

# The biology of Canadian weeds. 140. *Hesperis matronalis* L.

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Francis, A., Cavers, P. and Warwick, S. I. 2009. **The Biology of Canadian Weeds. 140. *Hesperis matronalis* L.** Can. J. Plant Sci. **89**: 189–204. The cruciferous weed *Hesperis matronalis*, dame's rocket (Brassicaceae), is an introduced Eurasian garden plant that began to escape shortly after its introduction to North America in the 19th century. It has gradually become naturalized across Canada and the United States, and has become invasive. It is not a major weed of crops, but is widespread in natural and conservation areas, particularly in thickets, open woodlands, forest margins and along streambanks, in parts of eastern and southern Ontario and western Quebec in Canada, and in New England and the midwest in the United States. In these habitats it can crowd out native vegetation and subsequently reduce biodiversity. Serving as an alternate host to a number of viruses, the species has the potential to infect cruciferous vegetable crops and garden plants. Despite its invasive potential, it continues to be sold at garden centres in both Canada and the United States.

**Key words:** *Hesperis matronalis*, dame's-rocket, julienne des dames, weed biology, invasive alien, HEVMA

Francis, A., Cavers, P. et Warwick, S. I. 2009. **La biologie des mauvaises herbes au Canada. 140. *Hesperis matronalis* L.** Can. J. Plant Sci. **89**: 189–204. *Hesperis matronalis*, la julienne des dames (Brassicacées), est une crucifère originaire d'Eurasie. D'abord cultivée dans les jardins, elle s'en est échappée peu après son introduction en Amérique du Nord, au XIX<sup>e</sup> siècle. Elle s'est progressivement acclimatée au Canada et aux États-Unis pour devenir envahissante. Il ne s'agit pas d'une mauvaise herbe importante, mais elle est largement répandue dans les aires naturelles et protégées, principalement les bosquets, les boisés ouverts, la lisière des forêts et le long des berges, dans certaines parties de l'est et du sud de l'Ontario ainsi que de l'ouest du Québec, au Canada, et dans les États de la Nouvelle-Angleterre ainsi que le Midwest des États-Unis. Dans ces habitats, la julienne des dames peut étouffer la végétation indigène, donc réduire la biodiversité. Elle est également l'hôte intermédiaire de plusieurs virus et pourrait infecter des crucifères maraîchères ou ornementales. Malgré sa capacité d'envahissement, cette plante continue d'être distribuée dans les centres de jardinage du Canada et des États-Unis.

**Mots clés:** *Hesperis matronalis*, julienne des dames, dame's-rocket, biologie des mauvaises herbes, plante exotique envahissante, HEVMA

## 1. Name

*Hesperis matronalis* L. — **dame's-rocket** (Darbyshire et al. 2000), common dame's violet, dame's violet, sweet rocket, mother-of-the-evening, damask violet, dames-rocket (US), damesviolet (US) (Darbyshire 2003); **julienne des dames** (Darbyshire et al. 2000), cassolette, damas, giroflée musquée, hespéride des jardins, hespéris matrone, julienne, julienne des jardins, roquette (Darbyshire 2003). EPPO (Bayer code): HEVMA. Brassicaceae (Cruciferae), mustard family, Brassicacées (Crucifères).

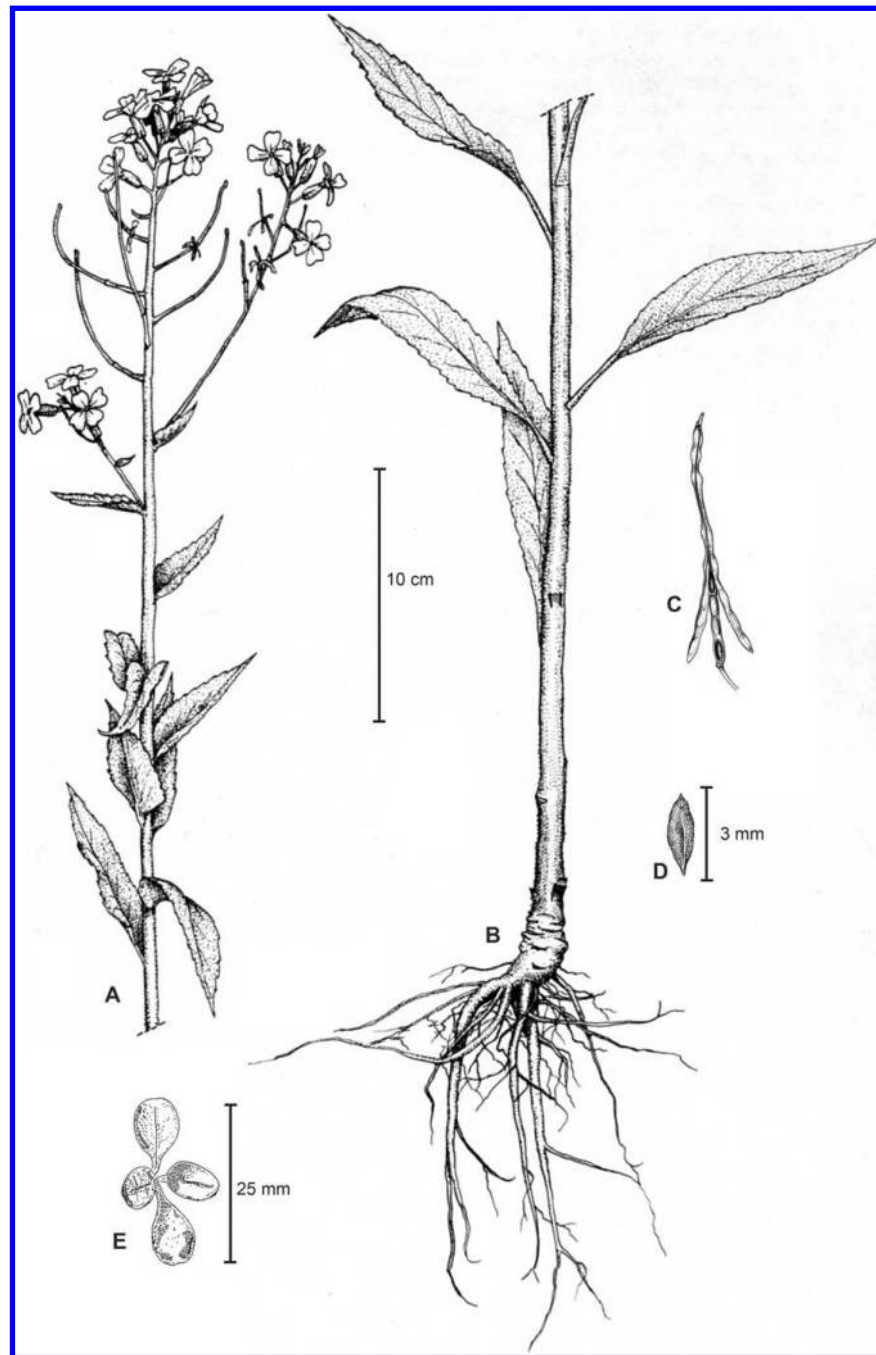
*Hesperis* is a genus of ca. 46 species (Warwick et al. 2006), only one of which is introduced in North America (Rollins 1993). The word *Hesperis* apparently was first used by Theophrastus (370–287 BC) and was taken from the Greek word "*hesperos*", meaning "western" because its fragrance is most pronounced in the evening when the sun is in the west (Clark 1973).

## 2. Description and Account of Variation

(a) *Species Description* — The following description is based primarily on information taken from the taxo-

nomic literature (e.g., Mohlenbrock 1980; Schultze-Motel 1986; Stace 1991; Alex 1992; Rollins 1993; Royer and Dickinson 1999; Cheo et al. 2001) and from herbarium specimens. Measurements are given as the typical range with unusual extremes in parentheses.

