areas with previously established plant-bacteria populations.

(c) Seed banks, seed viability and germination

The continued annual emergence of seedlings following strenuous attempts to eradicate the species indicated the presence of seed banks in infested areas of Utah (Evans et al. 1997), where 15 000–75 000 seeds m⁻² have been observed (Oldham 2009). Seeds germinate rapidly in 1–3 d when scarified and moistened in the laboratory [Patterson 1992; S. Mechanda, (unpublished data)], but germination may take several weeks under natural conditions. Seeds are known to remain viable in the soil for at least 5–10 yr (Evans and Ashcroft 1982). Seed dormancy, as with many Fabaceae, is primarily physical, with seeds germinating rapidly after physical or chemical scarification. Oldham and Ransom (2009) found nearly 100% seed germination after sulfuric acid scarification, but only 8% of un-scarified seeds germinated.

In Utah, greenhouse germination trials used seeds collected from the soil surface as well as seeds collected 26 yr earlier and placed in dry storage (Oldham and Ransom 2009). Seeds were planted at different depths from near-surface to 14 cm. The seeds exhibited dormancy of 80–93%, viability of 91%–100%, and were capable of remaining viable in dry storage for at least 26 y. Dormancy was estimated by comparing

germination of the old and new seed with and without sulphuric acid scarification. Of the untreated 26 yr old seed, 61% germinated, while maximum germination (99%) was achieved with a scarification time of 10 min. Only 23% germination occurred in untreated 6 mo seed, but reached 89% germination after 50 min of scarification treatment. These results indicated that dormancy was lower in old seed, although viability was similar in both age classes. Similar observations by Stebler and Schröter (1889) on the germination of “old” and “new” seeds planted for crops in Switzerland found that 12% of new seed and 21% of old seed (age and storage conditions not given) germinated; 88% of the new seed and 21% of the old seed remained hard (i.e., dormant) while the remainder of the old seed (58%) rotted. In Spain, a germination rate of 50% was observed after sandpaper scarified seed was sown (González-Andrés et al. 2004). Other factors have been shown to affect the germination of *G. officinalis*. In the Czech Republic (Moravcová et al. 2010), germination of freshly harvested seed was tested under three temperature regimes (25/10, 20/5 and 15/5 °C), and dry-stored plus cold-stratified (1–4 °C, 3–5 mo) seed at 25/10 °C (12 h light 12 h dark). Although details of the results were not given, germination under these various conditions ranged from 12%–56%. Testing the effect of temperature on germination in the laboratory, Patterson (1992) observed germination of scarified seeds was 47%–68% one day after planting, with lower germination rates occurring in the 26/14 and 34/14 °C regimes, but after three days, germination was 75%–81%, regardless of temperature conditions. Higher night temperature resulted in high germination rates. In Utah, seedling emergence was inversely related to burial depths; emergence was 93% at 0.5 cm soil depth, 87%–90% at 1–3 cm depth, 56% at 8 cm, and 21% at 10 cm, while no emergence occurred at depths below 12 cm (Oldham and Ransom 2009).

(d) Vegetative reproduction

Roots that survive winter temperatures will send up new shoots in the spring from buds on the caudex (base of the stem). In vitro experiments by Našinec and Němcová (1990) were able to regenerate plants from both callus formation and re-growth from node-bearing stem segments.

9. Hybrids

Naturally occurring hybrids between *G. officinalis* and *G. orientalis* have been reported in the Caucasus region where the two species are sympatric (Raig et al. 2001). Artificial hybrids between *Galega* species have been reported in the nursery trade; for example, the popular cultivars referred to as *G. hartlandii* or *G. officinalis* var. *hartlandii* (both are illegitimate scientific names) are reputed to be a hybrid cross between *G. officinalis* and *G. patula* Steven (although *G. patula* is usually considered a synonym of *G. officinalis*).

