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ARTICLE

The Biology of Canadian Weeds. 159. *Capsella bursa-pastoris* (L.) Medik.

Hafsa T. Ahmed, Ardath Francis, David R. Clements, Elyse Dyck, Natalie Ross,
Mahesh K. Upadhyaya, Linda M. Hall, and Sara L. Martin

Abstract: *Capsella bursa-pastoris* (L.) Medik, shepherd's purse, is a cosmopolitan summer or winter annual weed species distributed throughout temperate and subtropical regions of the world and is considered one of the most common plants on earth. It is an opportunistic annual that colonizes newly disturbed, open or dry environments and is ubiquitous in cultivated lands in Canada. In annual crops in western Canada, *C. bursa-pastoris* has been among the 20 most abundant weeds since the first weed surveys in 1970. It is most easily distinguished by its small white four-petalled flowers and its heart-shaped seed-pods, but exhibits considerable variation in leaf shape and flowering time. It has been used for food and medicine by numerous cultures. Its golden-brown seeds are produced in large numbers predominantly through self-pollination and can form a substantial seed bank, with reported values ranging to several hundred thousand seeds m^{-2}. While seeds usually disperse near the mother plant, long-distance dispersal by attaching to vehicles, people and other vectors may be facilitated by its mucilaginous coat. *Capsella bursa-pastoris* does not produce fertile hybrids with other species of economic or ecological significance. It is generally well controlled by soil-applied and foliar (post-emergence) herbicides although its presence in agricultural fields may result in substantial yield loss, as documented in cole crops in North America and grain crops in Europe. The species can host a wide range of insect, nematode, fungal, viral, and bacterial pests that may damage crop species.

Key words: Capsella bursa-pastoris, shepherd's purse, cole crops, weed dispersal.

Résumé : La bourse-à-pasteur [*Capsella bursa-pastoris* (L.) Medik,] est une adventice annuelle cosmopolite qu'on rencontre l'été ou l'hiver dans toutes les régions à climat tempéré ou subtropical du globe. On estime qu'il s'agit d'une des plantes les plus courantes sur la Terre. Opportuniste, l'annuelle colonise les endroits dégagés ou arides récemment perturbés et on la recense sur toutes les terres cultivées au Canada. *C. bursa-pastoris* figure parmi les vingt adventices les plus abondantes dans les cultures annuelles canadiennes depuis qu'on a commencé à répertorier les mauvaises herbes, en 1970. La plante se reconnaît aisément en raison de ses petites fleurs à quatre pétales et de ses gousses en cœur, mais la forme des feuilles et la période de floraison varient considérablement. Beaucoup d'ethnies l'utilisent comme plante vivrière ou médicinale. Les graines brun doré sont produites en grand nombre, principalement par autopollinisation, et peuvent constituer une importante réserve, susceptible d'atteindre, selon certains auteurs, plusieurs centaines de milliers par mètre carré. Bien qu'elles demeurent le plus souvent à proximité du plant mère, les graines peuvent se disperser sur de longues distances en adhérant aux véhicules, aux gens ou à d'autres vecteurs grâce à leurs téguments mucilagineux. *Capsella bursa-pastoris* n'engendre pas d'hybrides fertiles avec d'autres espèces d'importance économique ou écologique. L'application d'herbicide au sol ou aux feuilles (après la levée) est généralement efficace, mais la présence de cette mauvaise herbe sur les terres agricoles peut donner lieu à d'importantes pertes de rendement, comme on l'a observé dans les champs de crucifères en Amérique du Nord et ceux de céréales en Europe. L'espèce héberge une grande variété d'insectes,

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de nématodes ainsi que de parasites (champignons, virus et bactéries) susceptibles d'endommager les cultures. [Traduit par la Rédaction]

Mots-clés : Capsella bursa-pastoris, bourse-à-pasteur, crucifères, dispersion des semences.

1. Name

Capsella bursa-pastoris (L.) Medik. — synonyms: *Thlaspi bursa-pastoris* L., *Bursa bursa-pastoris* (L.) Schull, *Bursa pastoris* (L.) Weber. Common names: shepherd's purse (Darbyshire et al. 2000), case weed, common shepherd's-purse, pepper plant, pick-pocket, pickpocket, pick-purse, witches'-pouches, toothwort, shovel-plant, shepherd's bag, shepherd's purse, shepherdspurse (Hitchcock and Cronquist 1973; Darbyshire 2003); bourse-à-pasteur, bourse-à-berger, boursette, capselle, capselle bourse-à-pasteur, corne de lion, tabouret, tabouret des champs, thlaspi, thlaspi bourse à pasteur (Royer and Dickinson 1999; Darbyshire 2003).

2. Description and Account of Variation

(a) Species description

Capsella bursa-pastoris is a small summer or winter annual herb. It has adapted to a wide range of environments and is also phenotypically plastic contributing to wide variation in size and life history traits. It has a dominant white taproot with few lateral fine roots (Hitchcock and Cronquist 1973; Aksoy et al. 1998; Defelice 2001). A solitary or several erect stems, simple or branched, grow from the same root, generally from 10–60 cm tall but occasionally as high as 90 cm (Fig 1A). It forms a basal rosette with the first leaves at the ground surface, consisting of petiolate oblong leaves that narrow to the stalk and are usually hairy, varying from almost entire to shallowly or deeply toothed, 3–15 cm long and 4 cm wide, but occasionally longer with rosette diameters occasionally exceeding 40 cm (Neuffer and Hurka 1986*b*). The stem leaves are smaller than the rosette leaves, stalkless, alternate one per node, are roughly linear entire to shallowly toothed to lanceolate on upper stem, basal leaves sagittate (arrow shaped), amplexicaul (leaf grasping stem) or auriclate (ear-shaped) and densely to sparsely covered with fine star-shaped hairs or sometimes hairless (Hitchcock and Cronquist 1973; Schultze-Motel 1986; Frankton and Mulligan 1987; Alex 1992; Stace 1997; Defelice 2001; Damgaard et al. 2008; Al-Shehbaz 2012). Flowers are small (2.5–8 mm across), initially in rounded clusters at the ends of stems and branches (Fig. 1B). Sepals are green or reddish (1.5–2 × 0.7–1 mm). Petals are white, rounded, and larger than the sepals, generally 2–4 × 1–1.5 mm (occasionally slightly narrower or wider, ranging to 5 mm). Stamens number six, with tetradynamous filaments (1–2 mm) and with a shorter style (< 0.8 mm). Flowers are present on a short, glabrous terminal raceme and pedicels, generally 0.5–1.5 cm long at maturity (Defelice 2001; Damgaard et al. 2008). Fruits (silicles) 2-valved, up to 3× as long as wide (4–10 × 3.4–8 mm), flattened at right angle to the stem, triangular to heart-shaped, with straight to slightly convex sides, base cuneate, apex emarginate or truncate, notched at the top, valves each with subparallel lateral veins, divided by a narrow septum (membranous partition) (Fig. 1C). Seeds numerous, up to about 32 per fruit, oblong, 0.8–1 mm long, orange-yellow to light brown, surface dull and punctured (Fig. 1C) (Schultze-Motel 1986; Frankton and Mulligan 1987; Hurka and Neuffer 1991; Alex 1992; Stace 1997; Al-Shehbaz 2012). Mucilage layer visible on seed surface when wetted (Swarbrick, 1971). Pollen grains are small (< 25 mm polar axis), isopolar, tricolpate, prolate spheroidal to prolate and are distinct from other genera in the Camelineae in having interruptions in the tectum that create the appearance of dimples on the pollen surface (Sagun and Auer 2017).

(b) Distinguishing features

Capsella species are distinguished from other plants in the mustard family by their triangular or heart-shaped seed pods that have a narrow septum, or separating membrane, between the halves of the pod (Alex 1992). Refer to Hitchcock and Cronquist (1973) for a diagnostic key.

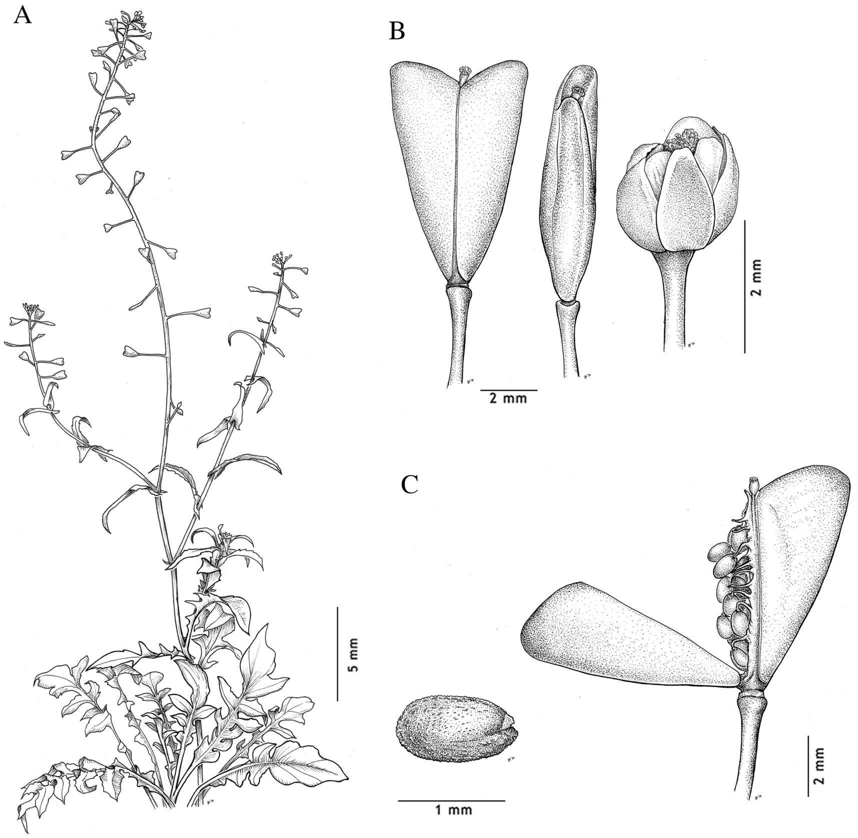
(c) Intraspecific variation

Capsella bursa-pastoris has been observed to have high intraspecific genetic, morphological, and phenological variability (Hurka and Neuffer 1991; Neuffer and Eschner 1995; Hurka and Neuffer 1997; Neuffer and Meyer-Walf 1996; Hawes et al. 2005; Neuffer et al. 2011; Wesse et al. 2021). However, no particular genetic, cytological, morphological, or phenological variants have been described within Canadian populations, although Wesse et al. (2021) incorporated Canadian accessions in their global analysis of variation in *C. bursa-pastoris*.

In Canada, a chromosome count of $2n = 32$ is based on cytological specimens from Ontario, Saskatchewan, and British Columbia (Mulligan 1957, 1984; Taylor and Mulligan 1968) and $2n = 32$ is given as the standard count in North America (Al-Shehbaz 2012) and Europe (Neuffer 1990; Slotte et al.2007). While counts of $2n = 16$ have occasionally been reported, these counts most likely represent counts for *Capsella rubella* Reuter, which has extremely similar morphology (Neuffer 1990; Slotte et al.2007). However, *C. rubella* has not yet been documented as occurring in North America.