Plants (Fig. 1) are biennial or short-lived perennials. Roots shallow, spindle-shaped, fibrous. Stems erect, leafy, 1 or rarely several, simple or sparingly branched, 40–80 (–130) cm tall, hairy with mixed simple and forked hairs, eglandular and often glabrous distally. Basal leaves, petiolate, rosulate, entire to dentate, withered by time of flowering. Middle and upper cauline leaves alternate, blade narrowing up the stem, narrowly oblong, lanceolate to ovate-lanceolate, (2–) 4–15 (–20) × (0.4–) 0.8–4 (–6) cm, sharply toothed, apex acute or acuminate, hairy with mixed simple and forked hairs, the lower long-petioled, upper often sessile. Flowers, sweet-scented in the evening, are borne in upper leaf axils and terminally in compound often somewhat corymbiform racemes; fruiting pedicels divaricate or ascending, (0.5–) 0.7–1.7 (–2.5) cm, eglandular;



**Fig. 1.** *Hesperis matronalis*. A. upper stem and inflorescence; B. lower stem, leaves and roots; C. seedpod; D. seed; and E. seedling. A, B, and C all have a 10-cm scale, D and E scales as shown. Adapted from Mohlenbrock (1980), Alex (1992), Royer and Dickinson (1999).

sepals pubescent, narrowly oblong,  $5-8 \times 1.5-2$  mm; petals obovate, white or pink to purple, 1.8–2.5 cm long. Stamens strongly tetradynamous (4 long and 2 short); filaments 2.5–6 mm; anthers linear, 2.5–4 mm; style 1. Nectaries 2, lateral, confined between 2 petals and long stamens, surrounding the short stamen in a complete annular ring. Fruits (siliques) terete, (4–) 6–10 (–14)

cm  $\times$  2–2.5 mm; valves glabrous, constricted between seeds; at maturity, the fruits split open from bottom to top, releasing the seeds and leaving a thin membrane in the middle. Seeds uniseriate, wingless, oblong, (2.5–) 3–4  $\times$  1–1.5 mm; seed coat reticulate, with a thin, polygonal reticulum, not mucilaginous when wetted. Cotyledons incumbent, 8–15 mm long, 5–8 mm wide,

ovate, dull green, covered with short white, branched hairs. The first seedling leaves are ovate and appear opposite, later leaves are alternate.

*Hesperis matronalis* has both diploid and polyploid populations. The chromosome number for this species varies with counts of  $n = 7, 8, 12, 14, 24$ , and  $2n = 14, 16, 24, 26, 28$  reported. North American counts include  $n = 12, 2n = 24$  for naturalized plants from Ontario (Mulligan 1984), and  $n = 8, 14, 16$  from Ohio (Easterly 1963). Bhattacharyya (1974) reported  $n = 7, 2n = 14$  for widely grown purple-flowered garden plants from Manitoba, and  $2n = 24$  for a white-flowered east European variety from Romania. Counts of  $n = 7, 8, 12$ , and  $14$ , and of  $2n = 14, 24, 26, 28$  have been reported for Europe (reviewed in Jalas and Suominen 1994; Warwick and Al-Shehbaz 2006), and  $2n = 24$  for China (Cheo et al. 2001) and India (Gohil and Raina 1987). Dvořák and Dadáková (1976) found that all Czech *Hesperis matronalis* populations examined had  $2n = 24$  chromosomes, but considerable variability in the length of the chromosomes in specimens from different localities suggested multiple genomes and varying cytotypes in this species. A detailed analysis of chromosome morphology and meiotic behaviour, led Gohil and Raina (1987) to further suggest that *H. matronalis* was a segmental allotetraploid, in which equal numbers of bivalent and quadrivalent chromosomal associations were observed, indicating that the two genomes making up its polyploid genome were closely related.

(b) *Distinguishing Features* — In North America, *H. matronalis* can be confused when in bloom with the 4-petalled white or purplish-pink flowers of the cruciferous garden plant *Lunaria annua* L. However, the leaves of the latter are broader, with cordate bases, and seedpods are distinctly flat, coin-shaped (Hilty 2004). It also flowers earlier, from mid-April in southwestern Ontario (Cavers, personal observations). *Hesperis matronalis* can also be confused with the native garden phlox, *Phlox paniculata* L., because of its similarly white to purple, fragrant flower clusters. However, phlox has more brightly coloured 5-petalled flowers, and is a long-lived perennial spreading vegetatively from rooting stolons, has opposite rather than alternate, entire leaves and blooms in late rather than early summer, producing single-seeded pods.

(c) *Intra-specific Variation* — Seven subspecies are currently recognized for *Hesperis matronalis*: subspp. *adzharica* (Tzvelev) Cullen, *cilicica* (Siehe ex Bornm.) Cullen, *cladotricha* (Borbás) Hayek, *matronalis* L., *nivea* (Baumg.) Kuszcz., *schurii* Soó and *voronovii* (N. Busch) P.W. Ball (Warwick et al. 2006). Subspecies are not usually identified in North American literature (e.g., Rollins 1993; Mulligan 2002). The type subspecies, *matronalis*, is the most widespread and naturalized type in western Europe (Ball 1993; Jalas and Suominen 1994), and therefore, most likely to have been intro-

duced from that region to North American gardens. Rothfels et al. (2002) reported intraspecific variation among three populations from roadsides and three from old-field sites near Hamilton, ON, in both plant size and response to soil treatments with NaCl and Mn.

Cavers (unpublished) surveyed more than three dozen large populations of *H. matronalis*, all in wooded sites beside the Thames River near London, Ontario, in the early 1970s and found plants with white and purple flowers in each. In several populations, pink-flowered and flowers with patterns of white and purple or white and pink were also found. In contrast, only purple-flowered plants were found in some areas of the Prairie Provinces, e.g., 10 populations observed during a field trip to the Qu'Appelle Valley of Saskatchewan in 1982 (Cavers, personal observations), and in Waterton Lakes National Park (Kuijt 1982), whereas in southern British Columbia, flower colours vary from white through various shades of pink, purple and violet (Douglas and Meidinger 1998).

A study in former Czechoslovakia suggested a relationship between chromosomal variants found within *H. matronalis* subsp. *matronalis* (see Section 2a) and traits such as flower colour, and leaf and hair morphology (Dvořák 1982). Gohil and Raina (1987) suggested flower colour variation was under the control of multiple alleles.

(d) *Illustrations* — *Hesperis matronalis* is illustrated in Fig. 1, based on Mohlenbrock (1980), Alex (1992), and Royer and Dickinson (1999).

### 3. Economic Importance

(a) *Detrimental* — As a garden escape inhabiting roadsides, thickets and open woodlands, *H. matronalis* is listed among invasive herbaceous plants in Canada, with its invasive potential ranked as “low level invasive” (Canadian Botanical Conservation Network 2008). In a survey evaluating invasive plants in natural areas in Canada, *Hesperis matronalis* was rated as a minor invasive alien of upland natural areas and was only a serious problem in southwestern Ontario (White et al. 1993). In Ontario, *H. matronalis* dominates open forest understorey and meadows, and is ranked among invasive exotic species “that can dominate a site to exclude all other species and remain dominant on a site indefinitely”, thus posing a threat to natural areas where they occur (Urban Forest Associates 2002). Densities of this species increase in disturbed areas such as roadsides (Rothfels et al. 2002) and it sometimes occurs in grain and legume crop fields in Ontario with potential to cause control problems, particularly under no-till systems (Murphy et al. 2006). In a Manitoba study of urban disturbed riparian forests, Moffatt et al. (2004) recorded low native understorey species diversity, and an abundance of exotics, particularly *H. matronalis* and *Solanum dulcamara* L. In Alberta, *H. matronalis* has escaped intentional plantings in Waterton Lakes

National Park and in the Crowsnest Pass (Alberta Invasive Plants Council 2008). Concern has been expressed concerning the susceptibility of *H. matronalis* as an alternate host to a number of viruses associated with cruciferous vegetable crops (Royer and Dickinson 1999); and particular concern has been directed to the species' potential to cause disease problems in vegetable-growing regions of British Columbia (Ford et al. 1988).