10. Population Dynamics

As a perennial, *G. officinalis* is not successful in annual crops of arable fields, but does well in un-cropped areas (including field margins) and uncut pastures where animals tend to avoid the species and more desirable fodder plants are overgrazed, leaving *G. officinalis* to spread as a result of the reduced competition (Tingey 1971; Evans 1984; Keeler et al. 1986). In a 4 yr study of horse grazing areas in Argentina, *G. officinalis* increased from 1% to 30% plant cover in improved pastures and from 15% to 47% in native grasslands under continuous grazing. Under controlled grazing intended to increase the use of bird's-foot trefoil (*Lotus tenuis* Willd.) as forage, the levels of *G. officinalis* remained at 1% in pastures and decreased from 15% to 5% in grasslands (Ansin 2001). Stebler and Schröter (1889) recommended that, as a forage crop, *G. officinalis* should be sown without a protective crop and would not survive if sown with grasses.

In Majella National Park of central Italy, *G. officinalis* was among dominant herbaceous species that appeared in a post-fire montane beech forests but was not detected in un-burned forests (Odoi 2009). It responded as a pioneer species after disturbance and prior to forest canopy maturation.

11. Response to Herbicides and Other Chemicals

Herbicide control has been used in a few regions where *G. officinalis* is considered particularly invasive or dangerous to animals. In parts of Europe there is little information on the use of herbicide controls to mitigate its spread. In southwestern France, where poisoning of livestock is a more serious problem, eradication of the species in pasturelands with the use of herbicides such as 2,4-D, bentazon, dicamba and MCPA has been recommended (Faliu et al. 1985). In Italy (Peiretti 2009, Peiretti and Gai 2006) and Spain (González-Andrés et al., 2004), where the species is valued for livestock feed and other uses, control has been limited to cutting or mowing before the flowering stage to limit accumulation of toxins (see Section 12). In the Hawke's Bay region of New Zealand, control of the species is required and the use of herbicides triclopyr or metsulfuron methyl in the spring or prior to flowering is recommended (Hawke's Bay Regional Council 2004). Since the caudex of herbicide-treated plants can remain viable for up to 7 yr, full control usually requires either re-treatment or uprooting (Miller 2003).

The most extensive use of herbicides to control *G. officinalis* has been in parts of the United States where control or eradication have become priorities. Various formulations of 2, 4-D were tested in Utah in the 1960s at various rates at different growth stages, but while 2,4,5-T was the most effective, 2, 4-D sprayed at relatively low rates was found to be effective enough (Tingey 1971). Spraying 2, 4-D, dicamba or a combination after cutting and repeating the treatment was found to be effective

in Utah trials, although it did not prevent new cohorts of seedlings emerging from the seed bank (Evans 1984). Effective control of plants was achieved with a mixture of these herbicides, applied twice a year for two years after mowing, at application rates of 565–568 g a.i. h⁻¹ of 2,4-D and 272–282 g a.i. h⁻¹ of dicamba (Evans 1984; Miller 2003). Further experiments with a number of herbicides were conducted in Utah (Oldham and Ransom 2011). Herbicides tested in a greenhouse were 2,4-D amine, dicamba, chloresulfuron, picloram, imazapyr, imazamox, aminopyralid and triclopyr, applied at gradually increasing doses from 0.125× to 2.0× typical field use rates. The species was most sensitive to the ALS inhibitors chloresulfuron (at 3.7 g a.i. ha⁻¹) and imazapyr (at 90 g a.i. ha⁻¹). In field trials at two infested pasture sites, the same herbicides were tested except that imazamox was replaced by metsulfuron methyl. On average, all tested herbicides, excluding 2,4-D and imazapyr, had greater than 93% control at both sites, and at one site, treatments not only controlled established *G. officinalis*, but also resulted in increased perennial grass cover. All treatments at one site decreased seedling cover, while aminopyralid and picloram also decreased seedling cover at the other site 11 mo after treatment.

