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**Leucanthemum vulgare** Lam.

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Clements, D. R., Cole, D. E., Darbyshire, S., King, J. and McClay, A. 2004. The biology of Canadian weeds. 128. *Leucanthemum vulgare* Lam. Can. J. Plant Sci. 84: 343–363. *Leucanthemum vulgare* Lam. (Asteraceae), known as ox-eye daisy, is a familiar perennial herb with white ray florets and yellow disc florets. It commonly inhabits roadside verges, pastures and old fields from Newfoundland to British Columbia, and also as far north as the Yukon Territory. Introduced from Europe, *L. vulgare* was well established in North America by 1800. The Canadian distribution of *L. vulgare* has expanded in many areas recently, particularly in western Canada. It can form dense populations that may reduce diversity of natural vegetation or pasture quality, and also serves as a host and reservoir for several species of polyphagous gall-forming *Meloidogyne* nematodes that feed on crops. It is considered a noxious weed under provincial legislation in Quebec, Manitoba, Alberta and British Columbia, as well as under the Canada Seeds Act. Control efforts are sometimes complicated by difficulties in distinguishing ox-eye daisy from some forms of the commercially available Shasta daisy (*L. × superbum*).

**Key words:** *Leucanthemum vulgare*, *Chrysanthemum leucanthemum*, *Leucanthemum ircutianum*, *Leucanthemum × superbum*, ox-eye daisy, CHYLE, marguerite blanche, Shasta daisy, Asteraceae, Compositae, pasture management


**Mots clés:** *Leucanthemum vulgare*, *Chrysanthemum leucanthemum*, *Leucanthemum ircutianum*, *Leucanthemum × superbum*, marguerite blanche, achyleux, ox-eye daisy, marguerite Shasta, Astéracées, Compositae, gestion des pâturages

1. Names


Asteraceae, Compositae, aster family (composite family), Astéracées, composites, tribe Anthemideae.
An article by Heywood and Humphries (1977) brought together a considerable amount of information pointing to the unnatural circumscription of many of the genera in the tribe Anthemideae. Bremer and Humphries (1993) conducted a detailed cladistic analysis of the tribe and further refined generic concepts into monophyletic groups. In a broad taxonomic sense, the genus *Chrysanthemum* contains about 200 species (Willis 1966), but with the assignment of many species to other genera, *Chrysanthemum* is now considered to contain only 2-4 annual species native to the Mediterranean area (Maberly 1987; Soreng and Cope 1991; Bremer and Humphries 1993). This realignment of the generic limits has been fuelled by evidence of relationships accumulated from seed anatomy and morphology, embryology, hybridization, and phytochemistry (Heywood and Humphries 1977; Bremer 1994). Summaries of the taxonomic realignment and nomenclature of the genus and its relatives are given by Anderson (1987) and Soreng and Cope (1991) and a key to the genera of the Anthemideae is given by Bremer and Humphries (1993). The genus name that should be applied to ox-eye daisy is *Leucanthemum* Mill. This genus is considered to have about 26-33 species of perennial herbs that have red (or reddish brown) root tips. Species of the genus occur naturally in Europe, North Africa and southwestern Asia. Under the International Code of Botanical Nomenclature, tautonyms are not allowed and so the name *Leucanthemum vulgare* must be used for ox-eye daisy.

2. Description and Account of Variation

(a) Physical description — *L. vulgare* is a glabrous to sparingly pubescent shallow-rooted perennial herb with conspicuous terminal flower heads (Fig. 1). Roots arise from a short creeping roostock with a curved main stem with many adventitious roots. Underground stems contain water-soluble red pigments in the xylem and pith tissues. Either short rhizomes or stout root crowns may give rise to stems. Seedlings (Fig. 2) bear cotyledons that open above the soil surface; the hypocotyl does not continue to elongate above the ground (Fig. 2A). Stems are erect, simple or slightly branching with usually 1-2 per plant, but may form thick clusters (Fig. 2B). The stems arise from stout roostocks and are decumbent at their base, usually 30-90 cm in height, reaching a maximum height of 2 m. Leaves are sparingly pubescent and three-nerved. Basal leaves are stalked, spatulate (spatula-shaped) to obovate (egg-shaped with the narrower end at the base), and irregularly dentate (sharp teeth) to regularly crenulate (rounded teeth) (10-25 cm long and 3-7 cm wide). Stem leaves are smaller, alternate, mostly sessile, obovate to narrowly lanceolate (lance head-shaped) becoming ligulate (strap-like) apically with coarse teeth and the base usually deeply lobed or fringed with slender segments (fimbriate). Flower heads (capitula) are erect, usually solitary on long terminal peduncles and are (2) 2.5-7.5 cm in diameter, with 1-15 inflorescences per plant. The flower heads are mainly heterogamous with female ray florets and hermaphrodite disk florets. White ray florets (Fig. 1B) number 15 to 30 per head and are 0.5-2.4 cm long, ligulate, the apex rounded or with 3 small teeth; the 400 to 500 yellow disk florets (Fig. 1C) are 4 mm long and tubular forming a dense, slightly domed centre. The numerous involucral bracts (Fig. 1E) are green, edged with brown, and surround the base of each head. Plants with discoid heads and lacking ray florets have been found in New Hampshire (Bogle 1983). Fruits (Fig. 1D) from both disk and ray florets are gray-silvery obovoid to cylindrical achenes (cypselas) with 5-10 equal raised ribs and are 2-3 mm long and 0.8-1 mm wide. The pappus is absent or reduced to a crown. Pollen grain structure was described and illustrated by Nilsson et al. (1977). When crushed, all parts of the *L. vulgare* plant have a disagreeable sour odour (Alex 1992).