Shull (1909, 1929) examined and measured variations in leaf morphology and segregated them into two species and ten subspecies. Similarly, Almquist (1923, 1929) divided *C. bursa-pastoris* taxa into some 200 microspecies

Fig. 1. Mature *Capsella bursa-pastoris* plant (A), flower and developing seed pod stages (B), and open capsule and seed (C). Illustrations by Jessica Hsiung.



based mostly on small variations in fruit structure (Neuffer and Hurka 1986*b*; Aksoy et al. 1999). In the British Isles approximately 25 segregates have been recognized showing variations in leaf and fruit shape (Stace 1997). An analysis by Iannetta et al. (2007) of populations in the United Kingdom (UK) concluded leaf-shape was not associated with geographical distribution and only loosely with life-history traits but studies in other regions such as the Swiss Alps have shown stronger associations (e.g., Neuffer and Bartelheim 1989; Neuffer 1990). Analysis of the genetic structure of these UK accessions using inter simple sequence repeat (ISSR) markers showed a surprisingly large amount, almost 60%, of the genetic variation was attributed to individuals within an accession (Begg et al. 2012); this result is similar to more recent work by Wesse et al (2021) where 79% of the variation was found within populations in a regional analysis. Begg et al. (2012) also found three genetically differentiated clusters, the most defined of which was associated with the southern region, earlier flowering and increased seed production and reduced secondary dormancy, but not intensive cropping (Begg et al. 2012). Given the key role of rosette morphology in life history, Neuffer et al. (2018) examined the geographical distribution of four distinct rosette leaf types across the globe and their association with morphological, anatomical and physiological characteristics under different conditions. This revealed a complex pattern suggesting local adaptation of rosette characteristics overlaid with other factors such as genetic background.

Numerous studies have examined intraspecific variation in phenology in *C. bursa-pastoris* plants and its genetic basis. In general, researchers have found that there are ecotypes with differentiated flowering times that occur in areas with different temperature regimes whether as a result of latitude or elevation. For example, temperature-dependent variations in time to flowering and phenotypic plasticity were observed in wild populations along a transect from northern to southern Europe (Neuffer and Hurka 1986*a*). In the Swiss Alps, variations in such features as germination, flowering time and vegetative growth forms were correlated with altitude. Later flowering genotypes replaced earlier-flowering forms as elevation increased resulting in later flowering winter annual forms at high altitudes (Neuffer and Bartelheim 1989; Neuffer 1990). Similarly, California populations with early-flowering seem to have arisen from ancestral Spanish populations, while later-flowering populations in temperate North America have arisen from cooler, wetter northern European gene pools (Neuffer and Hurka 1999). Karley et al. (2008) also found the two flowering time variants in UK material and noted a strong, but negative correlation between flowering time and seed production, but none between seed production and reproductive duration. Therefore, Karley et al. (2008) concluded short flowering time combined with greater resource allocation to reproduction was the reason behind high fecundity (seed output). The genetic pathways that lead to these two flowering time variants were investigated in early flowering types obtained from Taiwan and late flowering types obtained from Sweden by Slotte et al. (2007). They found that the expression of two circadian genes, *CCA1* and *TOC1*, and the modified function of the circadian clock function likely caused variation in flowering time, resulting in two extreme (early and late) flowering types. Linde et al. (2001) identified three quantitative trait loci (QTL) responsible for the onset of flowering. Given the likely linkage between flowering, rosette leaf development, and other factors (Linde et al. 2001), flowering induction is complex and more research is needed to elucidate the genetic pathway of flowering in *C. bursa-pastoris*. Overall the presence of both high dormancy/later flowering and low dormancy/earlier flowering appears to indicate a hedge betting strategy useful in variable environments.

An unusual heritable variant in floral morphology, first observed two centuries ago in Europe and described as *Capsella apetala* Opiz (Opiz 1821), is the recently rediscovered "decandric" or spermatogenesis-defective (*spe*) phenotype, in which all of the petals have been transformed into additional stamens (reviewed by Hintz et al. 2006; Hameister et al. 2009, 2013; Ziermann et al. 2009). A comparative study found that the flowers of the *spe* phenotype matured two weeks later in Germany, allowing stable coexistence with the wild type (Neuffer et al. 2020).

(d) Illustrations

The morphology of a mature *C. bursa-pastoris* plant, its basal and stem leaves, flower, seed pod and seed are shown in Fig. 1. Numerous photographic images are available online including: http://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=17109; http://linnet.geog.ubc.ca/Atlas/Atlas.aspx?sciname=Capsella%20bursa-pastoris; http://www.efloras.org/florataxon.aspx?flora_id=5&taxon_id=200009292; https://www.brc.ac.uk/plantatlas/plant/capsella-bursa-pastoris; https://www.calflora.org/cgi-bin/species_query.cgi?where-calrecnum=1472.

3. Economic Importance and Environmental Impact

(a) Detrimental

Capsella bursa-pastoris was the 20th most abundant weed in residual weed surveys in western Canada during the 2000s (Leeson et al. 2005). It was found in 9.2% of fields, in densities as high as 140 plants$\cdot$m^{-2}. It was most abundant in the Peace Lowland, Boreal Transition, Aspen Parkland and Fescue Grasslands ecoregions, and found in lower abundance in Interlake Plain, Moist Mixed Grassland and least in Mixed Grasslands and Lake Manitoba Plain. Globally, it is considered one of the most widespread plants on earth (Coquillat 1951; Zhou et al. 2001) and inevitably interferes with crop production, infesting winter cereals, horticultural crops, orchards, and forages (Aksoy et al. 1998).

Despite its observed frequency, research quantifying economic yield losses for *C. bursa-pastoris* alone has rarely been conducted. While it can contribute to yield losses of field crops in the Canadian Prairies, it is relatively non-competitive compared with other weeds in spring crops including cereals and canola (Welbank 1963). *Capsella bursa-pastoris* can cause serious yield losses in cole crops such as cabbage, broccoli, cauliflower or Brussel sprouts and in other horticultural crops such as onions because herbicides which control the weed would also cause crop injury (Freyman et al. 1992; Bitterlich et al. 1996; Dillard et al. 2004; Sikkema et al. 2007). However, it was less competitive than cultivated radish in pot experiments (Perera and Ayres 1992) and cabbage grown in narrow rows and in both narrow and wide rows with 10 cm planting intervals were unaffected by *C. bursa-pastoris* (Freyman et al. 1992). Due to its winter annual life cycle, however, *C. bursa-pastoris* is common in Canadian winter wheat fields. In a meta-analysis of herbicide trials conducted in Sweden, Milberg and Hallgren (2004) reported that *C. bursa-pastoris* was more economically detrimental in winter crops based on yield loss in cereal crops investigated in 1691 trials. They concluded that *C. bursa-pastoris* was one of the two worst weeds for autumn-sown cereal crops. Widespread infestation was also seen in Great Britain, where 23% of 2359 winter cereal fields were infested with *C. bursa-pastoris* (Marshall et al. 2003). Population densities of *C. bursa-pastoris* determined from barley and wheat fields over three seasons in New Zealand indicated a strong presence and high degree of competition with crops in their early developmental stages within fields undergoing normal crop management practices, including postemergence herbicide treatments (Bourdöt et al. 1998). In Denmark, the observed weed frequency of *C. bursa-pastoris* increased for spring barley, spring rape, winter rye and winter wheat in 2001–2004 compared with 1978–1989, but decreased in the multispecies assemblies of grass leys (Andreasen and Stryhn 2008). *Capsella bursa-pastoris* is generally a component of the common broadleaf weed assemblage for which a wide range of herbicides are available (see Section 11. Response to Herbicides and Other Chemicals).

A suspected nitrite poisoning of pigs in South Africa was attributed to consumption of *C. bursa-pastoris* (Wiese and Joubert 2001) and cattle grazing on a mixture of 40% *C. bursa-pastoris* and 60% *Sisymbrium irio* L., another member of the Brassicaceae, died from polioencephalomalacia, a neurologic disease of ruminants, as a result of the sulfur content of the plants (McKenzie et al. 2009). However, the plant is listed as having no known poisoning risk and moderate palatability to goats (Simmonds et al. 2000) and has been used as a folk remedy for treating ailments in livestock (see Section 3(b) Beneficial).

Populations of *C. bursa-pastoris* can pose a risk to crop health, production, and quality as it is a host to insect, nematode, fungal, viral and bacterial pests, including spore-forming bacilli (Iannetta et al. 2010; see Section 13. Response to Herbivory, Disease and Higher Plant Parasites).

(b) Beneficial

Because of its widespread availability *C. bursa-pastoris* has a long tradition of use as a potherb (a plant used in seasoning of food prepared by boiling in a pot) and in folk medicine in the majority of cultures around the world (Bussmann et al. 2019). Young leaves were cooked as greens or eaten raw as salad; seed pods were used as a peppery seasoning, seeds were dried and ground into meal, and roots were used as a ginger substitute. In Japan, the plant was an ingredient in a ceremonial barley–rice gruel (Facciola 1990; Defelice 2001) and it is eaten frequently in Korea, where its leaves and roots are consumed as vegetables (Lee et al. 2016). As a food plant, the species contains significant vitamins and minerals (Zennie and Ogzewalla 1977; Choi et al. 2014). However, an analysis of heavy metal content in wild food plants collected in an industrialized zone of Turkey showed higher than average levels of cobalt, lead, manganese, and iron in *C. bursa-pastoris*, placing it among plants hazardous to health if eaten in large quantities (Pehlivan et al. 2013).

Numerous medicinal properties ranging from analgesic to vermifuge (anti-parasite) have traditionally been attributed to extracts from the plant both for humans and livestock (Duke 2002), but it has primarily been associated with reducing internal or external bleeding. It has been used to staunch bleeding and to heal infected and bleeding wounds (Gerard 1633), and to treat such conditions as dysentery, bleeding, menstrual disorders and stomach problems, or as a diuretic (Defelice 2001; Kozub et al. 2012; Choi et al. 2014). Hartwell (1982) cited popular European sources dating to the medieval period on the use of infusions of *C. bursa-pastoris* to treat ulcers and cancers, including those of the stomach and uterus. Millspaugh (1974) indicated that the plant was used to treat diarrhoea in calves in England and its use was reported as folk-remedy for livestock in Switzerland (Bischoff et al. 2016). Based on these traditional uses, several studies have investigated *C. bursa-pastoris* or its extracts for these properties in cell culture; anti-thrombin (blood clotting) (Goun et al. 2002), anti-cancer (Mazzio and Soliman 2009; Lee et al. 2013), anti-bacterial (Fahey et al. 2002), and anti-inflammatory properties (Hur et al. 2013; Choi et al. 2014). For example, isothiocyanate sulforaphane extracted from crucifers was shown to inhibit antibiotic-resistant strains of the bacterium *Helicobacter pylori*, associated with gastric ulcers and stomach cancer in tissue culture (Fahey et al. 2002).