In Pennsylvania, mechanical measures to prevent flowering in combination with herbicide treatment is recommended (Pennsylvania Department of Conservation and Natural Resources n.d.). In Washington State, a combination of manual, mechanical and herbicide methods was recommended for control of the species, the most effective herbicides being 2,4-D, aminopyralid and dicamba, alone or in combination, applied in the early summer before the bud stage, and repeated again in the fall (King County 2018).

In Utah, Evans and Peitersen (1987) assessed the field use of sodium methyldithiocarbamate as a soil fumigation to inhibit *G. officinalis* seed germination. Scarified seed was placed at various depths and retrieved 48 h after treatment and tested for germination in the laboratory. Germination from untreated plots was reduced by 16%–72% with seeds buried at greater depths showing less germination. The fumigation treatment reduced germination by about 50%, but was not sufficiently effective to decrease the field population.

12. Response to Other Human Manipulation

Galega officinalis is unlikely to become a serious weed on tillable land if good agronomic practices, such as row cropping and crop rotation, are used. Although the species can spread rapidly in heavily-grazed pastures, regular mowing can keep the plants from producing seed and spreading (Tingey 1971). Mowing will limit its spread in alfalfa fields by preventing seed production, and will reduce plant vigour. However, mowing alone is unlikely to eradicate the species as seed can remain viable in soil for many years providing annual recruitment after mature plants have been eliminated (Evans 1984;

Evans et al. 1997). Crop rotation, mowing, clipping, cutting, digging and cultivation are most effective when used in an integrated approach including herbicides (Evans et al. 1997). Deep tillage to 12 cm or deeper can help to limit emergence from the seed bank, but the development of effective methods of seed bank control remains a challenge (Oldham and Ransom 2009). Alternate cropping and row crop systems can reduce the population size since cultivation interrupts the life cycle as well as depleting the seed bank by inducing germination.

In a production study in Spain, seedlings for transplanting were inoculated with strains of *N. galegae* isolated from root nodules of plants growing in a naturalized population, presumably symbiovar *officinalis* (González-Andrés et al. 2004). Both inoculated plants and non-inoculated plants receiving supplemental nitrogen, produced significantly more above-ground dry matter than plants inoculated with various *Rhizobium* or *Bradyrhizobium* strains that did not form effective nodules. The highest crop yields were obtained at a plant density of 160 000 plants ha⁻¹ (direct sowing) and a cutting height of 10 cm above ground. The lowest yields were from plants transplanted at 10 000 ha⁻¹ with a cutting height of 2 cm above ground level.

The rust fungus *Uromyces galegae* (Opiz) Sacc. was introduced from France to Chile in 1973 as a biological control agent against *G. officinalis* (Oehrens and González 1975) and has spread to Argentina (Ellison and Barreto 2004). Although the fungus successfully established in Chile, it did not reduce seed production (Ellison and Barreto 2004) and after a promising start, appears to have had no long-term impact on the weed (Barreto 2008).

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) Herbivory

(i) Mammals, including both domestic and wild animals

Horses, cattle and sheep may graze on young *G. officinalis* plants, but tend to avoid mature plants because of the bitter taste of the alkaloids (Reuter 1962; Oldham et al. 2011). However, animals may consume the plant when other forage is scarce, or when it is present as a contaminant in alfalfa or other fodder fed to animals as hay (Tingey 1971).

(ii) Birds and (or) other vertebrates

No information was located.

(iii) Insects

In 1892, *Galega officinalis* was grown in Kansas to test its forage potential. However, J.A. Sewall (in Vasey 1893) reported that the plants were eaten by grasshoppers.

Lepidoptera

In Argentina *G. officinalis* is one of a number of host plants for the neotropical soybean bud borer (*Crocidosema aporema* Walsingham) (Liljeström and

Rojas-Fajardo 2005). *Galega officinalis* is among food plants of the larvae of *Coleophora vicinella* Zeller, which also feeds on *Astragalus*, *Securigera*, and *Gypsophila fastigiata* L. It is also a host of the pea blue butterfly *Lampides boeticus* L. in the United Kingdom (Biological Records Centre 2014a).