*Leucanthemum vulgare* Lam. var. *vulgare* has a chromosome number of 2n = 18; *L. vulgare* var. *ircitanum* (DC.) Krylov is a tetraploid with 2n = 36 (Table 1). Both chromosome races are present in Canada (Mulligan 1958).

(b) Distinguishing features — Although the flower of ox-eye daisy clearly distinguishes it from most herbs, there are other plants with white ray florets and yellow disk florets including scentless chamomile, *Matricaria perforata* Mérat [= *Matricaria maritima* L. var. *agrestis* (Knaf) Wilmott], and stinking mayweed, *Anthemis cotula* L. (Frankton and Mulligan 1987). The flower heads of *M. perforata* are smaller (2-3 cm in diameter) and the leaves are fern-like and finely divided (Cranston et al. 1996). *Anthemis cotula* can be distinguished by the distinctive stem hairs below the smaller flower heads as well as the more finely dissected leaves. It also has a distinctive odour. English daisy (*Bellis perennis* L.) has a squat growth form, 2-20 cm tall, with elliptic to oval or circular leaves (Pojar and MacKinnon 1994). Some fleabanes (*Erigeron* spp.) also possess flowers with similar coloration, but the ligulate flowers are much narrower. Populations of *L. vulgare* can be detected by aerial remote sensing when in bloom (Lass and Callihan 1997).

The popular horticultural plant known as Shasta daisy, *Leucanthemum × superbum* (J.W. Ingram) D.H. Kent, was developed by Luther Burbank early in the nineteenth century. It is presumed by most workers to be a hybrid between *L. lactuca* and *L. maximum* (e.g., Ingram 1975). Hornbeck (1982), however, indicated from Burbank's records that the development of Shasta daisy was much more complicated, involving "wild" plants of *L. leucanthemum* from North America, *L. maximum*, *L. lactuca* and *Nipponanthemum nipponicum* (Maxim.) Kitam. (= *Chrysanthemum nipponicum* Maxim.). Since it was originally developed from hybridization of species mostly from within the *L. vulgare* complex and because many cultivars have been produced subsequently (Hornbeck 1982), some varieties (e.g., cultivar May Queen) can appear similar to ox-eye daisies, especially tetraploid forms of the latter. The thicker and more succulent leaves of Shasta daisy are coarsely and regularly toothed or crenulate and not deeply toothed or lobed as in ox-eye daisy. Stem leaves are not greatly reduced apically and, in the vast majority of varieties, are not lobed, fimbriate or pinnatifid at their base. Lower leaves are oblanceolate to 30 cm long including the petiole, which, if present, is usually winged. Upper leaves are lanceolate and sessile or slightly clasping. Flower heads are larger than in ox-eye daisy, being up to 10 cm or more across.

Shasta daisy is a hardy and popular garden plant in Canada. In spite of this, it rarely escapes cultivation and when established does not seem to persist. The only report that we have found of establishment in Canada is that by Cayouette et al. (1983) at Sainte-Foy, Québec (cf. Scoggan 1979; Boivin 1966),
where it was probably introduced through dumping of garden waste (J. Cayouette, pers. comm.). It may be that the plant reported by Kucyniak (1945) from Lachine, Québec, is also a form of *L. × superbium*.

(c) *Intraspecific variation*—The ox-eye daisy is part of a large species complex that ranges through most of Europe and western Asia. The remarks by Heywood (1976) in *Flora Europaea* provide an excellent summation of present taxo-
Fig. 2. Leucanthemum vulgare. A. Seedling with cotyledons and first two true leaves; bar = 1 cm. B. Young rosette; bar = 1 cm.

nomic understanding of this group. “An extremely variable species or species-complex which has been divided into a large number of taxa (given the rank of variety, subspecies or species) many of which are of restricted occurrence. The discovery of extensive cytological variation has led to intensive cytotaxonomic studies of the populations in various parts of Europe. Although some regional and local correlations between chromosome number and morphological variation can be detected, no overall treatment is at present possible and the recent tendency to recognize the various components of this complex as species is certainly premature and cannot be justified on practical grounds with our present knowledge. Since, however, it is desirable to draw attention to the main variants that deserve some recognition, they are listed below.” Fifteen of these named “variants” are then listed without a key for their identification: Leucanthemum praecox (Horvati) Horvati, L. leucoplepis (Briq. & Cavill.) Horvati, L. adustum (Koch) Gremli, L. heterophyllum (Willd.) DC., L. cuneifolium H.J. Coste, L. maximum (Ramond) DC., L. paliens (Gay) DC., L. crassifolium (Lange) Willk., L. subglaucum De Laramb., L. meridionale Legrand, L. laciniatum Huter, Porta & Rigo, L. delarbrei Timb.-Lagr., L. lacustre (Brot.) Samp., L. sylvaticum (Hoffmanns. & Link) Nyman, L. pluriflorum Pau.

Of the segregates in the L. vulgare species complex, the name L. praecox has sometimes been applied to tetraploid races of ox-eye daisy in Canada, although Heywood (1976) states that this taxon is diploid. The name L. vulgare var. ircutianum (DC.) Krylov was applied to tetraploid forms by Böcher and Larsen (1957). In the Canadian literature this latter name has sometimes been applied to tetraploids, or, if the name L. praecox is used, L. ircutianum is listed as a synonym. There are differences in morphology and flowering time between the different chromosome races (Fernald 1903; Mulligan 1958), but intermediate populations are known in Europe. Taxonomic distinction at a subspecific rank between the chromosome races in Canadian populations seems more reasonable than species ranking, at least until there is a better understanding of the entire L. vulgare species complex. Tzelev (1995) noted that throughout the range of the species there are many regional biotypes, varying in morphological characteristics such as pubescence and leaf shape. He discounted all these forms (including var. ircutianum) as being without taxonomic significance. Table 1 gives the main distinguishing characteristics between the two chromosome races present in Canada.