Weeds such as *C. bursa-pastoris* play a role in maintaining biological diversity within crop fields (Storkey and Westbury 2007; Begg et al. 2012). For example, the species' phenotypic and biochemical variability provides a heterogeneous resource for phloem-feeding aphids (Karley et al. 2008). Five insect families, 13 species, two of which are host specific, and three of which are pests, were associated with *C. bursa-pastoris* in winter cereal fields in Great Britain (Marshall et al. 2003). *Capsella bursa-pastoris* was also deemed important for 2–3 UK seed-feeding farmland birds and 11–25 invertebrates (Marshall et al. 2003). Andreasen and Stryhn (2008) suggest the increasing abundance of Brassicaceous weeds may improve food availability for birds and insects in arable lands.

Capsella bursa-pastoris extracts can be used as weed control against annual ryegrass and wild radish, though annual ryegrass is affected more (Seal et al. 2009). Extract concentrations of 5% or more were able to significantly inhibit growth for both aforementioned weeds, this includes root growth. A 400% concentrated extract was able to inhibit annual ryegrass shoot length and weight by more than 70% when grown in a tray filled with 50:50 sand:peat moss (Seal et al. 2009).

As an extremely abundant and widespread plant on the planet, *C. bursa-pastoris* is an important model organism for studies in a wide variety of areas including the evolutionary ecology of weeds (Nutt et al. 2006; Hintz et al. 2006; Choi et al. 2019; Žerdoner Čalasan et al. 2021) and genome evolution following hybridization and polyploidization (Hurka and Neuffer 1997; Slotte et al. 2007; Kasianov et al. 2017). Because it exhibits a wide range of genetic variation among populations, many studies have looked at patterns across its geographic range to examine the evolutionary mechanisms involved (Slotte et al. 2007; Neuffer 2011; Begg et al. 2012; Toorop et al. 2012).

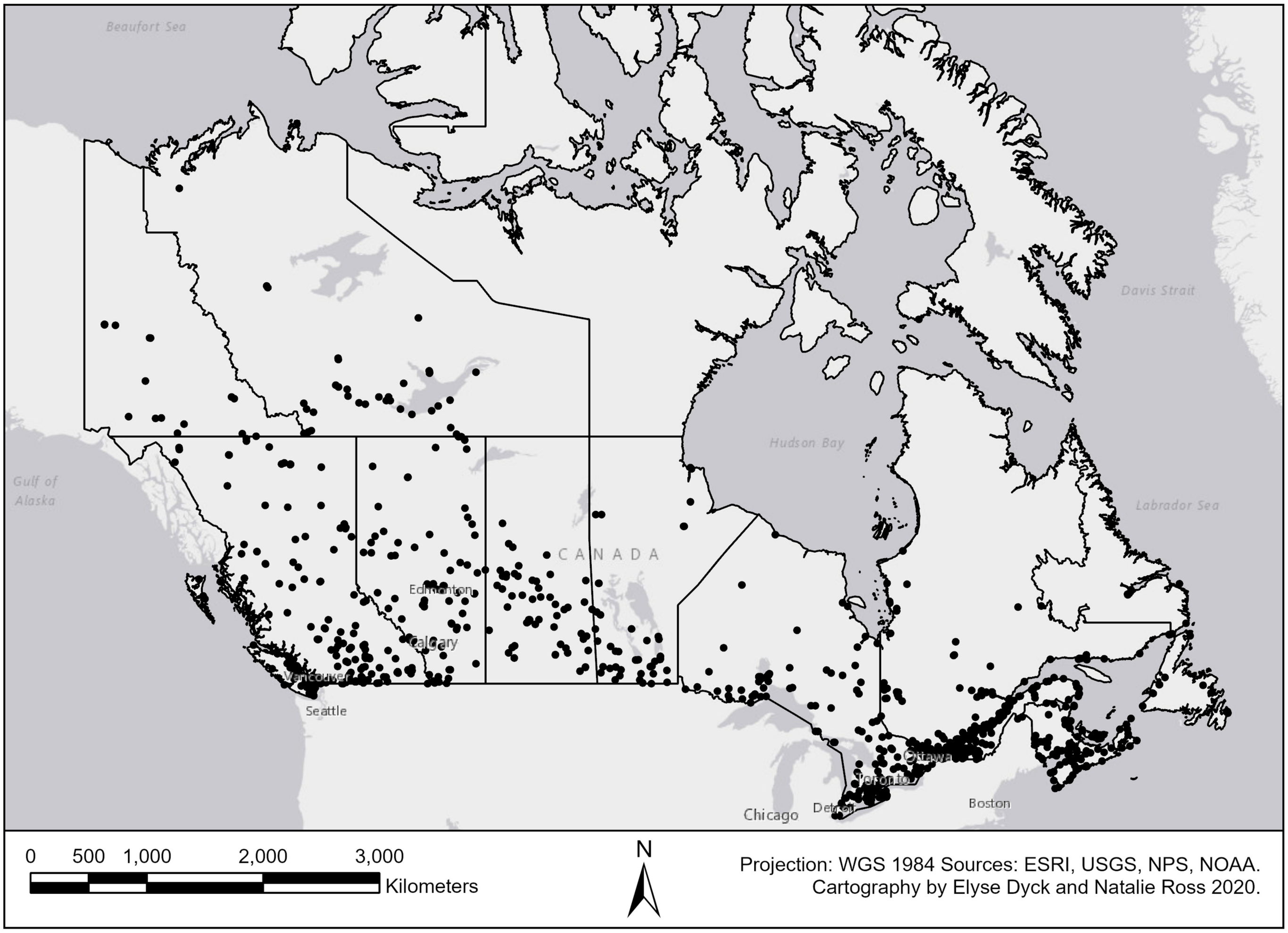
(c) Legislation

In Canada, *C. bursa-pastoris* is not listed under either the federal Plant Protection Act or the Federal Weed Seeds Order 2016, under the Seed Act. After its removal from Alberta noxious weed legislation, Manitoba remains the only province that has continued to designate the species a noxious weed (Noxious Weeds Act, CCSM c. N110 2010). In the United States, *C. bursa-pastoris* is not listed on either federal or state noxious weeds lists; but has been reported as invasive in several states [Invasive Plant Atlas of the United States (http://www.invasiveplantatlas.org/)].

4. Geographical Distribution

Capsella bursa-pastoris, a species of Eurasian, probably eastern Mediterranean origin, occurs broadly distributed around the world in temperate regions in both

Fig. 2. Distribution of *Capsella bursa-pastoris* in Canada based on herbarium collection from ACAD, ALTA, AUC, BABY, CAN, DAO, LEA, LKHD, MT, NHIC, OFRI, PMAE, QK, QUE, RBG, ROM, SASK, SSMF, UAC, UBC, ULF, UNB, V and WIN herbaria. See Holmgren et al. (1990) for institutional abbreviations. Esri Inc. *ArcMap* (Version 10.6.1). Software. Redlands, CA: Esri Inc, 2016. Basemap source: Esri, HERE, Garmin, Tinermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esric China (Hong Kong), © OpenStreetMap contributors, and the GIS User Community.



hemispheres and at scattered locations from tropical highlands to sub-arctic regions (Hultén and Fries 1986). In Canada, *C. bursa-pastoris* is present throughout agricultural regions in all provinces, including Newfoundland and Labrador, the Yukon and the Northwest territories (Darbyshire 2003; Fig. 2). Collections in Canadian herbaria show particular abundance in southern British Columbia, southern Manitoba, and throughout the Niagara Peninsula and the St. Lawrence Valley, as well as collections from eastern Alaska, southwestern Greenland, and the French islands of St. Pierre and Miquelon (Fig. 2).

It is relatively abundant throughout continental United States, with a presence in all 50 states (Al-Shehbaz 2012) and greatest abundance in the Atlantic, south-central and Pacific states (Hultén and Fries 1986). It is especially common in southwestern Mexico (Frankton and Mulligan 1987; Defelice 2001). Aksoy et al. (1998) considered it native to eastern Europe, while Mukherjee et al. (1984) considered all the populations in Switzerland, Afghanistan, Germany, Sweden, Finland, the Netherlands and Scotland at various altitudes and latitudes to represent native populations. Populations considered native were also studied along a latitudinal transect from the Kola Peninsula to the Caspian Sea and from northern and southern Scandinavia by Neuffer (2011).

Wesse et al. (2021) conducted a global survey of the genetic variation of *C. bursa-pastoris* from 1469 natural provenances from diverse locations in the native and introduced range. A moderate reduction in genetic diversity was observed among introduced populations, and it was concluded that there were two broad climatic variants, one adapted for warm arid conditions and the second to temperate humid conditions, and that by and large the world colonization was accomplished through multiple introductions of genotypes pre-adapted to diverse niches (Wesse et al. 2021).

5. Habitat

(a) Climatic requirements

Capsella bursa-pastoris is adapted to a wide range of micro-climates around the world but is commonly found growing in cool and warm (subtropical) temperate regions, as indicated by its broad range in Canada where it grows in all provinces and territories (Aksoy et al. 1998; Defelice 2001; Fig. 2). However, the species is also well-adapted to drought conditions (see Section 7(a) Morphology). Its presence was recorded in the Nile valley where the average rainfall was 20 mm in spring and mean temperature near 27 °C in May. In Germany, it survives as a rosette over winter, when the temperature can be as low as −12 °C (Aksoy et al. 1998). *Capsella bursa-pastoris* is restricted to flat or gently sloped regions but is more common on south-facing slopes (Grime et al. 2014).

(b) Substratum

Capsella bursa-pastoris grows in various types of soils, however it grows predominantly on fertile-disturbed, clay to sandy loam soil (Aksoy et al. 1998; Defelice 2001; Grime et al. 2014). It can tolerate soil with pH 5–8 (Aksoy et al. 1998) but is absent from regions with a soil pH less than 5 (Grime et al. 2014). Aksoy et al. (1998) curated a list of soil types where *C. bursa-pastoris* has been recorded including: serpentine soils in southern Urals (Brooks 1987), loess soil in Lublin, Poland (Lipecki 1989), alkaline sandy loam soils found in the Nile Valley in Egypt (El-Habibi and Youssef 1981), calcium carbonate enriched sandy loam soil in Turkey (Aksoy and Gemici 1993) and wet humus-rich soil in Korea (Kang 1983). *Capsella bursa-pastoris* has also been recorded growing on soil contaminated by cadmium (Liu et al. 2015).