Hymenoptera

In Utah, *G. officinalis* is a forage plant for the alfalfa leaf-cutter bee (*Megachile rotundata* Fabr.) (Guirguis and Brindley 1974). Throughout its range *G. officinalis* is a pollen forage plant for various types of medium and large sized bees, including *Bombus* spp., *M. rotundata* (Knuth 1908; Guirguis and Brindley 1974). It has been planted as forage for honeybees, *Apis mellifera* L. (see Section 3b.).

Thysanoptera

In Croatia, *G. officinalis* has been found as a host plant for the Western flower thrips (*Frankliniella occidentalis* Pergande) (Raspudić et al. 2009).

Coleoptera

Galega officinalis is a host plant for the seed beetle *Bruchidius imbricornis* Panz. in Hungary (Jermy and Szentesi 2003). In Romania, *B. imbricornis*, *B. varius* Olivier and other *Bruchidius* spp. have been found to infest 40%–80% of seeds of *G. officinalis*, with damaged seeds showing readily visible emergence holes (Perju and Moldovan 1981). In the former Czechoslovakia, Kocourek (1989) found 25% of seeds of *G. officinalis* were infested by *B. varius*. In the United Kingdom, *G. officinalis* has been reported as a host for the clover weevil (*Sitona hispidulus* Fabr.), the clover root weevil (*Sitona lepidus* Gyll.) and the alfalfa weevil (*Hypera postica* Gyll.) (Biological Records Centre 2014a).

Hemiptera

Galega officinalis is a reported host plant for the potato aphid [*Macrosiphum euphorbiae* (Thomas)] in Serbia and Montenegro (Tomanović et al. 2003; Holman 2009); and, the pea aphid (*Acyrtosiphon pisum* Harris) in eastern and central Europe (Holman 2009) and Great Britain (Biological Records Centre 2014a). The green peach aphid, *Myzus persicae* Sulzer, an insect vector of viruses, has been reported on *G. officinalis* in Chile [Apablaza et al. 2003; Section 13b (iii) Viruses]. It is also among the hosts of the cosmopolitan southern stink bug (*Nezara viridula* L.), a pest of soybean crops in Argentina (Liljeström and Rabinovich 2004).

In the state of Maryland, *G. officinalis* was reported as a host for the potato leafhopper (*Empoasca fabae* Harris) (Poos and Wheeler 1949; Lamp et al. 1994).

Diptera

In Great Britain, *G. officinalis* is a host of the leaf miner *Liriomyza congesta* Becker (Biological Records Centre 2014a).

(iv) Nematodes and (or) other non-vertebrates

No information was located.

(b) Diseases**(i) Fungi**

The rust fungus *Uromyces galegae* (Opiz) Sacc. is reported widespread on *G. officinalis* from France to Turkey (Tunali et al. 2006; Farr and Rossman 2018) and was released in Chile as a biological control agent (Oehrens and González 1975). Other rusts that have been reported on *G. officinalis* in eastern Europe and Turkey include *U. galegicola* Woron. and *U. pisi-sativa* (Pers.) Liro (Farr and Rossman 2018). *Galega officinalis* is reported as a host for *Ramularia galegae* Sacc., a disease transmitted by air-borne conidia that causes leaf spot lesions (Ingham 1986). The disease has been found on *G. officinalis* in much of Europe from Great Britain east to the Caucasus, in South America and in Asia (Baker et al. 1950; Ingham 1986; Jones and Baker 2007; Farr and Rossman 2018). The plant is one of many hosts for the powdery mildew fungus *Erysiphe trifolii* Grev. in eastern Europe and western Asia as well as in Argentina and Chile (Havrylenko and Takamatsu 2005; Nagy and Kiss 2006; Farr and Rossman 2018). Other powdery mildews that have been reported on *G. officinalis* in eastern Europe include *E. cruciferarum* Opiz ex L. Junell and *E. pisi* DC. (Farr and Rossman 2018). Farr and Rossman (2018) cite references to ten other fungi reported on *G. officinalis*: *Ascochyta galegae* Hollós (Romania); *A. phaseolorum* Sacc. (Bulgaria); *Cercospora galegae* Sacc. (Bulgaria); *C. radiata* Fuckel (Italy); *Oidium* sp. (Hungary); *Peronospora galegae* Săvul. & Rayss; *Phoma galegae* Thüm. (New Zealand); *Phomopsis tulasnei* Sacc. (Portugal); *Phyllosticta galegae* Garb. (Greece and Ukraine); and *Septoria galegae-orientalis* Lobik (Bulgaria).