Intraspecific taxonomy of ox-eye daisy in Canada has been confused by the varying applications of the name var. pinnatifidum. North American material of the diploid forms has sometimes been referred to under the name L. vulgare var. pinnatifidum (Lecocq & Lamotte) Moldenke (= C. leucanthemum var. pinnatifidum Lecocq & Lamotte) (e.g., Scoggin 1979). Böcher and Larsen (1957), however, stated that this taxon (described from southern France) is tetraploid and might be most closely allied to L. vulgare var. ircutianum. Löve and Bernard (1959) recognized tetraploid plants as a distinct species, and applied the name L. ircutianum var. pinnatifidum (Lecocq & Lamotte) D. Löve & J.-P. Bernard to this material. Under the impression that the tetraploid form represented the type, Fernald (1903) coined the superfluous name C. leucanthemum var. subpinnatifidum Fernald to apply to the diploid forms introduced to North America.

Ox-eye daisy is an extremely variable species. A variant with shallower leaf indentation is occasionally observed in the Atlantic provinces (Frankton and Mulligan 1987). Distinct maritime and high mountain ecotypes are found in Europe (Salisbury 1961). Bogle (1983) found a plant in New Hampshire with inheritable discoid heads without ray florets. Five subspecies and many additional variants were recognized by Howarth and Williams (1968) in central Europe. Böcher and Larsen (1957) regarded diploid (2n = 18) and tetraploid (2n = 36) forms as separate species, L. vulgare and C. ircutianum, respectively. The tetraploid race has a slightly larger flower head diameter and regularly toothed lower leaves, whereas the diploid race has irregularly alternating lobes or teeth on the lower leaves (Table 1). Kumar (1982) also distinguished between the two distinct groups of L. vulgare by flower size. He theorized that tetraploidy might have arisen through the diplloidization of autoploids rather than by hybridization and subsequent doubling of chromosomes. Mulligan (1968), examining diakinesis in pollen mother cells of tetraploid plants in Quebec, found one to four quadrivalents, leading him to conclude that they were probably autotetraploid. Böcher and
Counts from garden forms have been reported as in the strict sense, especially the decaploids. Although the correlation between chromosome number and maximum

Some of these counts may be based on garden forms of 90, 126, 148, 154, 160 and 171 by Dowrick (1952), (often reported under the name Chrysanthemum (sensu lato) (Dowrick 1952), a significant difference in pollen size was found between ox-eye daisy and Shasta daisy (Figs. 3–4). Following the methodology of Mulligan (1958), we repeated the measurements on the inside diameter of pollen grains from specimens at DAO previously studied and annotated by him. Diameters were found to range from 11.7 to 23.4 μm (16.7 μm average) for diploid ox-eye daisy (21 collections), from 13.7 to 27.3 μm (18.9 μm average) for tetraploid ox-eye daisy (10 collections), and from 13.7 to 42.9 μm (26.5 μm average) for Shasta daisy (27 collections not studied by Mulligan). Chromosome counts are not known for the cultivated forms examined, but the large size of pollen cells clearly reflects a significant difference in ploidy. Unlike the data reported by Mulligan (1958), a substantial overlap in pollen size range was observed (Fig. 4A), although mean size was significantly different (99% LSD) between ploidy levels (Fig. 4B). Although only 31 specimens were examined by us, compared with more than 191 by Mulligan, the data presented here are consistent with the overlapping size ranges between ploidy levels reported by Böcher and Larsen (1957).

Some cultivars sold as Shasta daisy, such as May Queen, are similar to tetraploid forms of ox-eye daisy, and may in fact be a sterile form of that taxon. The average pollen size of May Queen (20.7 μm; range 15.6–27.3 μm) was within the range of both ploidy levels of ox-eye daisy. Ox-eye daisy has well formed pollen, which stains well with lactophenol cotton blue (viability estimated at about 90%) (Fig. 3 A,B). May Queen, on the other hand, was found to have many misshapen and poorly stained pollen grains, suggesting a viability of much less than 50%. Furthermore, May Queen does not appear to produce viable seeds. Nurseries and gardeners do not report seed production in any of the varieties of Shasta daisy available in Canada. However, viable seeds are occasionally produced in some cultivars (Ingram 1975; Hornback 1982). The cultivation of diploid

<table>
<thead>
<tr>
<th>Category</th>
<th>Leucanthemum vulgare Lam. var. vulgare</th>
<th>Leucanthemum vulgare var. ircutianum (DC.) Krylov</th>
</tr>
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<tbody>
<tr>
<td>Chromosome number</td>
<td>Diploid, 2n = 18</td>
<td>Tetraploid, 2n = 36</td>
</tr>
<tr>
<td>Heads (capitula)</td>
<td>Usually solitary; 4–7 cm in diameter</td>
<td>Often more than one per stem; 5–7.5 cm in</td>
</tr>
<tr>
<td>Basal leaves</td>
<td>Spatulate, coarsely and irregularly toothed or lobed, often fimbriate basally</td>
<td>Spatulate-ovate, closely and regularly crenate, rarely lobed or fimbriate basally</td>
</tr>
<tr>
<td>Lower stem leaves</td>
<td>Narrowly spatulate, irregularly serrate or dentate, lobed or shallowly pinnate basally</td>
<td>Broadly spatulate to broadly ovate, regularly crenate or dentate, coarsely toothed basally with spreading teeth</td>
</tr>
<tr>
<td>Middle and upper stem leaves</td>
<td>Narrowly oblone or oblanceolate, irregularly coarsely toothed, usually distinctly fimbriate or somewhat pinnate (subpinnatifid) basally</td>
<td>Oblong to oblanceolate, regularly coarsely, toothed larger teeth basally but not fimbriate or pinnate</td>
</tr>
<tr>
<td>Pollen size</td>
<td>11.7–23.4 μm (inside diameter)</td>
<td>13.7–27.3 μm</td>
</tr>
<tr>
<td></td>
<td>16.7 μm (average)</td>
<td>18.9 μm (average)</td>
</tr>
</tbody>
</table>