In the United States, infestations of *H. matronalis* have been increasing rapidly in natural areas in the north central states, resulting in increasing competition with native species (Lym 2004). The species is reported as invasive in 12 states: Colorado, Connecticut, Indiana, Maryland, Massachusetts, Missouri, New Jersey, Pennsylvania, Tennessee, Virginia, Wisconsin and West Virginia (Massachusetts Department of Agricultural Resources 2006; USDA Forest Service 2006). It is considered a noxious and troublesome weed in North Dakota (Lym 2004), Colorado (Pitkin County Land Management Weed Advisory Board 2004), Wisconsin (Wisconsin Botanical Information System 2005), and is listed in the Invasive Plant Atlas of New England (2004), as frequent in riparian or wetland habitats, open woods, and along roads, where it is capable of crowding out native vegetation. Its inclusion in "wildflower" mixes is considered the biggest problem in these regions (Wisconsin Department of Natural Resources 2004; Mahr 2008). *Hesperis matronalis* is not widely recognized as an invasive species and consequently may not be recognized as a problem until it is well established, resulting in delays before measures are taken to control it (Wisconsin Department of Natural Resources 2004). It was present at low levels for many years in Michigan but now reported as spreading aggressively and subject to control measures in natural areas (Michigan Natural Features Inventory 2008), and indeed is cited as an example of a "sleeper" species for potential invasive in Washington State where it is undergoing range expansion (Mack 2002). It appears adapted to northern climes and has frequently escaped from gardens in Iceland (Grøntved 1942) and Alaska (Alaska Natural Heritage Program 2004).

(b) *Beneficial* — *Hesperis matronalis* is still widely marketed as a garden ornamental in Canada and the United States despite concerns about invasive ornamental plants by many in the horticultural industry (Peters et al. 2006). It is highly suited for commercial seed production and is sold in wild plant mixes for gardens or roadside beautification schemes (e.g., Johnson and Whitwell 1997). It was among species in wildflower mixtures that thrived in landfill restoration experiments in Virginia (Sabre et al. 1997), and produced good sods and rooting in fields plots for transplanting to provide cover and slope stabilization along highways in Massachusetts (Airhart et al. 1983).

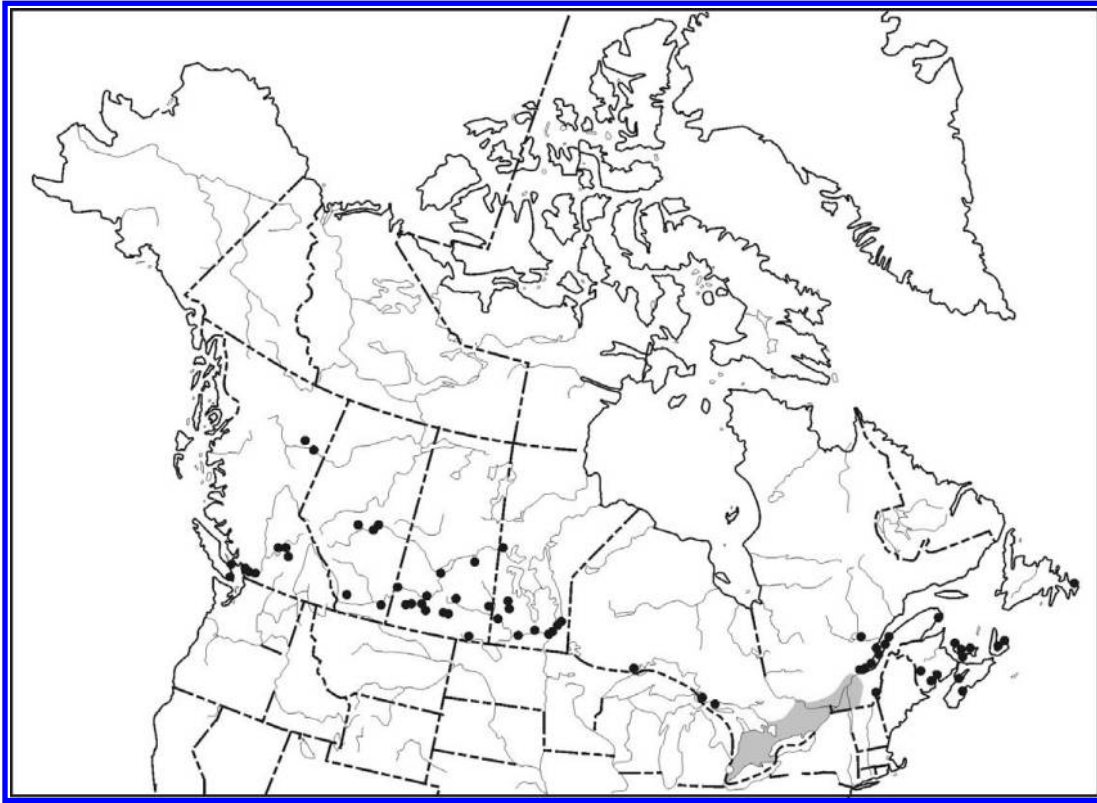
In Europe it is best known as a long-cultivated ornamental and occasional garden escape (e.g.,

Schultze-Motel 1986; Stace 1991; Ball 1993), and may also be planted expressly for other economic uses, such as the following. The leaves are used for medicinal purposes as an antiscorbutic, diaphoretic, diuretic, expectorant and to induce sweating (Bellardi et al. 1997; Plants for a Future 2004). Young leaves, rich in vitamin C, are eaten like cress in salads (Grieve 1959; Facciola 1990; Plants for a Future 2004), and sprouted seeds can be eaten (Facciola 1990). In the Netherlands, it is grown with fodder crops such as lucerne (*Trifolium* spp.), as the leaves are not poisonous to cattle and contain a good percentage of protein (Ouden 1956). The high percentage of oil in the seeds has potential for use as edible oil, and the high percentage of linolenic fatty acid has suggested possible use in the preparation of high-quality paints and varnishes (Kumar and Tsunoda 1980; see also Section 7c). The volatile oil, known as honesty oil, huile de julienne, or rotreps oil, is used in perfumery (Usher 1974; Facciola 1990; Bellardi et al. 1997). In Europe, the presence of *H. matronalis* in a crop field has been observed to lead to a reduction in pest nematode populations (see Section 13).

(c) *Legislation* — In Canada, *Hesperis matronalis* is not on any federal or provincial government noxious weed lists. However, it is treated as an invasive or potentially invasive plant in all provinces (Environment Canada 2001); and as a minor or local invasive alien in upland natural areas in Ontario, particularly in the southwest (Environment Canada 2003). In the United States, *H. matronalis* is not listed on the federal Noxious Weed List, but is on the B list of noxious weeds in Colorado (USDA, NRCS 2008a); is considered "invasive and banned" in Connecticut, subject to eradication efforts in that state (State of Connecticut General Assembly 2005; USDA, NRCS 2008a); and is among invasive plants subject to both an importation and propagation ban in Massachusetts (Massachusetts Department of Agricultural Resources 2006; USDA, NRCS 2008a).

#### 4. Geographical Distribution

*Hesperis matronalis* is found in all Canadian provinces (Fig. 2), and is particularly abundant in southwestern Ontario and along the St. Lawrence River in Quebec and eastern Ontario (Sabourin 1992; Warwick et al. 1999; Environment Canada 2002, 2003; Canadian Botanical Conservation Network 2008; Warwick, personal observations). Morton and Venn (2000) reported *H. matronalis* from Manitoulin Island and many small islands surrounding it in Lake Huron, Georgian Bay and the North Channel. It is common in southern British Columbia (Douglas and Meidinger 1998; Klinckenberg 2007), and described as frequent in southwestern BC, known from Vancouver Island and the adjacent mainland, rare in south-central BC, and locally frequent in westcentral and southeastern BC. It is rare along the Pacific Coast to the north and one record, on a gravel-shingle beach, was reported from the Queen



**Fig. 2.** Distribution of *Hesperis matronalis* in Canada, based on 136 herbarium specimens from DAO, UNB and UWO. Herbarium abbreviations in Holmgren et al. (1990). The shaded area on the map represents the area of greatest infestation.