(ii) Bacteria

The species was not susceptible to crown gall disease following inoculation with the bacterium *Agrobacterium tumefaciens* by De Cleene and De Ley (1976).

(iii) Viruses

Galega officinalis was among weeds in Chile found to be susceptible to viruses attacking field crops such as the alfalfa (alfalfa mosaic virus), capsicum (cucumber mosaic virus) and tomato (tomato mosaic tobamovirus) (Apablaza et al. 2003).

(iv) Other diseases

Phytoplasmas, the pathogenic organisms found primarily in the sieve elements of infected plants and usually spread by sap-sucking insect vectors (Lee et al. 2000), have been reported from South America. In Chilean vineyards, the phytoplasma subgroup 16SrVII was found in both the weed *G. officinalis* and its insect vector, the leaf-hopper *Paratanus exitiosus* (Beamer) (Cicadellidae) (Longone et al. 2011). The phytoplasma subgroup 16SrIII-J, transmitted by the same leafhopper

vector, was recently found on *G. officinalis* in a pear orchard in Chile (Zamorano et al. 2015).

(c) Higher plant parasites

No information has been located.

Competing Interests

The authors declare there are no competing interests.

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Author Contribution

S.D.: Investigation, Writing, Visualization, Project management. A.F.: Data curation, Writing. E.S.P.B.: Investigation, Writing. S.M.: Investigation, Data curation.

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Appendix A

DNA sequences from *Galega* spp. for nod factor 5 (*Nfr5*) and 2 fragments (positions 1–492 and 508–980 of 2522 bp) of the symbiotic gene nodulation receptor kinase (*NORK*); see Österman et al. (2011). Aligned consensus sequences of 11 individuals from each of *G. officinalis* and *G. orientalis*. Grey shading indicates unique species-specific markers. Lower case letters indicate nucleotide versus indel polymorphisms where the alternate state is a deletion.

NORK, 494 bp Fragment (Positions 1–492)

G. officinalis

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TTGTCAATCC CTTCAATTTCT CAGCTTGAAT TGAGGCCACT ACCTGAAGAA TACCTTCATG   60
ATTTTGTCTAA CAGTGTTTTA AAAGTATATA GCAGAAATAA TCTTGGGGAC TTAAGAATG   120
ACATCAGGTA TGTGATCTAT TTTATTTTGA CAGAGAGAGT GTATCTCTCA GCAAACCTAT   180
AAAGGCTTAG GGGTTGATAT TATCTA—AA GATCAACATA TTTTCTGTGA AGGGATACAA   240
ATTGTAATTC ATGTGTTATA TCAAACATAT TAAACCAAAA AATGAATTTG AGCAGCAAGC   300
ATGATGCATG AACCTTTTCA ACAAATGCAT GACATAACCT ATGTTTCACT TTATAGAAAG   360
AACTA—AAGA TGTGTGTGCA CCTTAATATT AATTT—TATC TTTGTGATA—C ATTGAGATGC   420

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ACCTGAATTT AATTAACAATA TAGAGAAGCA AGAATCCAATA ATCCATACCGT TCaATCCATG 480
ATAaTATGCA TCTCACT 497