Larsen (1957) found that the diploids were more prevalent in Northwestern Europe whereas the tetraploids dominated in northeastern Europe and the southern European mountains. In some areas such as Norway and central Europe, the races are intermixed (Favarger and Villard 1965; Knaaben 1982), but Favarger and Villard (1965) found that diploids begin flowering earlier than tetraploids and that the races occupy slightly different habitats. Fernald (1903) first reported the morphologically different tetraploid form as being restricted to eastern Canada and noted its similarity to the common form in central Europe. Mulligan (1958, 1968) found that the diploid race was most prevalent and widespread throughout North America. He found that the tetraploid race was locally common only in southern Quebec and Nova Scotia, but reported examining specimens collected from Labrador, Ontario, Manitoba, British Columbia, Minnesota and Washington. Lover and Bernard (1959) reported that the tetraploid form was most common at Otterburne, Manitoba, while the diploid was found to be rare in that area. Hexaploid and octaploid races occurring in Europe have sometimes been considered separate species, Leucanthemum graminifolium (L.) Lam. (= L. montanum (L.) DC.) and L. heterophyllum, respectively (Favarger 1959).

Mulligan (1958), reported that pollen size was different between plants of varying ploidy level (diploid: 16.3–19.5 μm; tetraploid: 19.5–22.8 μm; and hexaploid: 22.8–24.4 μm). Pollen size was measured from specimens at the DAO herbarium of cultivated Shasta daisy and some of the ox-eye daisy voucher specimens from Mulligan’s chromosome study (Mulligan 1958). The two purported parents of Shasta daisy (L. maximum and L. lacustre) are high polyploids, 2n = 90 and 198, respectively (Heywood 1976; Dowrick 1952) and chromosome counts of cultivated forms (often reported under the name C. maximum) are also high. Counts from garden forms have been reported as 2n = 85, 90, 126, 148, 154, 160 and 171 by Dowrick (1952), 2n = 153 by Shimotomi (1938) and 2n = 54 by Baksay (1960). Some of these counts may be based on garden forms of L. maximum in the strict sense, especially the decaploids. Although the correlation between chromosome number and cell size in polyploid series between species can be misleading, and chromosomes decrease in size with increasing ploidy in Chrysanthemum (sensu lato) (Dowrick 1952), a significant difference in pollen size was found between ox-eye daisy and Shasta daisy (Figs. 3–4). Following the methodology of Mulligan (1958), we repeated the measurements on the inside diameter of pollen grains from specimens at DAO previously studied and annotated by him. Diameters were found to range from 11.7 to 23.4 μm (16.7 μm average) for diploid ox-eye daisy (21 collections), from 13.7 to 27.3 μm (18.9 μm average) for tetraploid ox-eye daisy (10 collections), and from 13.7 to 42.9 μm (26.5 μm average) for Shasta daisy (27 collections not studied by Mulligan). Chromosome counts are not known for the cultivated forms examined, but the large size of pollen cells clearly reflects a significant difference in ploidy. Unlike the data reported by Mulligan (1958), a substantial overlap in pollen size range was observed (Fig. 4A), although mean size was significantly different (99% LSD) between ploidy levels (Fig. 4B). Although only 31 specimens were examined by us, compared with more than 191 by Mulligan, the data presented here are consistent with the overlapping size ranges between ploidy levels reported by Böcher and Larsen (1957).
and tetraploid races of ox-eye daisy is also popular in Canadian gardens. Not only is ox-eye daisy sometimes dug from wild populations, but it is also available from many seed companies. Gardens observed with transplanted ox-eye daisy, rather than Shasta daisy, usually have evidence of viable seed production; volunteer plants tend to escape the beds and spread readily.

(d) Illustrations—A mature plant, ray and disk florets, achenes and involucral bracts are illustrated in Fig. 1. Seedlings are illustrated in Fig. 2. Pollen variation is illustrated in Fig. 3. An illustration of a heavy infestation of *L. vulgare* is provided in Fig. 5. Additional illustrations are found in Frankton and Mulligan (1987).

### 3. Economic Importance

(a) Detrimental—*L. vulgare* does not generally cause major problems in annual crops in North America because its shallow root system is vulnerable to cultivation (Olson and Wallander 1999). In general, the ecological, environmental, economic and sociological impacts of *L. vulgare* are not well known (Olson and Wallander 1999). Holm et al. (1997) reported *L. vulgare* as a weed of 13 crops in 40 countries, in addition to its role as a major pasture weed. Contrary to Holm et al. (1997), *L. vulgare* is not usually reported to be a problem in annual crops in Canada. It is known to infest cereals in Austria and Tunisia, legumes in Tunisia and corn (*Zea mays* L.) in South Africa (Holm et al. 1997). Smith et al. (1999) found that in England, where *L. vulgare* was sown into uncropped field margins being
managed for biodiversity, it occasionally spread a short distance into adjacent cropped areas. However, they did not consider this to present any risk to crop production. It readily populates pastures, rangelands and roadside areas, where it reduces plant species diversity and hay or forage production (Olson and Wallander 1999). Fields become white with the flower heads of *L. vulgare* (Fig. 5). Once plants have established, the achenes may be spread widely as a contaminant in pasture seeds, hay or manure (Mitich 2000). Because of the relatively shallow root system of *L. vulgare* in comparison to those of perennial grasses, large populations of *L. vulgare* render areas vulnerable to soil erosion and deplete soil organic matter. In general, *L. vulgare* is avoided by cattle, and thus grazing encourages its proliferation (Olson and Wallander 1999). Milk from dairy cattle that have consumed *L. vulgare* may have a disagreeable taste (Frankton and Mulligan 1987). Gall-forming nematodes (*Meloidogyne* spp.) will use *L. vulgare* as a host (Townshend and Davidson 1960, 1962; Davidson and Townshend 1967; Belair and Benoit 1996; Mauch and Ferraz 1996), and thus *L. vulgare* may act as a reservoir for these pests (see also section 13). *L. vulgare* is one of the “priority exotic invasive species” for control in Yellowstone National Park (Ottilf et al. 2001).