Charlotte Islands (Calder and Taylor 1968). In Manitoba, it had escaped from cultivation and was established on the banks of the Saskatchewan River in The Pas in 1949 (Scoggan 1957). Hinds (2000) reported that it has commonly escaped to thickets and waste areas in New Brunswick, in the south and west of that province. *H. matronalis* has been found on roadsides and open woods in Prince Edward Island (Catling et al. 1985). It is found throughout Nova Scotia where it still persists patchily along roadsides and in waste places (Zinck 1998). A specimen collected from a hedge in Fort Providence, NWT, in 1955 was possibly a garden escape, but may have been planted (note by G. A. Mulligan in DAO herbarium).

In the United States (Fig. 3), it is widespread in temperate regions of the east and central states, less common west of the Rocky Mountains, and occurs in Alaska, where it has been recorded as a garden escape from southern and southeastern regions, as well as invading mesic meadows in the interior boreal region (Rollins 1993; Alaska Natural Heritage Program 2004; USDA, NRCS 2008a). Most likely originating in southern Europe and western Asia (Hultén and Fries 1986), it is now widespread in temperate western and Central Asia (Hultén and Fries 1986) and western Europe, spreading into northern Europe, but rarer and more localized from northern Spain through Italy, northern

Greece, the Balkans, European Turkey, Crimea, and Russia (Authier 1993; Ball 1993; Jalas and Suominen 1994; Stenberg 1995). It also occurs in Iceland, where it is one of the most frequently cultivated ornamental plants and it is often found on dumping grounds and as an escape from cultivation (Grøntved 1942). It is naturalized in New Zealand, occurring throughout, where it is occasionally persistent in waste land and old gardens, mostly in the South Island (Webb et al. 1988). In China it is established in Xinjiang province in the northwest (Cheo et al. 2001).

## 5. Habitat

(a) *Climatic Requirements* — *Hesperis matronalis* thrives in temperate zones with hot summers, enough precipitation to keep the soil moist, and where days are long in spring and early summer, when overwintered rosettes bolt and flower. Plants require moderate precipitation ranging between 80 and 150 cm and a minimum of 120 frost-free days, and can withstand winter temperatures as low as  $-23^{\circ}\text{F}$  ( $-31^{\circ}\text{C}$ ) (USDA, NRCS 2008c). *Hesperis matronalis* frequently occurs at sites subject to seasonal flooding, and studies below suggest that seeds are tolerant of inundation. On 11 different occasions from 1974 to 1999, seeds of *H. matronalis* in mesh bags were stored outdoors under water in London, ON, for 9 wk from late September to late November. At



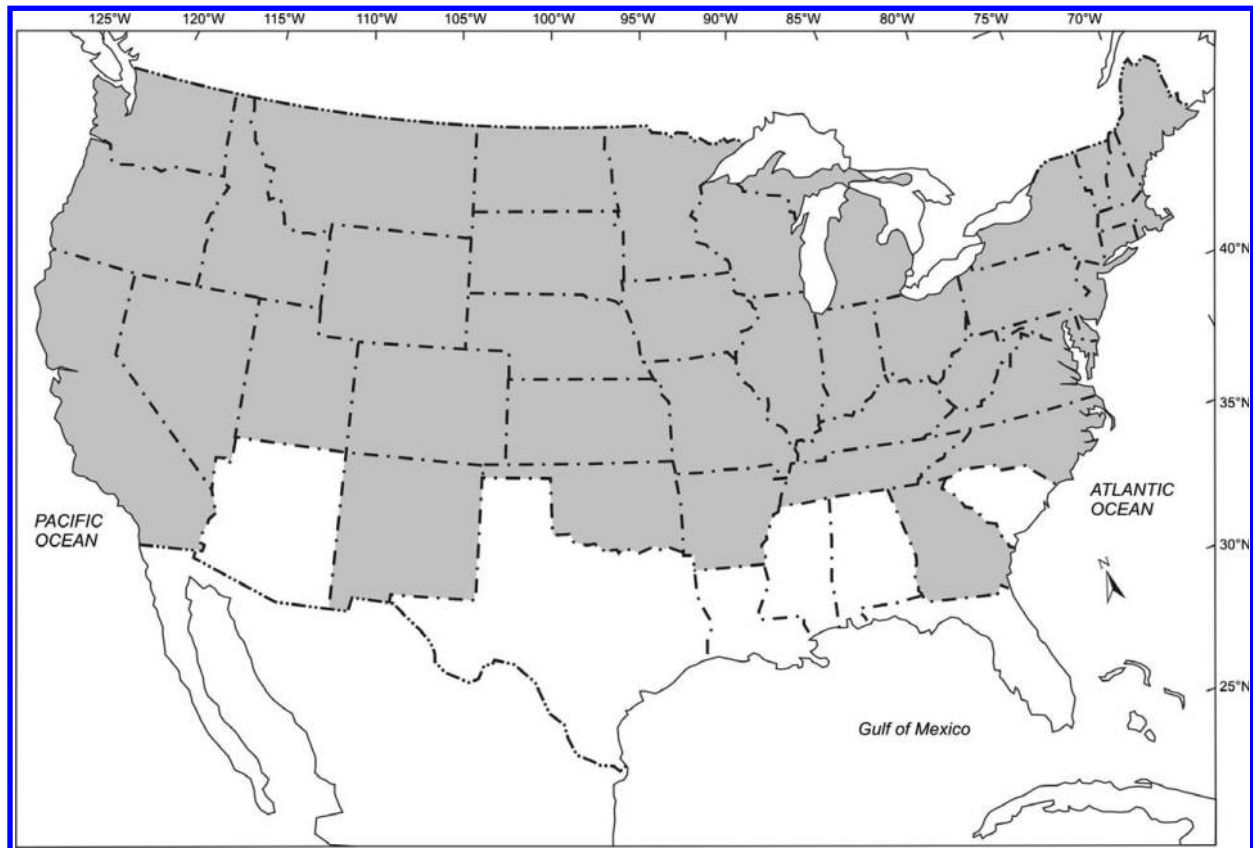


Fig. 3. Distribution of *Hesperis matronalis* in the United States, based on USDA, NRCS (2008a).

least 40% of the seeds remained viable after this treatment and in 10 of the tests 50–92% germinated in an incubator within 3 wk of removal from the water (P. Cavers and several undergraduate students, unpublished).

(b) *Substratum* — *Hesperis matronalis* is easily grown in well-drained fertile loamy soil in full sun to part shade (Hilty 2004). It is adapted to medium-textured soils with pH values from 5 to 7, and is most abundant on soils high in calcium (USDA, NRCS 2008b, 2008c). It also grows well on alkaline soils (Moffat et al. 2004), but has low tolerance for saline soils (Beaton and Dudley 2004).

(c) *Communities in Which the Species Occurs* — *Hesperis matronalis* has intermediate shade tolerance (USDA, NRCS 2008c). In Canada, it occurs as a weedy escape in old gardens and fields, thickets, rich moist woodlands, stream banks and flats, shingle and sand beaches, and along roadsides, railways and open disturbed areas (Alex 1992; Warwick et al. 1999). In southwestern Ontario, it has been a common component of disturbed riparian woodlands and other natural areas for more than 40 yr (Cavers, personal observations). In a degraded woodlot near Waterloo, ON, it grew beneath sugar maple (*Acer saccharum* L.), beech (*Fagus grandifolia* Ehrh.) and white oak (*Quercus alba* L.) in

association with garlic mustard (*Alliaria petiolata* (L.) Cavara & Grande, spring beauty (*Claytonia virginica* L.), dog-tooth violet (*Erythronium americanum* Ker.), Canada avens (*Geum canadense* Jacq.), herb-robert (*Geranium robertianum* L.), Canada bluegrass (*Poa compressa* L.) and woodland speargrass (*Poa nemoralis* L.) (Murphy 2005). In eastern Ontario (Warwick, personal observations), *H. matronalis* is frequent in disturbed deciduous wooded areas along the St. Lawrence River, along with the invasive *Alliaria petiolata*, and growing beneath red oak (*Quercus rubra* L.), shag bark hickory [*Carya ovata* (Mill.) K. Koch], basswood (*Tilia americana* DuRoi.), ash (*Fraxinus* sp.), and sugar maple (*Acer saccharum*). Rothfels et al. (2002) collected plants from old fields and roadsides in the Hamilton, ON, area. The old-field populations were dominated by mixed grasses and forbs (*Bromus inermis* Leyss., *Asclepias syriaca* L., *Dipsacus fullonum* L. and *Solidago* sp. were all common), while the roadside populations were all collected within 5 m of the edge of a major motorway, but *H. matronalis* was not abundant in any of them. *Hesperis matronalis* occupies mesic to dry roadsides, fields and disturbed areas in the lowland, steppe and montane zones in southern BC (Douglas and Meidinger 1998; Klinkenberg 2007).