G. orientalis

TTGTCAATCC CTTCAATTTCT CAGCTTGAAT TAAGGCCATT GCCTGAAGAA TACCTACATG 60
ATTTTGTCTAA CAGTGTTTTA AAAGTATAA GCAGAAATAA TCTTGGGGAC TTAAAGAATG 120
ACATCAGGTA TGTGATCTTT TTTATTTTGA CAGAGAGAGT GTATCTCTCA GCAAACCTAT 180
AAAGGCTTAG G—GTTGATAT TATCTAATAA GATCAACATC TTTTCTGTGA ACGAATACAA 240
ATTGTAATTC A—TGTTATA TCAAACATAT TAAAAACAAA AATGAATTTG AGCAGCAAGC 300
ATATATGCATG AACCTTTTCT ACAAATGAT GACATAACCT ATGTTTCACT TTATAGAAAAG 360
AACTAAAGA TGTGTGTGCA CCTTAATATT AATTTATATC TTTGTGATGC ATTGAGATGC 420
ACCTGAATTT AATTAACAATA TAGAGAAGCA AGAATCCaGA ATCGTACCGT TCAATCCATA 480
ATARTATGCA TCTCACT 497

NORK, 474 bp Fragment (Positions 508–980)

G. officinalis

TCTAGTATAG CCTTAGtTTT CTTTTGAAGT GATCTGTGCT TAGTGTTTAG TCTGCAACTT 60
TGTTTTGTTA TTCTGATACC ATGGACTATG TA—AATAGG CAGAAAGGTC TCATAATATC 120
GGTATCTATC AATTTTAGGT ACCCTGTTGA CAAAATGAT AGAATCTGGA AAGCAA—TTC 180
AACTCCATCA TCTGCTCTTC CCGTGTCTTT CAACGTCAGC AATGTGACC TCGAAGGCAA 240
AGTGACACCT CCTATAACAAG TCTTAAAAAC AGCTCTTACT CACCCTGAGC GATTGGAGTT 300
CATCCACAAC GGTCTCGAGA CCAACGATTA TGAATACTCT GTGTTTCTCT ACTTTCTTGA 360
ATTAATAGC ACTCTCAAAG CAGGTCAAAG GGTGTTTGGAC ATATATCTAA ACAATGAGAT 420
TAAACAGGAG AAGTTTGATG TATTGGCTGG AGGGTCCAAG TACAGTTACA TTGT 474

G. orientalis

TCTAGTATAG CCTTAGTTTT CTTTTGAAGT GATTTGTGCT TAGTGTTTAG TCTGCAACTT 60
TGTTTTGTTG TTCTGATGCC ATGGACTATG TaaaAATGGG AAGAAAGGTC TCATAATATC 120
GGTATCTATC AATTTTAGGT ACCCAAGTTGA CAAAATGAT AGAATCTGGA AAGCAA—TTC 180
AACTCCATCA TCTGCTCTTC CACTGTCTTT CAACGTCAGC AATGTGACC TCGAAGGCAA 240
AGTGACACCT CCTATAACAAG TCTTAAAAAC AGCTCTTACT CACCCTGAGC GATTGGAGTT 300
CATCCACAAC GGTCTCGAGA CCGAGGATTA TGAATACTCT GTGTTTCTGT ACTTTCTTGA 360
ATTAATAGC ACTCTCAAAG CAGGTCAAAG GGTGTTTGGAC ATATATCTAA ACAATGAGAT 420
TAAACAGGAG AAGTTTGATG TATTGGCTGG AGGGTCCAAG TACAGTTACA TWGT 474

Nfr5

Primers:

nft5_G_for2 5'-CGATCTTTTCGCCAATATATCCTA-3'

nft5_G_rev2 5'-AACTGATTCTTTGAAGGGCACC-3'