(c) Communities

Apart from the cultivated grain and vegetable crops where the species is a weed (see Section 3(a) Detrimental), *C. bursa-pastoris* is present in a variety of ruderal and disturbed communities wherever it occurs. This includes waste fields, demolition plots, manure piles, compost heaps, roadsides, and gravel parking lots (Alex and Switzer 1976; Aksoy et al. 1998). In Canada, it has been found in gardens, orchards, vineyards, pastures, meadows, and beaches (Canadian herbarium records). In the United States, the species, along with other winter annuals such as chickweed (*Stellaria media* L.), field pennycress, and henbit (*Lamium amplexicaule* L.) have been moving into crop areas (Hill et al. 2014). Within the United Kingdom, the species has been dominant in several vegetation communities: the chickweed–*Capsella* and the chickweed– nettle (*Urtica urens* L.) communities, and in the plantain (*Plantago major* L.) and bindweed [*Fallopia convolvulus* (L.) Á. Löve] – speedwell (*Polygonum aviculare* Poir.) subcommunities; and is a minor component of other communities of herbs including other crucifers such as field pennycress (*Thlaspi arvense* L.) and grasses, including meadow grass (*Poa annua* L.) and rye-grass (*Lolium perenne* L.) (Pigott et al. 2000); while in other parts of Europe it is among plant communities dominated by members of the Chenopodioideae such as *Amaranthus* and *Chenopodium* spp., and among such communities in alpine pine-spruce stands and in vineyards (Aksoy et al. 1998; Konstantinović and Blagojević 2014). The species is ubiquitous in Germany, along with other species in the above-mentioned communities (Hanzlik and Gerowitt 2012).

6. History

In Canada, *C. bursa-pastoris* was already established in Quebec when collected in Montreal in 1821 (Rousseau 1968); and it was recorded in Nova Scotia as early as 1829 (Groh 1947). It continued to spread in areas along the St. Lawrence River and by the 1950s was found at sub-arctic trading posts around James Bay. In Ontario, it was collected as early as 1885 and was widespread in the first half of the 20th century. It was established across the prairies with a record in Victoria, British Columbia, in 1894, and other early collections dated from 1899, 1911 and 1924 in Alberta, Saskatchewan and Manitoba, respectively. It had reached the Northwest Territories and Yukon by the 1940s with a record collected for Cape Dorset in Nunavut, in 1936 (Groh 1947; Canadian herbarium records).

The introduction of *Capsella bursa-pastoris* to the United States and Mexico occurred before introductions into Canada, very early in the colonial period and was likely introduced repeatedly. Indeed, on investigating the genetic makeup of populations in Europe (593 populations) and North America (88 populations – 7 Canadian), Neuffer and Hurka (1999) suggested *C. bursa-pastoris* was introduced to North America on at least 20 separate occasions. It was recorded as present in New England in 1672; and by the 19th century was referred to as "The commonest of weeds, introduced from Europe" (Gray 1848). It is believed to have been introduced to Mexico at the time of the Spanish conquest in the early 17th century; to have reached California following the establishment of the Spanish Missions there, particularly during the late Spanish and Mexican eras after 1824; and during the following gold rush, seeds could have come by transportation routes from the south and the east, as well as from Europe (Neuffer and Hurka 1999).

More broadly, the genus *Capsella* originated in the eastern Mediterranean, including Asia Minor as part of the diversification of the tribe Camelineae which also includes *Arabidopsis* and *Camelina* (Žerdoner Čalasan et al. 2019). *Capsella bursa-pastoris* is likely a 100 000–300 000-year-old hybrid originating from *Capsella orientalis* Klokov and *C. grandiflora* (Faucheé & Chaub.) Boiss. or *C. rubella* lineages. Maternal contributions were made from the *C. orientalis* lineage based on chloroplast DNA clustering while the *Capsella grandiflora*/*rubella* lineage made paternal contributions, resulting in an allopolyploid hybrid (Hurka et al. 2012; Douglas et al. 2015; Žerdoner Čalasan et al. 2021). An analysis by Žerdoner Čalasan et al. (2021) showed the hybridization resulting in *C. bursa-pastoris* took place in the southwestern East European plain during Late Pleistocene interglacial cycles. Early Neolithic records of *C. bursa-pastoris* seeds are reported in Turkey between 5850 and 5600 BC whereas in central Europe the earliest records date from the Neolithic, approximately 4000 BC (Willerding 1986 quoted in Hurka and Neuffer 1997). Presumably, it was spread from Central Europe via agriculture.

7. Growth and Development

(a) Morphology

Capsella bursa-pastoris, like other ruderal species, is characterized by phenotypic plasticity and genetic adaptability across a range of traits including height, rosette size, floral biology, and seed and fruit morphology (Hurka and Benneweg 1979; Neuffer and Hoffrogge 2000; Neuffer 2011; Neuffer and Paetsch 2013). Several common garden experiments have revealed variation in height is driven by both genetic differentiation and phenotypic plasticity (Neuffer and Hurka 1986*b*; Neuffer and Alberts 1996; Neuffer and Hoffrogge 2000). It forms a rosette, an adaptation for overwintering, and cold responsive (*COR*) genes have been shown to be promoted with rosette leaves in response to cold temperatures (Lin et al. 2016). Similarly, variation in petal size is strongly influenced by temperature, with warmer temperatures promoting larger petal growth (Neuffer and Paetsch 2013). Prolific seed production enables widespread dispersal of *C. bursa-pastoris* and seeds produce a mucilaginous sheath upon hydration (myxospermy), which can enhance water absorption, particularly in dry soil (Deng et al. 2015) and has likely played a major role in long-term dispersal success of the species (Neuffer et al. 2011). Its deep tap root (up to 33 cm) enables it to access water at considerable depth, also contributing to its ability to withstand drought conditions (Johnson et al. 2011).

(b) Perennation

Capsella bursa-pastoris is a summer or winter annual. It reproduces by seeds only (Neuffer 1990; Aksoy et al. 1998).

(c) Physiology and biochemistry

Capsella bursa-pastoris is a C_3, facultative winter annual that may overwinter as a rosette or emerge very early in spring. Cici and Van Acker (2011) investigated the freezing tolerance/recovery of several winter annual species and reported that *C. bursa-pastoris*, had lower cold tolerance than narrow-leaved hawksbeard, (*Crepis tectorum* L.), stinkweed/field pennycress (*Thlaspi arvense* L.), and field violet (*Viola arvensis* Murr.), but similar cold tolerance to downy brome (*Bromus tectorum* L.) and common chickweed [*Stellaria media* (L.) Vill.]. Specifically, *C. bursa-pastoris* plants showed 50% freezing damage at −14 °C with freezing tolerance mediated by a 21-fold increase in proline levels. Wani et al. (2018) analyzed cold stress responses of 30-day-old seedlings by exposing them to 10 °C and collecting plant tissues at 24, 48, 72, 96 and 120 h. Results indicated that cold stress reduced photosynthesis, but that turgor and osmotic pressure were maintained by increased levels of soluble sugars, saturated, and unsaturated fatty acids (Wani et al. 2018).

The performance of *C. bursa-pastoris* has been evaluated under light, water, and nutrient stress (Aksoy et al. 1998). The plant grows in both open and shaded areas, though leaf lengths were shorter under light flux reduction compared with full sun. *Capsella bursa-pastoris* had the highest total dry weight when it was watered for 4 consecutive days out of 14, compared with treatments with fewer or more (2, 6, 8, or 10) consecutive watering days. Nutrient requirements were tested in sand cultures over a 14 h day. Calcium treatments ranging from 5 to 200 $\mu g \cdot mL^{-1}$ increased total dry weight while calcium levels between 5 and 15 $\mu g \cdot mL^{-1}$ resulted in the rosette leaves to curl, indicating deficiency. Fertilization with phosphorus resulted in maximum root and shoot dry weight when supplied at 16 $\mu g \cdot mL^{-1}$. Nitrogen supplied at various concentrations increased total dry weight until 81 $\mu g \cdot mL^{-1}$ but declined significantly at 243 $\mu g \cdot mL^{-1}$. Potassium supplied at various concentrations increased total dry weight until 32 $\mu g \cdot mL^{-1}$, and then declined (Aksoy et al. 1998). Fertilization with ammonium nitrate may cause injury, with retention of the solution enhanced by trichomes on *C. bursa-pastoris* leaves (Bitterlich and Upadhyaya 1990).

The average lipid content of *C. bursa-pastoris* seed is reported to be 30%, though higher lipid contents are observed in plants from temperate regions compared with those from colder regions. The fatty acid profile has a relatively large proportion of very long-chain fatty acids ($> C_{18}$) as is characteristic of seeds from the Brassicaceae (Mukherjee et al. 1984). Specifically, the fatty acid profile of *C. bursa-pastoris* seed is dominated by 25%–40% linolenic acid (C18:3), 20% linoleic acid (C18:2) and has noteworthy levels of polyunsaturated fatty acids icosadienoic (C20:2; 10%–20%) and icosatrienoic acids (C20:3; 5%–15%), but has little erucic acid (C22:1), often a major component of brassicaceous seeds (Mukherjee et al. 1984; Moser and Vaughn 2012; Al-Snafi 2015). The roots and the aerial portions of the plants also contain these fatty acids (Al-Snafi 2015; Grosso et al. 2011). The levels of flavonoids, organic acids, and sterols among other chemicals have also been assessed, including their relationship to light and temperature at places of origin (Eschmann-Grupe et al. 1990; Grosso et al. 2011).

(d) Phenology

In Canada, *C. bursa-pastoris* can flower from early spring to late fall (Frankton and Mulligan 1987).

Aksoy et al. (1998) detailed the phenology of plants in Britain where seeds germinate primarily at the beginning of March, with a small germination event after August. The first rosette leaves are produced 12–14 d after germination. If germinated early, the rosette continues to grow until the beginning of June, while the first shoot appears by the beginning of May. Flower formation is initiated 3–4 d after shoot development starts, ripe seeds and fruits appear at the end of May with seeds released from June on (Aksoy et al. 1998). The time required before the onset of flowering has been reported to vary widely for European populations of *C. bursa-pastoris* (see section Intraspecific Variation). Iannetta et al. (2007) reported that early flowering variants required 70 d to flower, while other variants required >130 d.

(e) Mycorrhiza

Traditionally, plants of the Brassicaceae family, and *C. bursa-pastoris* in particular, were thought to be non-mycorrhizal (Gerdeman 1968; Medve 1983). Demars and Boerner (1994, 1995) observed vesicular-arbuscular mycorrhizal fungi colonization of *C. bursa-pastoris* in plants grown alone, and a greater level of colonization in plants grown in a grass matrix. However, this does not necessarily mean that *C. bursa-pastoris* is mycorrhizal, as it could mean that the mycorrhizae were attacking senescent roots. Alternatively, colonization did occur but only on a sporadic basis with the mycorrhizae mainly colonizing the grass species. Populations were sampled from both lawn and waste area habitats. Fungal colonization was significantly higher in lawn habitats, most likely due to the presence of strongly mycorrhizal plants. Internal hyphae, vesicles, chlamydospores and extramatrical hyphae were found from *C. bursa-pastoris* root segments investigated, but no arbuscles (Demars and Boerner 1994). Chawla et al. (2011) found arbuscules and extramatrical hyphae but no vesicular structures from populations in India and concluded *C. bursa-pastoris* may aid in maintaining mycorrhizal inoculum in the soil during winter.