Rollins (1993) reports *H. matronalis* as widely naturalized in rich moist woodlands, thickets, roadsides, waste places and gardens in the United States. It has further been reported from early successional floodplain and planted forests, pastures, herbaceous wetland, and wet meadows in New England (Invasive Plant Atlas of New England 2004), and in these and related sites such as riparian habitats, wetlands and rangelands further west (e.g., Lym 2004; Pitkin County Land Management Weed Advisory Board 2004; Wisconsin Department of Natural Resources 2004; Colorado Weed Management Association 2008).

## 6. History

*Hesperis matronalis* is generally believed to have been introduced from Europe to North America as a garden plant (e.g., Alex 1992; Mulligan 2002), but the first reports of its appearance as a garden escape did not appear until after the middle of the 19th century (e.g. Gray 1858; Rousseau 1968). In Canada, it was first reported in Quebec in 1862 at Château-Richer, Côté de Montmorency, naturalized in the vicinity of gardens (Rousseau 1968), and there are early Quebec collections dating to 1914 (DAO). In Ontario, early collections date to 1890 in Wingham (UWO) and to the 1920s in the Ottawa area (DAO). It has been a major understorey component of woodlands, riparian habitats and railway embankments in southwestern Ontario for more than 50 yr (Gaiser and Moore 1966; Cavers, unpublished data). In the prairies, one of the earliest reports was from Pine Ridge, near Winnipeg, MB, in 1939 (Scoggan 1957); and in British Columbia, there are collections from New Westminster and from Kamloops in 1930 (DAO).

In the United States, *H. matronalis* has subsequently spread through much of the temperate regions wherever it was cultivated as a garden plant (Rollins 1993). *Hesperis matronalis* was recognized as a resident alien in the Columbia Plateau of southern Washington State by 1937, having been introduced to the area as an ornamental (Mack 2002); but Rollins (1993) suggests that although widely naturalized, most of the established populations in the United States are east of the Rocky Mountains.

## 7. Growth and Development

(a) *Morphology* — See Sections 2a and 8a for vegetative and floral features of this species.

(b) *Perennation* — *Hesperis matronalis* survives the winter as seeds, vegetative rosettes and occasionally after flowering.

(c) *Physiological Data* — *Hesperis matronalis* is among cruciferous plants whose seeds produce a high percentage of oil, rich in linolenic acid and free from erucic acid, with an oil content of 32% and fatty acid composition as follows (numbers in parentheses refer to the length of the fatty-acid chain and the number of

double bonds in the chain): 7.3% palmitic (16:0), 2.2% stearic (18:0), 13.4% oleic (18:1), 23% linoleic (18:2), 55.3% linolenic (18:3), 0% eicosenoic (20:1), 0% erucic (22:1) and 0.9% other acids (Kumar and Tsunoda 1980). In Ontario, chemical analysis of the leaves of *H. matronalis* showed high (0.76  $\mu$ moles/50 g fresh green leaves) glucosinolate levels, although the glucosinolates were not identified in the study (Nair et al. 1976). In Denmark, the following glucosinolates were isolated from the seeds: 6-methylsulphinylnonylglucosinolate (glucohesperalin), 3,4-dihydroxybenzylglucosinolate (glucomatronalin), 3-O-apisylglucomatronalin, and a 3,4-dihydroxybenzoyl ester and a 3,4-dimethoxybenzoyl ester of 3-O-apisylglucomatronalin (Larsen et al. 1992); and from seedmeal of *H. matronalis*: 5-methylsulfinylpentyl- and 6-methylsulfinylhexyl glucosinolates (Daxenbichler et al. 1991). Hesperin, an ester, was identified in crude extracts from *H. matronalis* seedmeal, but yields were poor and the seedmeal was not considered a good candidate for hesperin production (Vaughan and Berhow 2005). Aromatic choline esters accumulated in seeds of *H. matronalis* showed a very high percentage of hesperaline and smaller amounts of vanillylcholine, p-coumaroylcholine and 3,4-dimethoxycinnamoylcholine; and an absence of sinapine, the dominant ester in *Sinapis alba* L., the other cruciferous species tested (Bjergegaard et al. 1993).

Flowers of wild *H. matronalis* plants in the Abkhazian Mountains of Russia contained 0.2% essential or volatile oil; while yield from plants in the lowlands was 3.9–5.0% (Esvandzhiya and Milianovskii 1975). Nielsen et al. (1995) identified 12 monoterpenes and five aromatic compounds from flowers of *H. matronalis* growing in Denmark: the four most abundant being 1,8-cineole, E- $\beta$ -ocimene, linalool, and benzyl acetate. Emissions of these volatiles varied with time of day and temperature. In the United States, Majetic et al. (2007) identified a total of 33 floral volatile compounds from *H. matronalis*, which could be divided into two main categories: aromatics (ester or alcohol-modified compounds with benzene rings) and terpenoids (composed of isoprene rings). Seven new aromatic compounds were identified including benzaldehyde, benzyl propionate, benzyl acetate, eugenol, methyl anthranilate, and phenyl acetonitrile. No differences were detected between white and purple colour morphs of *H. matronalis* in overall scent emission rates, but flowers of both morphs emitted more scent at dusk than at dawn, with a higher proportion of aromatic compounds at dusk (maximizing moth pollination) and higher terpenoid proportions at dawn. The white morph, however, exhibited significant differences between populations, whereas there was little variation in scent composition among purple morphs (Majetic et al. 2007).

In Ontario greenhouse studies (Rothfels et al. 2002; Beaton and Dudley 2004), *H. matronalis* plants grown from seeds collected from roadside populations showed no adaptation to high soil salinity during germination,

but one roadside population displayed a low level of manganese (Mn) tolerance, which was higher than that of old-field populations. There was high mortality in both the salt (43% seedling survival) and Mn treatments (53% seedling survival) compared with the control (71% seedling survival) in both roadside and old-field populations. There were no significant correlations between seed mass and either salt or Mn tolerance, but seedlings grown from seeds collected from roadside populations tended to have shorter roots than those collected from old-field populations, likely a reflection of the poorer roadside environment for seed production. Similarly, *H. matronalis* grown from seeds collected in the roadside were bigger as rosettes than plants grown from seeds collected from old-field sites (Rothfels et al. 2002).

A US study of the effectiveness of reproductive organs and leaves in screening ultraviolet radiation showed higher concentrations of ultraviolet-B absorbing compounds in pollen and ovaries of *H. matronalis* than in sepals, petals and leaves, suggesting that this species allocated more resources to protect gametes from damaging UV rays than to those organs involved in attracting pollinators or photosynthesis (Day and Demchik 1996). In a New York study, a level of proteinase inhibitory activity of 90 µg trypsin inhibited/mg protein was detectable in the foliage of *H. matronalis*, the lowest level among the wild cruciferous species tested (Broadway 1989). In a Russian study on water content and intensity of transpiration relative to surface area of leaves and fruits, *H. matronalis* was among plants whose dry fruits did not undergo any regular age-related changes in transpiration intensity (Antipov 1980).