G. officinalis

ATGGCTGTGTT TCTTYTTCC CTCTAGTTCT CAATGTCTTT TTCTTGCACT CATGCTGtTT 60
CTCACTAATA TCTCAGCTCA A—CACAACAG CTCAGTAGAA CMAACTTTAC ATGCCAGTG 120
GATTCGCCTC CTTCAATGTA AACCTATGTT ACATATATTG CACAGTCTCC AAATTTTTTG 180
AGTTCTAACAA ACATATCTAA TCTATTTGAT ATCAGTTCTT TATCCATTTT AAAAGCCAGT 240
AACATAGACG AGGATAGCAA GCTGATCCCA AACCAAGTCT TACTAGTACC TGTA—CTTGT 300
GGTTGCACTG GTAATCGATC TTTTCGCCAAT ATATCCTACT CAATCAAGAC TGACGATTAC 360
TACAAATTA TTTTCAGCCAC TTTATTTCAG AA—CTCACCA ATTATCTGGA AATGGAAGCT 420
GCCAA—CCAA GTCTAAATCC AAATCTATTG CCACTAGATG CCAAAGTTGT AGTCCCTTTA 480
TTCTGCAGGT GCCCTTCAA GAATCAGTTG AACAAAGGAA TCAAGTATCT GATTACTTAT 540
GTGTGGAAGG CTAATGACAA TGTTACTCTT GTAAGTTCCA AGTTTGGTGC ATCACAAGGA 600
GACATGTTAA CCAAAATAA CTTCACTGCT GCAGCCAACC TTTCAATTTT GATCCCAGTG 660
ACAAATTTAC CAAAATTTAA TCAACCACCT TCAAA—TGGA GTAA—AAGCAG CAGAAAAAAA 720
YTTCTGTTA TAATGGTAT TAGCCTAGGA AGT—CTTTTT TCATTGT—CGT GTTAAC—CTA 780
TCACTTGTTT ATGTTTATTG TCTGAAAATG AAGAGATTGA ATAGGAGTAC TTCATTAGCT 840

G. orientalis

ATGGCTGTGC TCTTCTTCC CTCTAGTTCT CAATGTCTTT TTCTTGCACT CATGCTGTTT 60
 CTCACATAATA TCTCAGCTCA AACACAACAG CTCAGTAGAA CCAACTTTAC ATGCCAGTG 120
 GATTCGCCTC CTTTATGTGA AACCTATGTT ACATATATTG CACAATCTCC GAATTTTTTG 180
 AGCCTAACTA ATATAGCTAA TCTATTTGAT ATCAGTTCTT TATCCATTTT AAAAGCCAGT 240
 AACATAGACG AGGATAGCAA GCTGATCCCA AACCAAGTCT TACTAGTACC TGTAACCTGT 300
 GGTGCACTG AAAATCGATC TTTCGCCAAT ATATCCTACT CAATCAAGAC TGACGATTAC 360
 TACAAATTA TTTTACCCAC TTTATTTCAG AACCTCACCA ATTATCTGGA AATGGAAGAT 420
 GCCAAATCCAA GTCTAAATCC AAATCTATTG CCACTAGATG CCAAAGTTGT AGCCCCTTTA 480
 TTCTGCAGGT GCCCTTCAAA GAATCAGTTG AACAAAGGAA TCAAGTATCT GATTACTTAT 540
 GTGTGGAAGG CTAATGACAA TGTACTATT GTAAGTTCCA AGTTTGGTGC ATCACAAGGA 600
 GACATGTTAA CCCAAAATAA CTTCACTGAT GCGGCCAACC TTCCAATTTT GATCCCAGTG 660
 ACAAATTTAC CAAAACCTTGA TCAACCACT TCAAGTGgaa gtaTAAGCAG TAGTAAAAAA 720
 CTTCTGTTA TAATTGGTAT TAGCCTAGGA AGTCTTTTT TCATTGTAGT GTTAACACTA 780
 TCACTTGTKT ATGTATATTG TCTGAAAATG AAGAGATTGA ATAGGAGTAC TTCATTAGCT 840

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