8. Reproduction

(a) Floral biology

Capsella bursa-pastoris is self-compatible and primarily self-pollinating (autogamous), the extent to which varies with environmental conditions and other interactions. Nearly exclusive self-pollination occurs when the atmospheric humidity is high, temperature is over 15 °C and light intensity is low. Outcrossing is favoured under dry, sunny conditions (Hurka et al. 1976) with up to 10% outcrossing recorded under field conditions (Hurka et al. 1989). Sterile fruits are produced under extremely cold or hot conditions and this has been attributed to the failure of the anthers opening. Compared with self-incompatible *Capsella* species such as *C. grandiflora*, *C. bursa-pastoris* has smaller petals, lower pollen production, shorter styles and more rapid fertilization after pollination from compatible pollen (Hurka et al. 1976; Neuffer and Paetsch 2013). Examples of flower insect visitors included hoverflies (Syrphidae), bees (Apidae), beetles (Coleoptera) and thrips (Thysanoptera) for a population studied in Germany (Ziermann et al. 2009). The unique *spe* floral type where petals are replaced by stamens tends to attract hoverflies rather than bees as typical of the wild type (Neuffer et al. 2020). Homeotic mutants with stamenoid petals found close to Mainz, Germany exhibited half the number of insect visitations and no emission of volatile monoterpenes and benzenoids compared with wild type plants. Both the mutant and wild type plants attracted the same types of visitors (Ziermann et al. 2009). Day-length influences the onset of flowering time; *C. bursa-pastoris* behaves as a facultative long-day plant (Hurka et al. 1976).

(b) Seed production and dispersal

Capsella bursa-pastoris is a prolific seed producer, but production per plant is highly variable. Hurka and Neuffer (1991) reported seed production from individuals from seven European populations ranging from 100 to 91 000 seeds plant^{-1}. Hill et al. (2014) reported seed production from naturally occurring stands at 800 to 40 000 seed m^{-2} from 40 to 230 plants·m^{-2}. Individual plant seed production ranged from a minimum of 5000 to a maximum of 90 000 seeds in a German study (Hurka and Haase 1982). Seed production per plant was increased by fertilization, and linked to increased branching (Yang 2018). The seed is 1 mm long and weighs approximately 0.1 mg on average but is highly variable. Seed weights reported for a variety of environments are relatively consistent. Mukherjee et al. (1984) reported seed weights from 0.093–0.156 g per 1000 seeds for material collected from a variety of elevations (10 to 2400 m) and latitudes (36 to 69 °N). Similarly, Werle et al. (2014) reported weights of 0.0110 ± 0.0001 and 0.0108 ± 0.0002 g per 100 seeds in two different years (2010 and 2011) from a farm field in Nebraska, USA, and Benvenuti (2007) reported 0.092 ± 0.071 per 1000 seeds from farm fields in Asciano, Italy. Seed size affects the germination rate and hypocotyl length of seedlings, with hypocotyl length longer in seedlings from larger seeds (Hurka and Benneweg 1979). Seed count varies from 10 to 40 seeds per fruit. Seeds are dormant at the time of dispersal. When the seed pod is ripe, it opens along its septa, but the seeds are not released immediately, lengthening the time over which seeds disperse and seedlings emerge (Hurka and Haase 1982). The small spherical, smooth seeds disperse unassisted within 50 cm of the parent plant (Aksoy et al. 1998), while for wind-aided dispersal, 80% of seed fell within 50 cm but 20% was scattered between 50 and 105 cm. The size and shape of the seed increases the probability of seed burial, even in the absence of tillage (Benvenuti 2007). It was observed the seeds were equally distributed in the first

10 cm of the soil, after which the frequency declined. No seeds were observed at 40 cm soil depth; this was attributed to the soil conditions at the field station (Hurka and Haase 1982). The mucilaginous sheath around the seed may enable long-distance dispersal by facilitating attachment to animals, vehicles, and people. Earthworms (*Lumbricus terrestris* L.) ingest the seeds and release them in their casts. This contributes to short-distance vertical dispersion and germination (Hurka and Haase 1982).

(c) Seed banks, seed viability and germination

Capsella bursa-pastoris has a persistent seed bank that can vary in size. Hurka and Neuffer (1991) reported a broad range of seed banks, from 500 to 300 000 seed m^{-2} in various German environments. Sanderson et al. (2014) reported seed banks (as determined by germinable seeds) in organic dairy hay, permanent and recently established pastures at between 11 to 8580 seed·m^{-2}. In cotton–tomato rotations in California, seed banks ranged between 8 and 1220 seed·m^{-2}, with the highest seed bank exhibited in conservation tillage treatments with cover crops (Shrestha et al. 2015). Larger seed banks may be favored by a lack of soil disturbance, as viable seeds survive longer in undisturbed soil than in cultivated soil. In experiments conducted in the United Kingdom, *C. bursa-pastoris* seed was buried in disturbed and undisturbed soil and seed emergence and viability monitored over 6 years (Roberts and Feast 1973). In cultivated soil, they recorded 18% and 12% emergence in the first and second years, with a total of 46% emergence over the 6 years of the study and 4% of the seeds remaining viable in the soil. In uncultivated soil the emergence rates were lower, 5% and 1% in the first and second years and 12% total emergence over the 6 years, however 23% of the seeds remained viable in the seed bank. Similarly, Kivilaan and Bandurski (1981) reported that *C. bursa-pastoris* remained viable in Dr. Beal's Alaska seed viability experiment for >35 yr, while Conn and Deck (1995) reported that seed germination declined from an initial 48% germination rate to 42, 42, 30, 9 and <1% after 2.7, 3.7, 4.7, 6.7 and 9.7 years, respectively. However, after this initial sharp decline in germination rate, seeds showed long-term persistence with viability remaining at a constant low level to 24.7 years. Specifically, viability for *C. bursa-pastoris* was 1.3% at 19.7 yr and 2.8% at 24.7 yr and further, unlike the majority of species tested, over a third of the seed still exhibited dormancy after 24.7 yr (Conn and Werdin-Pfisterer 2010). Baskin and Baskin (2006) combined data from the Duvel experiment, which lasted 39 yr and the Beal experiment which lasted 120 yr and suggested *C. bursa-pastoris* seeds can remain viable in the soil after 39–40 yr. However, the seed half-life according to Roberts and Feast (1973) is 5 yr which is further reduced to 1 yr if the soil is annually disturbed through cultivation (Aksoy et al. 1998). This suggests that in the absence of seed bank replacement, seed banks decrease more rapidly in cultivated soils, while *C. bursa-pastoris* can persist longer in wastelands, rights-of-way, and perennial crops.

Temperature alters germination success with low temperatures inhibiting germination and growth (Wani et al. 2018). Seed germination of populations from Scandinavia, the European Alps and the Middle East was tested in growth chambers and greenhouses under five to seven different temperature treatments, showing a trend in greater germination with increased temperature (Neuffer and Hurka 1988). Neuffer and Hurka (1988) also observed that seed age influenced both germination capacity, the proportion of seed that germinated, and germination rate, the time taken for 50% of the seeds to germinate, with decreased germination with seed age. Seed dormancy level also influences germination timing (Neuffer and Hurka 1988; Toorop et al. 2012). Germination occurred from 10–30 °C, while soil pH ranged from 3 to 11 for seeds collected from a wheat field from Qarakheyl Crop Research Station, Iran (Rezvani et al. 2014). At 30 °C, the greatest germination rate was obtained under a 12/12-h light/dark treatment. In another study conducted in the Nile delta, the highest germination rates were obtained at 30–35 °C (Rayia et al. 2020).

Germination rates, seedling fresh mass, fresh root length and other traits indicative of germination and establishment were found to be higher when the plants were germinated in the presence of nematodes (Roberts et al. 2018).

In Canada, *C. bursa-pastoris* is a facultative winter annual with two distinct emergence peaks in late summer/fall and in spring. Cici and Van Acker (2009) reported that in Ontario, seeds from seedlings that emerged in August flowered in early spring (mid-April) and seeds from seedlings that emerged in spring flowered in May. In a Michigan study, seed maturity, expressed as 50% of seed release from the plant, occurred by 31 May and 28 May for 840 and 920 growing degree days (GDD), with a base temperature of 0 °C, in 2009 and 2010, respectively (Hill et al. 2014).

Dormancy triggers (release and re-entry) and germination triggers are an ecological adaptation mechanism that prevents germination under conditions unfavourable for survival of *C. bursa-pastoris*. Freshly harvested seed is almost completely dormant (primary dormancy) (Popay and Roberts 1970*a*; Baskin et al. 2004; Hill et al. 2014) and not all seed is released from dormancy in one year. After release from primary dormancy ungerminated seed may become conditionally dormant, depending on environmental conditions. Seed dormancy, both primary and (or) conditional, must be minimal to allow for seed germination. Baskin and Baskin (1989) reported that *C. bursa-pastoris* seed freshly harvested (dormant) in May became non-dormant (afterripening) and capable of germinating after being exposed to high temperatures (25/15 to 35/20 °C day/night temperatures). Seeds that fail to germinate in fall or become conditionally dormant at 5 °C germinate in spring. Baskin et al. (2004) reported that seed collected from spring and fall germinated plants grown at high latitudes was dormant and neither was capable of germination in the fall, but rather it was only possible in spring the following year.

In the case of a small seeded species, depth of seed placement can be critical. Popay and Roberts (1970*b*) reported *C. bursa-pastoris* germination is influenced by light (red light stimulation), increased temperature, fluctuations between cool and warm temperatures, carbon dioxide (anoxia), soil nitrate and nitrite concentration, all of which could be influenced by depth of seed placement or by tillage. Under field conditions, Cici and Van Acker (2009) reported the primary microsite conditions; temperature, moisture and light were modified by CO_2, nitrate, and nitrite concentrations. Optimal soil depths are reported to be < 2 cm.

In agricultural systems *C. bursa-pastoris* co-evolved with crops and predictable periodic disturbance (by tillage and/or herbicide). Annuals respond to the environment via dormancy/release, germination, and phenotypic plasticity to avoid disturbance, and successfully produce seed. Predictable emergence patterns may be useful for guiding the timing of weed control (Cici and Van Acker 2009). Werle et al. (2014) planted seeds of *C. bursa-pastoris* in July at four sites over two years in Nebraska and measured emergence for one year. For *C. bursa-pastoris* 30% emerged in fall with a further 70% emerging in late winter and spring. Soil temperature was the most useful parameter in modeling emergence, although soil moisture was necessary for germination. The time of emergence of the maternal plant may affect the seed germination and morphology of the seed and plant. Van Acker and Cici (2012) reported that spring emerging plants produced seed that germinated faster, flowered earlier, and resulted in differential allocation of biomass to roots and reproductive tissue.

(d) Vegetative reproduction

This species does not reproduce vegetatively.

9. Hybrids

Natural triploid hybrids, between the tetraploid *C. bursa-pastoris* and its diploid relative *C. rubella* Reut. (*C.* × *gracilis* Gren.) have occurred in mixed populations. In the UK such hybrids tend to have very long inflorescences, but very little seed (Stace 1997) indicating failure of the seed to develop. Successful hybrids are thought to be unlikely for several reasons: the chromosome number difference; *C. bursa-pastoris* and *C. rubella* are both primarily self-fertilizing; both possess very small nectaries reducing insect visitation; and the species have differences in flowering time with a tendency for the tetraploid species to flower earlier than the diploid (Neuffer and Eschner 1995; Hawes et al. 2005).