(d) *Phenology* — *Hesperis matronalis* develops from seed in late spring to late summer, overwinters as a rosette, and flowers the following spring. Under some conditions, plants may survive through a second winter. Cavers observed that almost half of the plants flowered in 2 successive years in several southern Ontario sites. It flowers from mid-May to August in eastern Canada (Alex 1992; Sabourin 1992), in late June and early July in the Qu'Appelle Valley in Saskatchewan (Cavers, personal observations) and in July and early August in Waterton Lakes National Park in Alberta (Kuijt 1982). Morton and Venn (2000) recorded that it flowered from the first week in June until the second week in July on Manitoulin Island, but they also recorded it as flowering there throughout October. The flowering period is from April to July in parts of the United States (Rollins 1993). In southern Ontario, seeds mature from late spring to October and are dispersed from August to November (including some that are retained on the parent plant until after the first frosts). Since stratification can delay germination (Section 8c), germination often takes place in the spring (Cavers, personal observations). Seedlings establish and reach the rosette stage before overwintering, and the growth cycle resumes in early spring of the

following year when reproductive organs begin to form after bolting (Evtikhova 1985).

(e) *Mycorrhiza* — *Hesperis matronalis*, like the majority of cruciferous species tested, is nonmycorrhizal (Medve 1983). It was among three cruciferous species studied for arbuscular mycorrhizal development, grown both alone and with a matrix of living roots of the mycotrophic grass *Sorghum sudanense* (Piper) Stapf (DeMars and Boerner 1995). The percent of root length colonized was least in *H. matronalis*, and colonization levelled off or decreased at the end of 90 d for plants grown alone, but continued to increase for plants grown in the matrix, suggesting that progressive root senescence contributed to spread of the inoculum from the matrix. No arbuscules were observed in the roots of *H. matronalis* at any time, suggesting that arbuscular mycorrhizae were non-functional in this species.

## 8. Reproduction

(a) *Floral Biology* — *Hesperis matronalis* is largely self-incompatible (Mitchell and Ankeny 2001), with hand-cross pollinated flowers producing 12 seeds/fruit, while selfed or unpollinated flowers produced only 2 seeds/fruit. Susko and Clubb (2008) also noted in an Ontario study that significantly fewer seeds were produced via inbred crosses. These were significantly heavier and more than twice the number germinated compared with those from cross-pollinations. Susko and Clubb (2008) also found that seed maturation within fruits depended significantly on the pollination regime and ovule position. When self-pollinated, the resultant fruits matured significantly fewer mature seeds at the tip of the fruit than at the base, whereas the opposite pattern was observed following cross-pollination.

*Hesperis matronalis* is adapted to both day and night pollinators, and is pollinated by a variety of long- and short-tongued bees, butterflies, syrphid flies, and moths including *Bombus* spp., *Apis mellifera* L., other bee species, and several species of Lepidoptera, including Sphingidae and white-veined butterflies (*Pieris rapae* L.) (Conner and Sterling 1995; Mitchell and Ankeny 2001; Majetic et al. 2007; Susko and Clubb 2008). There appears to be a complicated relationship between flower colour and scents in attracting different kinds of pollinators (Majetic et al. 2007), and a high glucose:fructose ratio and a much lower sucrose:hexose ratio in the two lateral nectaries also lead to discrimination among pollinators (Davis et al. 1998). *Hesperis matronalis* lacks median nectaries, and nectar carbohydrate production per flower was low in spite of its large flower size compared with other crucifer species studied (Davis et al. 1998). *Hesperis matronalis* is well adapted for both day and night pollinators, with day pollinators resulting in double the seed-set of night pollinators (Sahli 2007).

Unlike three other species studied, *H. matronalis* did not show phenotypic correlations among floral traits, such as increased filament-corolla tube lengths, which



would potentially optimize anther placement to enhance pollination, and none of the species studied showed evidence of selection for optimal stigma placement (Conner and Sterling 1995). Conner and Sterling (1996) confirmed for *H. matronalis* and four other species the hypothesis that flower size in insect-pollinated plants should be selected to remain constant, regardless of the size of vegetative structures, so that flowers match the sizes of their pollinators for effective pollination. Experiments suggest that deviations from perfect symmetry in *H. matronalis* also do not affect seed production in this species, instead insects use flower size as a primary cue to discriminate among plants, but not among flowers within a plant (Weeks and Frey 2007).

(b) *Seed Production and Dispersal* — Each pod contains between 20 and 35 seeds; and a plant is capable of producing up to 20 000 seeds (Royer and Dickinson 1999). The number of seeds per pound has been estimated at 224 000 (=492 800 seeds kg<sup>-1</sup>) (USDA, NRCS 2008c). In a South Carolina commercial seed production trial, *H. matronalis* yielded 2920 kg ha<sup>-1</sup> of viable seeds (Johnson and Whitwell 1997). There is no evidence that plant density, dense 60 vs. sparse 6 stems within 3 m of the focal plants, has any significant effect on the reproductive success of *H. matronalis* (Mitchell and Ankeny 2001), with a mean seed set of 11 seeds per fruit. No difference was detected between colour morphs, i.e., purple versus pale white to light pink, in seed or fruit set (Mitchell and Ankeny 2001). In a Delaware study, seed weight was 422 seeds g<sup>-1</sup> (Pill et al. 2000). Salisbury (1942) gave the average seed weight of *H. matronalis* from American samples as 0.002025 g.

Seeds of *H. matronalis* are usually dispersed close to the parent plant, since wind dispersal is not effective nor is dispersal by water. It was observed that seeds sank quickly in agitated water, although some seeds could float for minutes, or even a few hours, in still water and some could be dispersed in small lumps of soil attached to human footwear (P. Cavers and undergraduate students, unpublished observations). Seeds of *H. matronalis* are reportedly eaten and dispersed by ground-foraging birds (USDA Forest Service 2006).

(c) *Seed Banks, Seed Viability and Seed Germination* — Many seeds of *Hesperis matronalis* can survive the winter following their production and, at least in some sites, the species has a weakly persistent seed bank (Cavers, unpublished data). There is almost no information on seed longevity in the literature.

Experiments with multi-year (1974–1999) seed collections of *H. matronalis* from London, ON, averaged 87% viability, although germination was often slow and irregular (P. Cavers and undergraduate students, unpublished observations). Fresh seeds collected in September had a range of 0.5 to 29% germination in light at 25/10°C after 7 d and 63 to 100% germination after 35

d, with slightly higher germination percentages and much faster germination obtained at 35/20°C, whereas seeds stored for 8 wk at room temperatures (20–25°C) yielded 66 to 89% germination after 7 d at 25/10°C and 75 to 97% germination after 14 d. In laboratory studies, Susko and Hussein (2008) observed maximum germination of fresh seeds (>80%) of *H. matronalis* collected from an old field near Windsor, ON, at alternating temperatures 25/15°C in both light/dark and continuous darkness, enhanced germination at low alternating temperatures after cold stratification at 4°C for 4 to 16 wk, and greater than 94% germination after 1 yr of dry storage. They also found that at burial depths of 1 to 5 cm, emergence was greater than 56%, with maximum emergence at 0–2 cm. Germination exceeded 60% at pH 3–10, reaching almost 100% with pH 5–8, suggesting some adaptation to both alkaline and very acidic soils, and although reduced below 50% at osmotic potentials (MPa) below –0.6, there was nevertheless considerable tolerance of marginal water stress conditions.

Mitchell (1926) found that light was beneficial for germination, but Cavers and his students (unpublished) found that percent germination in total darkness was equal to or exceeded the totals obtained in the light (both fresh seeds and seeds stratified outdoors for 12 wk in the fall were tested). Steinbauer et al. (1955) suggested that seeds should be exposed to a 0.2% solution of potassium nitrate for optimal germination, but Cavers (unpublished) found that such solutions did not stimulate germination and exposure to a solution of 1% potassium nitrate slowed germination. Cavers (unpublished) found that germination was not stimulated in Petri dishes moistened with either 0.1 or 0.01% gibberellic acid. Germination totals were not affected but, at least in 0.1% gibberellic acid, germination was slower.