The mosquito *Aedes aegypti* is attracted to the odour of *L. vulgare* flowers and feeds on their nectar (Jepson and Healy 1988), but a methylene chloride extract of the flowers is not attractive to another mosquito species, *Culex pipiens* L. (Mauer and Rowley 1999). *L. vulgare* is a strong sensitizer in guinea pig tests, suggesting that it is likely to cause allergic contact dermatitis (Zeller et al. 1985). Many species in the tribe Anthemideae produce sesquiterpene lactones and this class of compounds has been implicated as a cause of contact dermatitis (Mitchell et al. 1971). A few cases have been reported, both in Europe and North America, where ox-eye daisy has been a cause of contact dermatitis (Mitchell and Rook 1979). Although the pollen is not airborne, occasional cases of hay fever symptoms have been reported after direct contact (Wodehouse 1935).

There are increasing concerns that escaping Shasta daisies may hybridize with *L. vulgare*, or be confused with *L. vulgare* where they grow. An “ox-eye daisy task force” based in Alberta made the following recommendations to horticulturalists in 2000: prevent seeding of all white daisies, avoid buying wildflower seed mixes, buy Shasta daisy grown from cuttings—not seeds, choose other types and colours of daisies or perennials, do not exchange any "naturalized" daisies, and set up displays in garden centres and other appropriate locations to educate people about invasive plants and the concern over ox-eye daisy specifically (Cole, pers. obs.).

(b) Beneficial—The aesthetic appeal of *L. vulgare* is well known. Mitich (2000) wrote that it has been “beloved by prince and peasant in the Orient and the Western world” as seen in the innumerable folk names it has been given throughout the world. It is often intentionally spread as an ornamental and grown in decorative gardens (Tzvetev 1995; Holm et al. 1997; Olson and Wallander 1999) and is a reported parent of the
Shasta daisy. It is often included in commercial "wild-flower" seed mixes, and is well suited for bouquets.

*L. vulgare* has been used to produce both infusions prescribed for internal disorders and lotions to apply to external wounds and sores (le Strange 1977). Fresh flowers distributed on floors were used in Europe during the medieval period to repel fleas. Taken internally, extracts of *L. vulgare* are valued for their antispasmodic, diuretic and tonic qualities. It was utilized in England for treatment of running eyes, cholera, ulcers and "as an application to the secret parts" (Culpeper 1953). *L. vulgare* infusions are still prescribed by herbalists for treatment of asthma, whooping-cough and nervous excitability, and lotions are recommended for ulcers and sores (le Strange 1977).

Young leaves are occasionally incorporated into salads (le Strange 1977) and a 100 g sample of leaves from *L. vulgare* contains more than 500 units of vitamin A (Zennie and Ogzewalla 1977). More mature leaves have an acid flavour and the flowers are bitter. According to Fernald et al. (1958), "Some European authors state that the young leaves of the Ox-eye Daisy make a palatable salad.... The odor of our plants suggests, however, that fondness for this particular salad is an acquired taste."

Areas with large populations of *L. vulgare* provide habitat for wildlife. For example, spiders use them as hunting sites (Morse 1999). *L. vulgare* is one of the species commonly sown as a means of maintaining biodiversity within agricultural land, such as in "ecological compensation areas" in Switzerland (Keller and Kollmann 1999) and in species-poor grassland in England (Coulson et al. 2001). It is also one of the species used in wildflower seed mixes sown on former arable land, roadsides and land adjacent to developments in the United Kingdom (Spearman et al. 2000). The flowers attract some beneficial insects; *L. vulgare* is among the most attractive plants to adult syrphid flies, whose larvae feed on aphids (Weiss and Stettmer 1991). However, the flowers were not found not to be a suitable nectar source for the parasitoid wasp *Pimpla turionellae* L. (Wickers et al. 1996). Powdered inflorescences of *L. vulgare* added to grain at 2% are effective repellents for grain weevil, *Sitophilus granarius* L., and rice weevil, *S. oryzae* L. (Ignatowicz 1998). Because it is intolerant of heavy metals, *L. vulgare* has been successfully used to monitor levels of Pb, Zn, Mn, Cu, Cr and Cd along a heavily used highway in Italy (Badino et al. 1998).

(c) Legislation—*L. vulgare* is classed as noxious within Alberta under the Alberta weed control act (Anonymous 1991) and in Manitoba under the Noxious Weed Act (Anonymous 1996). In British Columbia, *L. vulgare* is classified as noxious within the Cariboo, North Okanagan and Peace River districts, but not within other parts of the province (Cranston et al. 1996). It is listed as a noxious weed in Quebec in the Agricultural Abuses Act (Division IV—Noxious Weeds) whether it occurs in agricultural lands (cultivated fields and pastures) or in ruderal habitats (transportation corridors, vacant lots, etc.) (Anonymous 1981). In the Canada Seeds Act (Agriculture Canada 1986) it is listed as a Class 2 Primary Noxious Weed Seed for most crop seed commodities and as a Class 5 Noxious Weed in turf and groundcover seed commodities. No *L. vulgare* seed is permitted in Canada Foundation, Registered or Certified seed of most crop categories. It has also been declared noxious in other parts of the world (Holm et al. 1997).