Several studies have investigated the inter-compatibility of *C. bursa-pastoris* and the emerging oilseed *Camelina sativa* (L.) Crantz, another member of the Camelineae tribe (Al-Shehbaz 2012), to assess the risk of transgene introgression. Séguin-Swartz et al. (2011) observed that when *C. sativa* was the male parent pollen tubes grew to the ovules indicating that no pre-fertilization barriers appear to exist between the species. Julié-Galau et al. (2014) recorded the production of eight hybrids in hand from 95 hand crosses (1 hybrid for 15 ovules pollinated) with *C. sativa* as the male parent, though the use of a hemizygous *C. sativa* marker (DsRed) to detect hybridization may mean that even this high estimate of hybridization could have underestimated the number of hybrids produced. The stamens in these hybrids failed to elongate and did not produce pollen. Martin et al. (2015) produced seven hybrids with pollination of Canadian accessions of *C. bursa-pastoris* by *C. sativa*, detected by DNA content using flow cytometry and species specific internal transcribed spacer (ITS) markers, from 1864 crosses and estimated a much lower hybridization rate of 1.5 hybrids per 10 000 ovules pollinated. As with those produced by Julié-Galau et al. (2014), hybrids had low pollen viability based on staining with a 2% acetocarmine solution and neither pollination by the parental species nor intentional self-pollination resulted in viable seed, leading to the conclusion that genome duplication may be the only route to F_2 progeny between the species (Martin et al. 2015). Zhang and Auer (2020) obtained hybrids at rates lower than Julié-Galau et al. (2014) but higher than Martin et al. (2015), which produced low pollen and ovule numbers from bidirectional crosses with *C. sativa* as both the female (3.1 hybrids per 1000 ovules) and the male parent (2.9 hybrids per 1000 ovules). These hybrids also were unsuccessful in backcrosses.

Tissue culture techniques have also been used to attempt wider crosses. For example, somatic hybrids from *C. bursa-pastoris* protoplast and rapid-cycling *Brassica oleracea* have been generated to determine the potential for transferring *Alternaria brassicicola* resistance to the crop. Hybrid lines that resulted in rooted plants were planted in the soil and grown until flowering. They displayed combined morphological features, leaves were lanceolate with trichomes similar to *Capsella* and had serrated margins, similar to *B. oleracea*. Flowers showed intermediate morphology, but male sterility. When hybrids were pollinated with *B. oleracea*, no seed production was observed, indicating poor fertility. *Alternaria brassicicola* resistance was detected among one of the hybrids tested, indicating its use for breeding resistance. Unfortunately, these plants did not survive for a long period in the greenhouse (Sigareva and Earle 1999).

10. Population Dynamics

Capsella bursa-pastoris is an opportunistic annual plant that can colonize newly disturbed, open or dry environments, forming a high percent cover and is found ubiquitously in cultivated lands in Canada. In annual crops in western Canada, *C. bursa-pastoris* has been one of the 20 most abundant weeds since weed surveys were first conducted in 1970. In Canada, plants tend to emerge in two peaks in spring and late summer/fall (see Section 8(c) Seed banks, seed viability, and germination). It is found growing in various climates and niches; however, abundance decreases in less disturbed areas to exclusion once perennial grasses establish (Bosbach et al. 1982; Aksoy et al. 1998; Begg et al. 2012). For example, Monzeglio and Stoll (2005) describe *C. bursa-pastoris* as a weak competitor and determined that the species has higher fitness when in a monoculture than when mixed with other annual species. By evaluating accessions of *C. bursa-pastoris* from both a colonization front and from the core area of the natural range, Orsucci et al. (2020) demonstrated that although the ecotypes from the colonization showed less fitness, as measured through various growth and reproductive parameters, they were better able to avoid competition due to a shift in phenology.

11. Response to Herbicides and Other Chemicals

Capsella bursa-pastoris is susceptible to most foliar (post-emergence) herbicides recommended for the control of dicot annual weeds in a range of crops (OMAFRA 2020; Saskatchewan Guide to Crop Protection 2020). Herbicide resistant populations have been selected but are generally managed through the use of alternative herbicides or herbicide mixtures.

Capsella bursa-pastoris can be controlled with most broadleaf herbicides. Exceptions include group 3 mitotic inhibitors; group 4 auxinic herbicides in the pyridine carboxylic acid family; and group 6 photosystem II inhibitors. Control is influenced by the timing of herbicides application(s) in relation to annual and winter crop rotations and the time of emergence of this facultative winter annual weed. Residual control is often desirable, because multiple flushes of emergence usually occur throughout the spring and fall emergence period. It can be readily controlled by non-selective herbicides, such as glyphosate pre-seeding and glyphosate and glufosinate and with group 2 ALS inhibitors in herbicide resistant crops with the exception of ALS resistant populations (see below).

Capsella bursa-pastoris can be controlled (< 90%) in alfalfa and alfalfa grass mixtures with metribuzin applied in fall, spring applied imazethapyr and imazamox; while spring applied MCPA provided an average of 81% control (Wilson and Orloff 2008). In turf grass there are many available herbicides for control, the most commonly used herbicides are 2,4-D, 2,4-DP, mecoprop and dicamba (PennState Center for Turfgrass Science, accessed 10 July 2021, https://extension.psu.edu/weed-management-in-turf#section-47). *Capsella bursa-pastoris* presents challenges to postemergence herbicide control in certain crops, such as cole crops, because of its similarity to the crop (Freyman et al. 1992).

Capsella bursa-pastoris has been selected for resistance to a number of herbicides. Resistance to ALS inhibitors was reported in Israel in 2000 (imazapyr), in Canada in 2008 (imazamox, imazethapyr, thifensulfuron method and tribenuron methyl), in China in 2009 (tribenuron-methyl), in Demark in 2012 (florasulam and tribenuron-methyl), and in Norway in 2019 (iodosulfuron-methyl-Na) (Wang et al. 2011; Zhang et al. 2017; Heap 2021). Resistance to ALS inhibitor tribenuron methyl in populations from China was due to a single amino acid change at position 197 (Jin et al. 2011; Cui et al. 2012).

Resistance to the herbicide hexazine was reported in Oregon due to a change in the PSII target site change from Phe to Ile in the *psbA* gene at position Phe255 (Perez-Jones et al. 2009). This alteration conferred 22-fold resistance to hexazine compared with the susceptible population. The hexazinone-resistant population was cross-resistant to metribuzin but susceptible to atrazine, diuron and terbacil. Other reported cases of *C. bursa-pastoris* herbicide resistance include simazine-resistance in 1984 in Poland (Heap 2021).

12. Response to Other Human Manipulations

Many agronomic factors including tillage timing and intensity, nutrient regime, crop type, use of cover crops all can influence populations of *C. bursa-pastoris*. Increasing competition through cover crops or green manure and changing row spacing and flaming can be effective means of controlling or suppressing growth. The density of *C. bursa-pastoris* increased in the upper soil layer that was subjected to reduced tillage relative to conventional tillage in a study conducted to observe the effects of tillage on weed density in California (Fennimore and Jackson 2003).

A variety of cover crops and green manures have been reported to reduce *C. bursa-pastoris* emergence or density. *Brassica napus* L. or *Sinapis alba* L. planted in fall and incorporated into the soil in spring prior to planting of peas provided 76% and 97% suppression of *C. bursa-pastoris* emergence, respectively in Mt. Vernon, Washington, USA (Al-Khatib et al. 1997). In Germany in organic *Triticum aestivum* L. fields, legume cover crops, a mixture of *Trifolium repens* L., *Trifolium subterraneum* L., *Medicago truncatula* Gaertner and *Lotus corniculatus* L., were able to suppress *C. bursa-pastoris* at one site compared with the control treatment (Hiltbrunner et al. 2007). Buckwheat residues reduced emergence and growth of *C. bursa-pastoris* compared with bare soil, by reducing available nitrogen, but the addition of nitrogen fertilizer negated this effect (Kumar et al. 2008). Mennan et al. (2009) reported that cover crop residue from grain sorghum [*Sorghum bicolor* (L.) Moench], sudangrass [*Sorghum* × *drummondii* (Nees ex Steud.) Millsp. & Chase], hairy vetch, (*Vicia villosa* Roth), grain amaranth (*Amaranthus* sp.), or pea (*Pisum sativum* L.) residue suppressed emergence of

C. bursa-pastoris for organic kale production. Franczuk et al. (2010) reported that cover crops phacelia (*Phacelia tanacetifolia* Benth.), vetch (*Vicia sativa* L.), serradella (*Ornithopus sativus* Brot.), and oat (*Avena sativa* L.) suppressed *C. bursa-pastoris* emergence in onion (*Allium cepa* L.) and cabbage (*Brassica oleraceae* L.) crops. Planting cabbage at higher densities can also reduce *C. bursa-pastoris* growth between the rows (Freyman et al. 1992). Weed flaming can also effectively control *C. bursa-pastoris* in the cotyledon stage but requires a higher flaming dose in the rosette stage (2 to 5 leaves) (Sivesind et al. 2009). Harvest weed seed control promises to provide a tool for reducing populations of seed banking plants like *C. bursa-pastoris*; a Danish study identified it as a reasonably good target, i.e., "intermediate," for this control method (Bitarafan and Andreasen 2020).

Capsella bursa-pastoris is common in annual pastures and perennial forages in western Canada. It was reported to be more common in annual than perennial forages, especially in the spring with increased grazing intensity leading to increased density (Harker et al. 2000). Disturbances and fertilizer application generally increase *C. bursa-pastoris* abundance and fecundity in pastures. While soil compacted due to trampling results in short and twisted roots, trampling provided better dispersal, rapid germination, and establishment (Ellenberg 1988; Aksoy et al. 1998). Neuffer and Meyer-Walf (1996) reported that by comparison to an arable field, *C. bursa-pastoris* growing in a trampled area exhibited later but more plastic flowering onset with more vigorous rosettes, and greater variation in other growth parameters, but less seed production. Plants in the trampling area also showed a greater response to nutrient additions.

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) Herbivory

(i) Mammals

In annual cattle pastures in Alberta, *C. bursa-pastoris* and other annual forbs declined in numbers over the season because although the cattle grazed mainly on sown forage grasses, grazing removed the apical meristem of the weeds, leaving little opportunity for the weed seedlings to re-establish later in the season (Harker et al. 2000). In Great Britain, *C. bursa-pastoris* grazed by cattle, sheep, and other grazers such as yaks (Aksoy et al. 1998) and by rabbits in grasslands had reduced populations and exhibited delayed flowering in damaged plants for up to four weeks (Crawley 1990).

(ii) Birds or other vertebrates

Marshall et al. (2003) recorded feeding by several bird species on seeds of *C. bursa-pastoris*.