In South Carolina, *H. matronalis* was among plants in wildflower mixes studied for commercial production potential with the highest germination percentages and most even maturation period: 98% of seeds from plantings on 1993 Oct. 07, which flowered the following April and were harvested on 1994 Jul. 01 (Johnson and Whitwell 1997). Cold stratification is not required for germination (USDA, NRCS 2008c), and observations by Cavers (unpublished data) suggest that cold stratification actually inhibits germination as moist seeds stratified for 9 wk at 5°C germinated more slowly and to much lower totals than seeds stored at room temperature for the same length of time before testing. In a Delaware study on improving wildflower establishment of seeds of *H. matronalis* by altering water potential of a vermiculite matrix hydrated with water, there was no significant effect on percent germination regardless of seed:vermiculite weight ratios tested (ratios 1:0.5 to 1:4). Percent germination ranged between 90 and 92%, the same as the control. There was only a slight reduction in the number of days to 50% seedling emergence (less than 2 d from 2.3) and only slight

increases from 90 to 98% by exposure to gibberellic acid during the priming (Pill et al. 2000).

(d) *Vegetative Reproduction* — *Hesperis matronalis* reproduces only from seed.

## 9. Hybrids

There is no evidence of interspecific hybridization in *H. matronalis*; but many cultivars have been produced through intraspecific breeding. Crossing of *Alliaria petiolata* with *H. matronalis* by means of in vitro fertilization produced a small number of embryos on *Alliaria petiolata*, but no hybrid seedlings (Zenkteler 1992).

## 10. Population Dynamics

Cavers (unpublished) has conducted a 40-yr study (1967–2007) of the ground flora in a deciduous riparian woodland beside the Thames River in London, ON. In sites disturbed primarily by flooding and human trampling the most abundant species was goutweed (*Aegopodium podagraria* L.), but both *Hesperis matronalis* and garlic mustard (*Alliaria petiolata*) were common. During the study, populations of *H. matronalis* tended to remain in the areas where they were first recorded in the 1960s, and the relative abundance of this species did not change markedly. Increases were noted along the woodland edge on the eastern side. The great variety in flower colours, purple, pink, white and variegated (mottled), was maintained in most sites.

Comparative studies of populations in abandoned farm fields undergoing succession and along roadsides in southern Ontario (Rothfels et al. 2002) showed that, regardless of localized stresses, larger plants were more likely to bolt in all areas, and that old-field plants were less likely to bolt than roadside plants. High-density treatments led to earlier bolting (up to 78% in roadside and between 40 and 55% in old-field plants) and longer internodes, consistent with the tendency of this species to avoid full shade, and the addition of water to the soil produced a higher bolting proportion in both roadside (60–80%) and old-field (30–43%) populations than either manganese or salt treatments, where bolting was greatly reduced. It appeared that selection pressure at the seedling stage was more intense than at the adult stage, as shown by the high mortality of juvenile plants on roadsides, whereas unbolted rosettes were more likely to successfully delay reproduction for an additional year in old-field populations.

In Colorado, Hwang and Lauenroth (2008) studied the effects of *H. matronalis* on neighbouring native perennial species *Campanula rotundifolia* L. and *Muhlenbergia montana* (Nutt.) A.S. Hitchc. at various levels of neighbour density, nitrogen and water. *Hesperis matronalis* clearly reduced aboveground growth of the neighbouring species and maintained its competitive advantage across all treatments even when biomass of

the other species increased under certain levels of water or nitrogen.

## 11. Response to Herbicides and Other Chemicals

There is little detailed information on the use of herbicides to control *H. matronalis*. The USDA Forest Service (2006) recommends applying any of several readily available general-use herbicides, such as glyphosate, in late fall, when the leaves of the rosettes are still green. In Michigan, it was suggested that foliar herbicide applications could be effective in early spring or late fall while native species are dormant (Michigan Natural Features Inventory 2008). In Wisconsin, it was similarly suggested that herbicides be applied in late fall when rosettes are still green to avoid damaging nearby native vegetation (Wisconsin Department of Natural Resources 2004). In Colorado, the herbicides clopyralid+metsulfuron methyl or dicamba formulations at recommended commercial rates have been proposed for application from spring and onwards as long as the plant is actively growing (Pitkin County Land Management Weed Advisory Board 2004).

## 12. Response to Other Human Manipulation

No-tillage management of corn, soybean and winter wheat crops in southern Ontario has resulted in increased weed species diversity, including the presence of *H. matronalis*, and increased competition among winter annuals, biennials and perennials (Murphy et al. 2006). Physical removal and cutting of *H. matronalis* are recommended by the Canadian Botanical Conservation Network (2008). Immediate removal of plants before seed set is considered the best means of depleting the seed bank and preventing the spread of *H. matronalis*; and combined herbicide or mechanical removal of rosettes with removal of seed heads is also recommended (Pitkin County Land Management Weed Advisory Board 2004; Colorado Weed Management Association 2008). In Nebraska, roadside mowing practiced as a means of maintaining roadside vegetation dominated by grasses and mixed with planted wild flowers, including *H. matronalis*, had the following effects on the latter: mowed plants survived, but plant vigour was reduced, the height of lateral shoots was shorter, blooming was delayed, the blooming period was extended by a month, and the number of buds, flowers, and seed pods of this early blooming species was significantly reduced following May 15 and May 29 mowing dates (Salac et al. 1973). Burning can be effective where there is enough leaf litter or other fuel available (USDA Forest Service 2006). The USDA Forest Service also recommends pulling or the use of a dandelion digger when the soil is moist, combined with bagging flower heads for landfill or drying and burning them where permissible. There is no information regarding possible biological controls (e.g., Pitkin County Land Management Weed Advisory Board 2004).

### 13. Response to Herbivory, Disease and Higher Plant Parasites

#### (a) Herbivory

(i) *Mammals, including both domestic and wild animals* — Despite a high protein potential, *H. matronalis* reportedly has low palatability for browsing or grazing animals (USDA, NRCS 2008c).

(ii) *Birds and other vertebrates* — Seeds are reportedly eaten and dispersed by ground-foraging birds (USDA Forest Service 2006).

(iii) *Insects* — Of 13 cruciferous weed species studied under field conditions in Ontario for infestation by the cabbage maggot, *Hylemya brassicae* (Bouché) (Diptera: Anthomyiidae), *H. matronalis* was among five species that elicited oviposition and supported development of the larvae (Nair et al. 1973, 1976). Also in Ontario, the introduced moth, *Plutella porrectella* L. (Lepidoptera: Plutellidae), a close relative of the diamond-back moth, *Plutella xylostella* L., completed two generations per year and overwintered as early-instar larva within apical buds of *H. matronalis*, its only recorded host plant in North America (Smith and Sears 1984). *Hesperis matronalis* is also the principal larval food plant of this moth in Great Britain, which pupates on the underside of the leaves (Kimber 2007). In Great Britain, *H. matronalis*, although poor for larval survival, attracted more eggs from the seed-feeding orange tip butterfly *Anthocharis cardamines* L. (Lepidoptera: Pieridae) compared with the more suitable and abundant host *Alliaria petiolata*; higher egg deposition was attributed to its large, persistent inflorescences (Courtney 1982). In a study of the “edge effect” where outlying host plants received proportionately more attention from insect herbivores, *H. matronalis* not only attracted an unusually large number of eggs from *A. cardamines*, but also deposits from a competing pierid butterfly *Artogeia napi* L. (Courtney and Courtney 1982). *Hesperis matronalis* was also a reported host of *Anthocharis cardamines* in Sweden (Wiklund and Åhrberg 1978). In northern Scotland, *H. matronalis* was a host of *Rhigognostis incarnatella* Steudel (Lepidoptera: Yponomeutidae) and showed leaf damage from the larvae (Agassiz and Langmaid 1992).