4. Geographical Distribution

The present distribution of *L. vulgare* is throughout southern Canada from Newfoundland and Labrador to British Columbia, and as far north as Dawson City in the Yukon Territory (Fig. 6). Porsild and Cody (1980) reported it from "near Ft. Smith", but the specimen on which this report was
based was not located. Other than this reference, it has not been recorded from the Northwest Territories or Nunavut. As recently as the 1980s, it was referred to as "rare in most of Alberta" (Frankton and Mulligan 1987). It is now fairly common in western, west-central and northeastern Alberta, and also occurs in the Peace River region (L. Darwent, pers. comm.; Frankton and Mulligan 1987). It is common in southern areas of British Columbia, Ontario and Quebec and in the Maritime Provinces. In a weed survey of spring cereals in New Brunswick conducted in the late 1980s, L. vulgare occurred in 54% of fields surveyed and ranked fourth in terms of relative abundance (Thomas et al. 1994). Frick et al. (1990), surveying weeds in southwestern Ontario under different tillage regimes, found ox-eye daisy at low frequencies in soybean fields under conventional tillage (1.4% frequency). It was not detected in reduced tillage systems nor in corn or wheat crops.

Widely distributed throughout the United States, it is especially common in the northeastern states and in northern states down to California (Muenscher 1953), but is less common in southern states (Olson and Wallander 1999). Taylor (1990) referred to L. vulgare as the most common roadside weed in the Pacific Northwest, where the range of L. vulgare continues to expand (Olson and Wallander 1999, R. Cranston, pers. comm.).

Native to Eurasia, L. vulgare is found from northern Italy to Scandinavia (Howarth and Williams 1978) and extends eastward through Russia and central Asia (Hultén and Fries 1986). From Europe, it has been introduced to many other parts of the world, including North America, South America, New Zealand, Australia, Hawaii, Tunisia, China and Pakistan (Holm et al. 1979).

5. Habitat
(a) Climatic requirements—In both North America and Europe, L. vulgare thrives in a variety of climatic regimes, living as far north as 70°N in Scandinavia (Howarth and Williams 1968). Baldwin (1958) reported it to be quite abundant in the Ontario-Quebec clay belt just south of James Bay. Although more abundant in moist climates, L. vulgare is drought-tolerant, and often colonizes habitats subject to soil drying late in the season (Grime et al. 1988; Olson and Wallander 1999). It is tolerant of light frost when actively growing (Olson and Wallander 1999).
(b) *Substratum*—In general, *L. vulgare* tolerates a relatively wide range of soil types (Olson and Wallander 1999). Howarth and Williams (1968) noted that in Great Britain *L. vulgare* was widespread on both nutrient-rich clays and in limestone grasslands where it is more common on basic or neutral soils than in acid soils. Ferdinandsen (1918) classed it as a basophile growing best at pH 6.5 to 7.0. Neutral soils than in acid soils. Howarth and Williams (1968) noted that in Great Britain *L. vulgare* grows well in pasture land with a pH of 5.9–6.1 (Cole 1998). Soil fertility levels have limited effects on growth of *L. vulgare* and its nitrogen requirement is described as moderate (Howarth and Williams 1968; Olson and Wallander 1999). In fact, *L. vulgare* frequently grows better on poor soils (Sanders 1993; Cole 1998).

When growing under moist conditions, the short rootstock of *L. vulgare* can elevate the rosette above the soil surface, with the adventitious roots stabilizing the plant. The seedlings are relatively drought tolerant (Mitich 2000). Drought tolerance is illustrated by observations of the deeper-rooted *Taraxacum officinale* Weber (dandelion), which has been observed wilting before adjacent plants of *L. vulgare* (Howarth and Williams 1968).

c) *Communities*—*L. vulgare* occurs mainly on roadsides, native grasslands, rangeland, pastures, hay fields, abandoned croplands, railway embankments, rocky shores, rock outcrops, forest openings and waste ground but also is found in cultivated land, gardens and lawns (Dorn 1984; Alex 1992). The diploid form has been observed to be more shade tolerant and associated with mesic conditions, whereas the tetraploid form was associated with more ruderal habitats, such as dry disturbed areas and roadsides (P. Morisset, unpublished). Grime et al. (1988) recorded the most common habitats where *L. vulgare* occurred in Europe as 28% limestone quarries, 19% meadows, 15% limestone wasteland, 14% cinder heaps and 9% rock outcrops. It is not common on cultivated land. It also grows sparsely in thickly vegetated areas because of its low shade tolerance (Olson and Wallander 1999). In an abandoned pasture in southern Ontario, Reader (1991) observed that *L. vulgare* was more abundant on ridges than in more densely vegetated hollows. Howarth and Williams (1968) list 25 frequent associates of *L. vulgare* in the United Kingdom, including species it also associates with in Canada such as *Achillea millefolium* L., *Centaurea nigra* L., *Hieracium pilosella* L., *Leontodon autumnalis* L., *Plantago lanceolata* L., *Prunella vulgaris* L., *Ranunculus acris* L., *Rumex acetosa* L., *Taraxacum officinale*, *Trifolium pratense* L., and *T. repens* L.