(iii) Insects

Lepidoptera

Capsella bursa-pastoris is among the more frequently visited wild cruciferous plants by the butterfly *Ancharis cardamines* L. (Pieridae) (Wiklund and Friberg 2009). Eggs are laid on the flowering ramets which provide food for the developing larvae as the fruits mature. Over a five-year study period 9.3%–12.4% of larvae survived on *C. bursa-pastoris*, with the leading causes of larval mortality being starvation in very dry summer periods and attacks by braconid wasps. Compared with other summer-flowering mustards, *C. bursa-pastoris* encountered less herbivory by *Pieris rapae* L., the cabbage white butterfly and supported less relative growth rate of the first instar in common garden conditions (Lariviere et al. 2015). Similarly, *C. bursa-pastoris* is among brassicaceous host species of the diamondback moth *Plutella xylostella* (L.) (Plutellidae) and despite supporting low insect growth and survival rates, their overwintering seedlings can be bridge hosts until more-favourable annual wild or crop plants become available (Sarfraz et a. 2011). In British Columbia vineyards, *C. bursa-pastoris* is a host of the climbing cutworm pest of grapevines, *Abagrotis orbis* (Grote) (Noctuidae) (Mostafa et al. 2011) but the cutworm larvae did not survive beyond the third instar on *Capsella*, suggesting that it could reduce cutworm damage to the vines. In China, female adults of *P. xylostella* produced more eggs (over 300 per adult) on *C. bursa-pastoris* than on other wild host plants (Niu et al. 2014).

Hymenoptera

The parasitoid wasp *Cotesia saltator* Thunb. (Braconidae) frequently feeds on and kills the larvae of the butterfly *Anthocharis cardamines* found on *C. bursa-pastoris* and other wild cruciferous plants (Wiklund and Friberg 2009). *Anaphes iole* Girault (Mymaridae), a wasp parasitic on the eggs of *Lygus* spp., was not able to obtain meaningful food resources from *C. bursa-pastoris*, an important host of *Lygus lineolaris* P. Beauv. (Williams and Hendrix 2008). Among hosts of diamondback moth larvae, parasitism by the wasp *Diadegma insulare* (Cresson), as well as its growth rates and longevity, are lowest on *C. bursa-pastoris* (Sarfraz et al. 2012).

Thysanoptera

The western flower thrips *Frankliniella occidentalis* Pergande is the primary vector of viruses that infect crops and crop weeds, including *C. bursa-pastoris*, in California (Kuo et al. 2014; Section 13(b) *iii* Viruses).

Coleoptera

Different species of ground beetles (Carabidae) feed on the seeds of *C. bursa-pastoris* in many parts of the world, while at least one feeds on *C. bursa-pastoris*' roots. *Calathus ruficollis* Dejean and *Tanystoma maculicolle* Dejean show very high seed predation rates in California vineyards: the highest rates of 64% ± 9% for the former and of 41% ± 11% for the latter occurred in the cover crop and untreated control (Sanguankeo and León 2011). Indeed in a lab experiment, Sanguankeo and León (2011) showed *C. bursa-pastoris* was one of the two out of eight weed species that was voluntarily eaten by carabid beetles. In the Czech Republic, seed consumption by *Amara aenea* DeGeer, *A. familiaris* (Duftschmid), *A. similata* (Gyllenhal) and (*Pseudophonus) Harpalus rufipes* DeGeer was more discriminating at the larval than at the adult stages: *A. similata* preferred seeds of *C. bursa-pastoris* at the first instar and adult stages, and *A. aenea* and *A. similata* showed higher reproductive rates on either single-seed *Capsella* diets, or mixed-seed diets (Saska 2008*a*; Klimeš and Saska 2010; Saska et al. 2014). The weevil *Ceutorhynchus typhae* (Herbst) feeds on seeds of *C. bursa-pastoris* in Europe and in eastern Canada (Muller et al. 2011). In Japan (Sasakawa 2011), *C. bursa-pastoris* is a food source for *A. chalcites* Dejean and *A. congrua* Morawitz, with 73% survival rates of the former and 60% of the latter. Mixed seed and larval diets were somewhat more important than single-seed diets in development and growth of new adults. Root herbivory by *Phyllopertha horticola* (L.) has been documented to result in substantial biomass loss (Gange and Brown 1989).

Hemiptera

Capsella bursa-pastoris is an accidental host of the cabbage aphid *Brevicoryne brassicae* L. (Aphididae), permitting short-term development of the aphid following stylet penetration and sap ingestion, and a considerable delay between finding and accepting the phloem by the insect, suggesting a deterrent factor in the sieve elements of the plant (Gabryś and Pawluk 1999). The aphid *Myzus ascolonicus* Donc. (Aphididae) is known to transmit the beet mild yellowing virus (BMYV) and the beet western yellows virus (BWYV) to *C. bursa-pastoris* in Europe (Stevens et al. 1994). In China, *C. bursa-pastoris* is host of the small brown planthopper *Laodelphax striatellus* (Fallén) (Delphacidae) (Qiao et al. 2009). Three aphid species have been reported on *C. bursa-pastoris* in Indonesia: *Aphis craccivora* Koch, *Myzus ornatus* Laing and *Rhopalosyphum padi* L. (Noordam 2004). Intraspecific variation within *C. bursa-pastoris* resulted in differential responses by the phloem-feeding aphids *Aphis fabae* Scopoli and *Myzus persicae* Sulzer (Aphididae) to such variants as greater tissue water content, a low carbon/nitrogen ratio or lower phloem nitrogen (Karley et al. 2008). In arable field plots, sap-feeding insects were more attracted to early-flowering than to late-flowering ecotypes of *C. bursa-pastoris* (Karley et al. 2011). *Capsella bursa-pastoris* is a spring host of the tarnished plant bug *Lygus lineolaris* P. Beauv. (Miridae) in cotton crops in the Mississippi Delta (Snodgrass et al. 2006). The species is also a host of the wheat bug *Nysius huttoni* White (Lygaeidae) which damages wheat and cultivated cruciferous crops (Wei 2008). However, *C. bursa-pastoris* showed resistance towards *Lipaphis erysimi* (Kalt.) in a caged pot experiment (Singh et al. 2014).

Diptera

In cruciferous vegetable crops in southern Ontario, *C. bursa-pastoris* was among hosts of the swede midge *Contarina nasturtii* (Kieffer) (Cecidomyiidae) (Hallett 2007). Flower galls have been produced on *C. bursa-pastoris* by the gall midge *Gephyraulus capsellae* Skuhrava (Cecidomyiidae) (Skuhrava 2011).

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

Capsella bursa-pastoris was among weed hosts of the sugar-beet nematode *Heterodera schachtii* Schmidt in Germany; cysts were formed regularly and root diffusates increased hatching of the larvae (Gleissl et al. 1989). In Ohio soybean crops, *C. bursa-pastoris* was identified as a minor alternative host of the soybean cyst nematode, *H. glycines* Ichinohe, but was one of only four such hosts on which reproduction of the nematode occurred (Venkatesh et al. 2000). Attention has recently focused on alternative hosts of *H. glycines* among winter annual weeds such as *C. bursa-pastoris*, which have the potential to provide a niche for reproduction and population increase of this nematode pest in the seasonal absence of the soybean crop (Johnson et al. 2008). There is evidence of *C. bursa-pastoris* root consumption by ectoparasitic nematode species *Trichodorus* and *Paratrichodorus* (Iannetta et al. 2010). The land slug *Agriolimax caruanae* Pollinera ate whole, or parts of, leaves of *C. bursa-pastoris*, resulting in reduced plant size, but almost never in death of the plant (Dirzo and Harper 1980). Herbivory by slugs on crucifers, including *C. bursa-pastoris*, resulted in a significant reduction in stem mass and fruit production (Rees and Brown 1992). The land slugs *Arion lusitanicus* (= *A. vulgaris* Mabille) and *Deroceras reticulatum* (O.F. Müller) are attracted to *C. bursa-pastoris*, and presence of the weed in oilseed rape (*Brassica napus* L.) crops considerably reduced the number of rape plants destroyed by the slugs (Frank and Friedli 1999). Indeed, the leaves of *C. bursa-pastoris* are highly palatable to *D. reticulatum*, as shown in leaf preference tests between *C. bursa-pastoris* and *Triticum aestivum* L. (Cook et al. 1996). The woodlice *Armadillidium vulgare* Latreille and *Porcellio scaber* Latreille, species of terrestrial isopods, were observed feeding on seeds of *C. bursa-pastoris* in crop fields and adjacent non-crop habitats (Saska 2008*b*; Saska et al. 2014).

(b) Diseases

(i) Fungi and oomycetes

Capsella bursa-pastoris is host to numerous fungal pathogens, listed in detail in Farr and Rossman (2020). These are summarized according to the type of disease transmitted to the plants. Unless otherwise indicated, the reference is (Farr and Rossman 2020).

Black leg

Both virulent and weakly-virulent strains of *Leptosphaeria maculans* (Sowerby) P. Kaarst, isolated from symptomless canola (*Brassica napus* L.), *C. bursa-pastoris* and other weeds in Saskatchewan, could act as a reservoir of inoculum of black leg disease in the absence of a canola crop (Petrie et al. 1995). This fungus has been reported in New Zealand.

Club root

Plasmodiophora brassicae Woronin was reported in Canada (Connors 1967), a few US states, Australia, and New Zealand.

Leaf curl and wilt

The seed-borne *Verticillium dahlia* Kleba was reported in British Columbia, Canada (Ginns 1986). It is a major cause of wilt in lettuce crops in California, where virulent isolates of this fungus in *C. bursa-pastoris* and other weeds serve as inoculum in crops (Vallad et al. 2005).

Leaf spot

Mycosphaerella brassicicola (Duby) Lindau is a source of ringspot in Saskatchewan (Ginns 1986). *Pseudocercosporella capsellae* (Ellis & Everh.) Deighton produced white leaf spot in Ontario (Braun 1995), Saskatchewan (Ginns 1986), a few central states in the US, several countries in northern Europe, and in South Korea. *Cylindrosporium capsellae* Ellis and Everh. was reported in several central US states south to Texas. *Sphaerella passeriniana* Sacc. was reported in Spain, and *Cercospora nasturtii* var. *capsellae* Pass. in the former Soviet Union and Ukraine.

Mildews

Capsella bursa-pastoris can be host to powdery mildews of *Erysiphe* spp., particularly *E. cruciferarum* Opiz ex L. Junell, which are widespread in Europe, and have also been reported from Japan and India. As well as the downy mildews *Hyaloperonospora* (= *Peronospora)* spp., notably *H. parasitica* (Pers.) Constant., were reported from British Columbia and Saskatchewan in Canada (Ginns 1986), from Alaska (Connors 1967), from throughout the northern US, from Europe (Constantinescu and Fatehi 2002), Algeria, Central Asia, China, and India. Additionally the species has been reported to host *Golovinomyces cichoracearum* (DC.) V.P. Heluta was reported in Korea; *G. orontii* (Castagne) V.P. Veluta in Switzerland, Germany, Poland (Farr and Rossman 2020) and Slovenia (Radisek et al. 2018); and *Oidium* sp. in Australia.