In a Danish study of host plant relationships of *Phyllotreta nemorum* L. (Coleoptera: Chrysomelidae) (Nielsen 1977), no larvae were found on *H. matronalis* under natural field conditions and no larvae survived on this species when transferred artificially. The Euro-Anatolian pollen-beetle *Meligethes matronalis* Audisio & Spornraft (Coleoptera: Nitidulidae) is distinguished from closely related species by its strict host association with *H. matronalis* in early summer (Audisio et al. 2001). In Serbia, *H. matronalis* served as host to the pollen beetle, *Meligethes reitteri* Schilsky (Coleoptera: Nitidulidae) (Stevanovich and Audisio 1999). In northwestern Europe, the weevil *Ceutorhynchus inaeffectatus* Gyll.

(Coleoptera: Curculionidae) is monophagous on *H. matronalis*, feeding on leaves in the spring and later on buds, flowers and pods, where the larvae develop (Larsen et al. 1992). Volatiles from the flowers seem to be important in initiating oviposition by this weevil in flowers and on pods (Nielsen et al. 1995). In Central Europe, *H. matronalis* has been subject to fruit and stem galls caused by *Ceutorhynchus inaeffectatus* and to leaf curl caused by the aphid *Aphis brassicae* L. (Homoptera: Aphididae) (Schultze-Motel 1986).

(iv) *Nematodes and other invertebrates* — *Hesperis matronalis* is not a susceptible host of nematodes, but the beet-cyst nematode *Heterodera schachtii* Schm. has a limited parasitic relationship in which larvae can reach the third but almost never the fourth larval stage on this species and, in fact, *H. schachtii* populations showed high declines (66%) under *H. matronalis* compared with 38% under cereals (Ouden 1956; Shepherd 1959). A 9-yr field study in the former Czechoslovakia also found that *H. matronalis* resulted in decreased numbers of viable *Heterodera schachtii* cysts in the soil (Vinduška 1978). In studies of various crops in the Netherlands, roots of *H. matronalis* were invaded by the yellow beet cyst eelworm, *Heterodera* spp., but the nematode did not multiply in them (Anonymous 1976). Field experiments in the Netherlands, which tested host specificity of green manure crops to the northern root knot nematode *Meloidogyne hapla* Chitwood, found that the nematode population decreased by 80–100% under *H. matronalis* and *Tagetes minuta* L., whereas it remained unchanged or increased under all other dicot species tested (Lamers and Roosjen 1993).

#### (b) Diseases

(i) *Fungi* — *Hesperis matronalis* is not listed as a host of fungal pathogens in Canada (Ginns 1986), although Connors (1967) reported downy mildew, *Peronospora parasitica* (Pers. ex Fr.) Fr. from a cultivated plant in Ontario and *Rhizoctonia* sp. associated with basal rot and wilt in a cultivated plant from Saskatchewan. Reports from the United States, dating between 1923 and 1959, include *Albugo candida* (Pers.: Fr.) Kuntze from New York, *Peronospora parasitica* from New York, Pennsylvania and Wisconsin, and *Plasmopara brassicae* Wor. (probable error for *Plasmodiophora brassicae* Wor.) from New Jersey (Farr et al. 2006). All other reports on *H. matronalis* (Farr et al. 2006) are from Europe or western Asia. These include *Erysiphe communis* (Wallr.: Fr.) Link (= *Erysiphe pisi* DC.) from Finland; *Erysiphe cruciferarum* Opiz ex L. Junell from Austria, Belarus, the former Czechoslovakia, Finland, France, Germany, Hungary, Italy, Norway, Poland, Romania, Sweden, Switzerland and the former USSR; *Oidium* sp. from the former USSR; *Peronospora hesperidis* Gäum. from the Czech Republic; *P. parasitica* from Scotland; *Ramularia matronalis* Sacc. (= *R. armoraciae* Fuckel) from Sweden; and *Septoria hesperidis* (no

authority located, possible error for *Peronospora hesperidis* Gäum.) from Armenia. *Hesperis matronalis* has also been reported among hosts to *Ramularia armoraciae* (location not specified) (David 2004). In the United Kingdom, *H. matronalis* has been reported as parasitised by *Erysiphe cruciferarum* and infected or damaged by *Leptosphaeria maculans* (Desm.) Ces. & de Not. (Storey 2006). In Central Europe, *H. matronalis* is subject to infection by *Plasmodiophora brassicae*, a cause of club root disease (Schultze-Motel 1986). In Italy, *H. matronalis* was a newly identified host of the wilt disease *Verticillium dahliae* Kleb. (Frisullo et al. 1987).

(ii) *Bacteria* — No information was located.

(iii) *Viruses* — In Canada and the northern United States, *H. matronalis* is an alternate host for beet, cauliflower, radish, squash and turnip mosaic viruses (Royer and Dickinson 1999). Symptoms of turnip yellows disease or turnip mosaic potyvirus TuMV exhibited by *H. matronalis* and other infected species include chlorotic local lesions, mosaic, mottling, puckering or rugosity (Brunt et al. 1996). In Ontario, the common turnip mosaic virus strain (TUMV-S1) does not infect *Hesperis matronalis*; however, the strain of turnip mosaic virus isolated from *Alliaria petiolata* (TuMV-A1) can be transmitted to *H. matronalis* by aphids in the field and cause mosaic mottling, flower flecking and stunting (Stobbs and Van Schagen 1987; Stobbs and Stirling 1990). In British Columbia, turnip mosaic virus (TuMV), cucumber mosaic virus (CMV) and ribgrass mosaic virus (RMV) were isolated from both cultivated and wild specimens of *H. matronalis* (Ford et al. 1988). CMV and RMV produced only local lesions or no symptoms, while TuMV produced local lesions and severe mosaic symptom that persisted as the leaves aged; more severe symptoms such as stunting and leaf curling were induced by simultaneous inoculation with TuMV and either CMV or RMV, and marked stunting and occasional necrosis followed inoculation with all three viruses. No seed transmission of any of the viruses occurred in seedlings grown from infected plants (Ford et al. 1988). *Hesperis matronalis* was not among inoculated hosts susceptible to the cauliflower mosaic virus, but was one of two symptomless hosts of a Quebec strain of CMV (Berkeley and Tremaine 1954). In a Florida study, a distinct strain of TuMV, originally isolated from *H. matronalis* in Ontario, was designated TuMV-D on the basis of capsid and cylindrical inclusion proteins (McDonald and Hiebert 1975). Two strains of CMV were reported to cause mosaic disease of *H. matronalis* in a Wisconsin study (Pound and Walker 1948).

In Germany, tests showed that the aphid-transmitted turnip yellows virus disease could be transmitted to ornamental plants, including *H. matronalis* (Heinze 1967). In Central Europe, *H. matronalis* is subject to

cabbage ringspot, stock virus, and cucumber and watermelon mosaic diseases (Schultze-Motel 1986). In Hungary, the species was a symptomless host of tomato black ring virus TBRV (Shukla and Schmelzer 1971). In the former Yugoslavia, *H. matronalis* was a host of the cauliflower mosaic virus CaMV (Mamula and Milicic 1968). In Italy, *H. matronalis* was among medicinal and aromatic plants infected by aphid-transmitted viruses, among them CMV, broad bean wilt fabavirus (BBWV) and TuMV (Bellardi and Rubies-Autonell 1997; Bellardi et al. 1997). Symptoms of combined infections by TuMV and CMV included pustules, malformation and chlorotic yellowing of the leaves, and reduced growth of the plant (Bellardi et al. 1997).

(iv) *Phytoplasmas* — In Alberta, a new yellows disease caused by an unidentified phytoplasma (a mycoplasma-like organism) was found in the phloem tube cells of *H. matronalis*, and produced such symptoms as chlorosis, stunting, a bladder-like deformation of the seed pods and phyllody (abnormal development of leaves from petals) of the inflorescences (Chang et al. 1996). These pathogens are believed to have been carried by leafhopper vectors migrating from the midwestern states into Alberta and is the first report of a phytoplasma being associated with disease in *H. matronalis*.

(c) *Higher Plant Parasites* — No information was located.

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