6. History

The recorded history of ox-eye daisy dates back to Far Eastern legends (Mitich 2000). In Europe, achenes have been identified in excavations dating to the Iron Age and the Roman period (Howarth and Williams 1968). According to Howarth and Williams (1968), it appears to have spread along with increasing habitation of Europe. A common plant in Europe, *L. vulgare* was widely used in medieval medicine (see section 3b). The English name, ox-eye daisy, first appeared in print in *The Academy of Armory* by Randle Holme in 1688 (Mitich 2000). Margaret of Anjou had ox-eye daisies embroidered on her robes and those of her attendants before sailing to England in 1445 to marry Henry VI. Subsequently, she led his troops in the Wars of the Roses, with her banners bearing the image of the daisy (Haughton 1978). Later, as a result, it acquired the name "Marguerite." A woody relative from the Canary Islands, *Argyranthemum frutescens* (L.) Schultz-Bip. (= *Chrysanthemum frutescens* L.), is also called marguerite, Paris marguerite or Paris daisy. This similar species may also have had a role in the origins of the emblem.

Frankton and Mulligan (1987) reported that *L. vulgare* was introduced from Europe “at a very early date.” According to tradition, it was an escape from Governor Endicott’s garden in Massachusetts (Haughton 1978). It arrived in North America both as a contaminant in seed and as an ornamental, becoming naturalized first in the northeastern United States (Olson and Wallander 1999). By 1785, it was known as a problematic weed around Boston (Fernald 1903). By 1800, *L. vulgare* was well established throughout many regions of North America, and it was utilized extensively in herbal medicine during the nineteenth century. It was introduced into the northwestern United States as a contaminant of forage and grass seeds in the late 1800s and by 1937 it occurred in more than 50% of northwestern United States counties (Forceilla 1985).

The rapid spread of *L. vulgare* throughout North America was facilitated by moist, disturbed conditions within roadside ditches, which facilitated the spread of seeds via air and water (Howarth and Williams 1968). As mentioned previously, the penetration of *L. vulgare* into drier regions of North America, such as the interior plains, has been less rapid as it is reliant on favourable agricultural practices, such as irrigation of pasture land. Substantial populations have only developed recently in Alberta (in the last several decades), and it does not seem to be a weed of concern in Saskatchewan (D. Cole, pers. obs.).

7. Growth and Development

(a) *Morphology*—Howarth and Williams (1968) described ox-eye daisy as a shallow-rooted perennial herb that spreads by rhizomes and seeds. Germination is epigal with the pericarp carried above the ground. The seedling root system starts to be replaced by a well-developed system of relatively shallow lateral roots at about the 6-leaf stage (Howarth and Williams 1968). There is limited rooting of more prostrate basal stems or rhizomes. Subsequent to the development of basal stem rooting, the main root system is reduced in importance.

In a greenhouse experiment, *L. vulgare* seedlings growing at 20/18°C day/night temperatures were 2 to 5 cm tall with 4 to 7 leaves at 16 d after seeding. After 5 wk of growth, the plants were 7 to 12 cm tall with 5 to 10 basal vegetative branches and 24 to 56 leaves. At 15 wk, plants had as many as 55 basal branches and 319 leaves (Cole 1998). In a field experiment in Alberta, seedlings that germinated in early July had reached a height of 18 cm with 24 basal stems by mid September (Cole 1998).

When growing as single-spaced plants, at the end of two growing seasons, individual ox-eye daisy plants had attained a volume of 0.68 m³ and produced an average of 75
stems and 392 flower heads per plant. In the same test, plants growing in competition with meadow bromegrass (Bromus riparius Rehm.) were one-tenth the volume with 7.5 stems and 26 flower heads (King and Cole, unpublished data). In Australia at an altitude of 600 m, the leaf life span was 66 d as compared to 42 to 95 d for other low altitude perennial herbaceous plants (Diemer et al. 1992).

Many features of L. vulgare show xeromorphic adaptations, such as having leaves with stomata on both sides, and a tendency toward succulence (Howarth and Williams 1968; Grime et al. 1988). Biotypes adapted for salt-spray conditions on the coasts of the United Kingdom retained their characteristic features when cultivated (Howarth and Williams 1968). The xeromorphic characteristics were also induced in response to nitrogen shortage.

The flower heads are usually solitary on long terminal peduncles and are 2.5 to 7.5 cm in diameter. In pastures, there are typically one to three flowering stems per plant, though a single plant growing in the absence of competition can produce more than 100 stems (Cole and King, unpublished data).

(b) Perennation—Classed as a hemicryptophyte, L. vulgare reproduces by seed and by limited rooting and budding at the decumbent bases of the stems, both above and below the soil surface (S. Darbyshire, unpublished data). Extended spread is by seeds from second and subsequent year flowering plants. Both the plant and its achenes are able to over-winter, but seeds only persist under certain environmental conditions (see section 8c).

(c) Physiology—Heide (1995) described a dual induction requirement for flowering. The primary induction is a low temperature vernalization response, the optimum temperature being 6–9°C. Subsequently, a period of long days induces inflorescence initiation and stem elongation. Approximately six weeks of exposure to vernalization was required for 100% flowering. Long days (LD) were required for inflorescence initiation and stem elongation at 9°C. More than 16 LD cycles were required for normal stem elongation (bolting).

L. vulgare is able to adjust leaf position through modulations in petiole development (Howarth and Williams 1968). When grown under shade cloth at 24% of full light intensity, plants devoted energy to reproduction at the expense of root growth and production of late-season leaves (Boutin and Morisset 1988).

Bungener et al. (1999) found that L. vulgare was sensitive to ozone concentrations of double the ambient level, exhibiting decreased biomass in the first year of growth. In contrast, Mortensen and Nilsen (1992) found that L. vulgare biomass did not decrease with exposure to enhanced ozone levels, but exposed plants did exhibit chlorosis.