Moulds

Cultural filtrates of the saprophytes *Penicillium* sp. and *Aspergillus niveus* Blochwitz suppressed the growth of seeds of *C. bursa-pastoris* in Ukraine (Savchuk 2012). The yeast-like saprophyte *Tilletiopsis minor* Nyland, identified in British Columbia, Canada, forms colonies on leaves (Urquhart et al. 1997). The saprophytes *Trichoderma koningii* Oudem. and *T. viride* Pers., reported in Poland, cause green mould rot. *Sclerotinia* spp., reported on *C. bursa-pastoris* in alfalfa fields in Maryland, US, caused leaf and stem blight (Morgan 1971). Other reports of white and grey moulds on *C. bursa-pastoris* include *Sclerotinia sclerotiorum* (Lib.) De Bary in China and Taiwan, *Botrytis cinerea* Pers. in China; and *Cladosporium cladosporioides* (Fresen) G.A. de Vries and *Scopulariopsis brumptii* Salv.-Duval in Poland.

Root rot

Capsella bursa-pastoris was among hosts of *Lagena radicicola* Vanterp. & Ledingham from Nova Scotia west to Alberta in Canada (Barr and Désaulniers 1990). *Rhizophydium graminis* was reported on the species in Ontario (Ginns 1986). Other root rot fungi in Canada include *Ligniera pilorum* Fron & Gaillet in Ontario; *Pythium* spp in British Columbia; and *P. polymastum* Drechsler in Saskatchewan. The saprophytic soil-borne pathogen *Rhizoctonia solani* Kühn, reported from Washington State, causes lesions on the collet between the stem and root, progressing from collar to root rot, and also attacks seeds [United States Department of Agriculture (USDA) 1960]. *Aphanomyces euteiches* Drechsler was reported in New Zealand and *Humicola grisea* Traaen in Poland.

Rusts

White blister rusts caused by the parasitic fungus *Albugo candida* (Pers.) Kuntze (= *A. cruciferarum* (DC) A. Gray; *Cystopus candidus* (Pers.) Lév.) result in white or cream-coloured sori found on leaves, shoots and flowering parts of *C. bursa-pastoris* (Heller and Thines 2009; Mirzaee and Sajedi 2015). The species is the type host of race 4 of this fungus, and is among Brassicaceae that became resistant to their particular race of *A. candida* following transfer of the white rust resistance gene *WWR4* from *Arabidopsis thaliana* (L.) Heynh. (Borhan et al. 2008, 2010). Virulent isolates from *C. bursa-pastoris* cells revealed very rapid spread and development of this fungus, including sporangia production in the absence of host cell necrosis (Soylu et al. 2003). In Canada, *A. candida* has been reported in British Columbia and Saskatchewan (Ginns 1986) and is common on all continents. A new species, *A. koreana* Y.J.Choi, Thines & H.D.Shin infecting *C. bursa-pastoris* was identified in Korea (Choi et al. 2007). A case of white blister rust caused by *A. candida* and *A. koreana* has been reported in Iran (Mirzaee and Sajedi 2015). The rust *Puccinia aristidae* Tracy is found on *C. bursa-pastoris* in several US states. Double infection by *A. candida* and *Hyaloperonospora parasitica* (= *Peronospora*) has been observed in diseased inflorescences of *C. bursa-pastoris* (Sansome and Sansome 1974) and may reduce the number of individuals in established stands and any recruitment for future generations (Alexander and Burdon 1984). Of the 17 races or pathotypes of *A. candida*, races Ac1 to Ac6 were found to be specific to the host *C. bursa-pastoris* in Australia (Petkowski et al. 2010). A strain of *A. candida* isolated from *C. bursa-pastoris* in western Australia was pathogenic on *Brassica juncea* (L.) Czern., but the *B. juncea* isolate was not pathogenic on *C. bursa-pastoris* (Kaur et al. 2011).

Stem disease

Colletotrichum dematium (Pers.) Grove was reported to have infected *C. bursa-pastoris* in Saskatchewan (Ginns 1986). In the United Kingdom, C. *bursa-pastoris* was among weed hosts of crown and stem rot diseases caused by *Fusarium* spp., particularly *F. avenaceum* (Fr.) Sacc., pathogenic to seedlings of winter wheat (Jenkinson and Parry 1994). Seedling blight for *C. bursa-pastoris* was caused by *F. culmorum* (W.C.Sm.) Sacc. in Poland.

(ii) Bacteria

Wild hosts, including *C. bursa-pastoris*, of *Spiroplasma citri*, a bacterial causative agent of brittle root disease of horseradish (*Armoracia rusticana* Gaertn. Mey. & Sherb.), were found to be sources for transmission of the bacterium by the beet leafhopper (*Circulifer tenellus* Baker) in Illinois (O'Hayer et al. 1984). The bacterial pathogen *Xanthomonas campestris* pv. *campestris* was recovered from *C. bursa-pastoris* in cruciferous crop fields in Oklahoma, and was found to be the only weed that harboured bacterial pathogens in those fields (Zhao et al. 2002). The survey indicated that *C. bursa-pastoris* was not only an alternative host for this pathogen but might also play a role in the secondary disease cycle of black rot and leaf spot of cruciferous field crops. Other causal agents of bacterial leaf spots were not recovered from *C. bursa-pastoris*. In California almond orchards, *C. bursa-pastoris* has been infected by the bacterium *Xylella fastidiosa*, a cause of almond leaf scorch, usually transmitted by hemipteran vectors such as the blue-green sharpshooter *Graphocephala atropunctata* Signoret (Shapland et al. 2006). The bacterium *Rhizobacter dauci*, the causal agent of carrot bacterial gall, produced galls on the roots of a wide range of host species, including *C. bursa-pastoris*, in Japan (Kawarazaki et al. 2012).

Lee et al. (2016) identified nine species of spore-forming bacilli bacteria from fresh samples of *C. bursa-pastoris* in South Korea: *Bacillus drentensis*, *B. acidiceler*, *B. aryabhattai*, *B. asahii*, *B. firmus*, *B. pseudomycoides*, *B. psychrodurans*, *B. simplex*, *Bacillus* sp., *Paenibacillus lautus*, *P. barcinonensis*, *P. tundra*, and *Brevibacillus reuszeri*. These bacteria are ubiquitously present in nature, their endospores are generally found in soil and all isolates are able to produce enzymes that are responsible for food spoilage and can make the consumption of plant materials a food safety concern (Lee et al. 2016).

(iii) Viruses

Certain strains of the aphid-transmitted beet western yellows virus (BWYV) caused severe yellowing and stunting of infected *C. bursa-pastoris* (Falk and Duffus 1984; Sanger et al. 1994). Severe symptoms following inoculation with the BWYV strain ST9 did not arise from any change in confinement of the infection to the phloem. In Great Britain, *C. bursa-pastoris* was susceptible to BWYV and to beet mild yellowing virus (BMYV), but not to beet yellows virus (BYV) (Stevens et al. 1994). When a California legume isolate of BWYV was purified from *C. bursa-pastoris*, root tissue yielded four times as much as the shoots (D'Arcy et al. 1983). The satellite RNA of Barley Yellow Dwarf Virus-RPV is transmitted to *C. bursa-pastoris* by aphids, but only in conjunction with BWYV and its ST9 strain (Rasochová et al. 1997). A very small percentage of *C. bursa-pastoris* plants were infected by BWYV in sugarbeet seed crops in Oregon (Hampton et al. 1999). BMYV is able to overwinter on *C. bursa-pastoris*, and the latter is susceptible to most strains of beet yellowing viruses except for a strain of BMYV now classified as a new species, beet chlorosis virus (BChV) (Stevens et al. 2005) and the BMYV-2ITB isolate (Lemaire et al. 1995). A German isolate of BMYV used for both agrinoculation and aphid transmission of the virus produced systemic infection of *C. bursa-pastoris* by both methods (Stephan and Maiss 2006). Visible symptoms included both yellowing and leaf-rolling of older leaves. Artificially infected *C. bursa-pastoris* is able to transmit beet mosaic virus through the aphid, *Myzus ascalonicus* Doncaster (Semal 1956). As one of the more abundant weeds in areas adjacent to potato and onion crops in New York State, *C. bursa-pastoris* is host to the potato virus Y (PVY) and the potato leafroll virus (PLRV), both transmitted to crops by aphids, particularly the green peach aphid, *Myzus persicae* (Selzer) (Homoptera: Aphididae) (Smith et al. 2012). Several genotypes of that aphid are common on *C. bursa-pastoris* in Greece (Blackman et al. 2007). In contaminated soil, *C. bursa-pastoris* is among alternative hosts for the beet necrotic yellow vein virus (BANYVV), the beet soil-borne virus (BASBV) and spores of their protozoan vector *Polymyxa betae* Keskin (Mouhanna et al. 2008). *Capsella bursa-pastoris* is a potential alternative host of the blackberry yellow vein associated virus (BYVaV) in the United States (Poudel et al. 2013). In California lettuce-growing areas, *C. bursa-pastoris* is among crops and weeds infected by the thrips-transmitted disease *Impatiens* necrotic spot virus (INSV); and as a winter annual, is a probable virus reservoir and source of primary inoculum for lettuce planted in early spring and for maintaining the virus between summer- and fall-planted crops (Kuo et al. 2014). Curly top disease (CTD) caused by viruses in the genus *Curtovirus* and spread by leafhoppers, severely infects *C. bursa-pastoris* causing stunted growth and distorted and twisted leaves and stems (Chen and Gilbertson 2009; Chen et al. 2011). *Capsella bursa-pastoris* is also susceptible to the tobacco rattle virus TRV (genus *Tobravirus),* which is spread by nematodes, species *Trichodorus* and *Paratrichodorus* (Iannetta et al. 2010). TRV has a well-known persistent history of causing economic damage to potato tubers which appears as arcs of discolouration referred to as spraing.

(iv) Other diseases

The beet leafhopper *Circulifer tenellus* (Baker) (Cicadellidae) transmits the phytoplasma BLTVA, the causal agent of the potato purple top disease, to both crops and several weeds, including *C. bursa-pastoris* (Munyaneza et al. 2006). The causal agent of clubroot disease on *Brassica* spp., *Plasmodiophora brassicae* Woronin (Rhizaria) has been found on *C. bursa-pastoris* in oilseed rape fields in China, with an incidence of 6.2% and 100% respectively. Rapid spread of the disease in both the weed and a cabbage crop was observed (Kim et al. 2011; Ren et al. 2014).

(c) Higher plant parasites

Capsella bursa-pastoris is host of the field cow-wheat, *Melampyrum arvense* L., a hemi-parasite which attaches itself by haustoria to the roots of the host plant to obtain additional moisture and nutrients (Lechowski 1995). There are unconfirmed data from Bulgarian floras that *Capsella* is a host of the parasitic species *Orobanche nana* Noë (Stoyanov 2005). A greenhouse study done in Dijon, France showed that *Phelipanche ramosa* (L.) Pomel, a parasitic plant, had a low number of successful infections relative to other species in the study (Moreau et al. 2016).

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