Seeds are rich in linoleic acid and, while devoid of starch and tannins, contain 24% protein and 26% fats (Earle and Jones 1962). Surface extracts from L. vulgare flowers contained the flavonoids apigenin, acacetin, and apigenin 7-glucuronide, while extracts from leaf and flower tissue contained acacetin 7-diglucuronide, apigenin 7-glucuronide, kaempferol 5-glucoside, kaempferol 5-glucuronide, luteolin 7-glucuronide, quercetin 5-glucoside, quercetin 5-glucuronide, quercetin 7-glucoside, and quercetin 7-glucuronide. The relative proportions of these compounds may be of taxonomic value (Williams et al. 2001). The presence of the cyclitol L-leucanthemitol was reported by Plouvier (1963). Sagareishvili (2000) isolated a variety of compounds from the flowers of plants growing in the country of Georgia, including: the flavonoids apigenin, cosminoside, apigenin 7-O-β-D-glucuronide, vitexin, rutin, hyperin, quercetin, luteolin, isorhamnetin, chrysirin 7-O-β-D-glucuronide and chrysirin; four methylsterols, the principal one being 24-ethylidenolozenphenol; the pyrrolizidine alkaloids platiphylline and seneconine; and choline.

(d) Phenology—The majority of ox-eye daisy seeds germinate in the spring, with sporadic germination throughout the growing season (Howarth and Williams 1968). In the first year of growth, the plant forms a vegetative basal rosette, typically under 5 cm in height. In the second and subsequent years, flowering stems are produced. L. vulgare is an obligate long-day plant (Spector 1956). Bolting and flowering typically occur from June to August, though in Québec, Boutin and Morisset (1989) observed that flower production continued into September. Seedling plants have a short juvenile phase of only four weeks. In west-central Alberta, heavily infested hay and pasture land may be completely white with L. vulgare in July (J. King, pers. obs.). After the development of flowering stems, a further increase in rosette leaves may be observed towards the end of July in Québec as the plant puts energy into perennating structures that will survive the winter (Boutin and Morisset 1989). Seeds are shed in August and September when the inflorescences are senescent and desiccating. In late fall, most plants die back to the crown, though in milder climates the basal rosette leaves can persist throughout the winter.

(c) Mycorrhiza—Kuehn et al. (1991) observed L. vulgare to be heavily infected with vesicular-arbuscular mycorrhizae (VAM) in Germany.

8. Reproduction

(a) Floral Biology—L. vulgare is chiefly insect-pollinated. Outcrossing is promoted by a male stage preceding the female stage (protrandry) within the disk florets (Howarth and Williams 1968), but there is a possibility of automatic self-pollination (Knuth 1908; Grime et al. 1988). If not pollinated early by insects, the stigmas will recurve towards the anthers as the stigmas are self-pollinated as they mature. The disk florets contain nectar, and during the male stage, the brushes on the style direct the pollen up the anther tube. Marie-Victorin (1997) stated that, although the flowers are nectariferous, they are not visited by honeybees, but only by small insects. Regardless, reported pollinators of L. vulgare include bees from the Halictidae and Anthophoridae, as well as Diptera (especially Calliphoridae, Conopidae, Stratiomyidae, and Syrphidae), Lepidoptera, and Thysanoptera (Howarth and Williams 1968; Ginsberg 1984). Dicks et al. (2002), in England, found that the most common insect visitors to L. vulgare flowers were the bumblebee Bombus lapidarius (L.), the flies Empis livida L., Eristalinus sepulchralis (L.), Helophilus sp., Tropida scita, and...
Phaonia incana (Wiedemann), and the butterfly Maniola jurtina (L.). Knuth (1908) reported more than 100 species of Coleoptera, Hymenoptera, Diptera and Lepidoptera visiting ox-eye daisy in central Europe. He also cited references to observations of slugs of the genus Limax on flower heads in wet weather and thus serving as possible pollen vectors.

(b) Seed Production and Dispersal—Under optimal conditions, Salisbury (1942) recorded annual achene production by an individual L. vulgare plant of about 26,000 achenes. In Europe, Salisbury (1942) observed that plants produced an average of 14 flower heads, but not all flower heads produced achenes. He reported between 1 and 15 inflorescences per plant in meadows with 111 to 290 viable seeds formed per inflorescence and 2689 seeds per plant. Coulson et al. (2001) found a mean of 251 seeds per inflorescence. In Denmark, Dorph-Petersen (1925) recorded 1300 to 4000 L. vulgare seeds per plant, with vigorous plants producing up to 26,000 seeds. L. vulgare may accumulate a large seed bank, both in the soil and on the soil surface. Parsons (1973) calculated that, in Australia, a pasture infested by L. vulgare could produce 10,710 seeds m\(^{-2}\) (= 107.1 million ha\(^{-1}\)). In the United Kingdom, Howarth and Williams (1968) reported that 1000 achenes weighed 0.38 ± 0.16 SD g. Grime et al. (1988) reported a mean seed weight of 0.33 mg.

Achene maturation occurs within 10 days after flowers open. Achenes are not generally dispersed far from the parent plant. In a study of equally spaced plants, up to 100 seedlings established in the vicinity of 2-year-old parent plants, largely in a downwind position (King and Cole, unpublished data). Coulson et al. (2001) found that few seeds dispersed more than 0.6 m from the parent plant. Dispersal distance was not affected by mowing or sheep grazing treatments. No seeds were found in dung of sheep that had grazed in plots containing L. vulgare (Coulson et al. 2001). Mature plants may retain many seeds on the plant (Grime et al. 1988), but few seeds are retained over winter (Cole, pers. obs.). Considerable dispersal occurs through movement of hay containing fruiting plants (Mitich 2000) or grass seeds (Salisbury 1961). Furthermore, the achenes are capable of remaining viable after passing through the digestive tracts of farm animals, thus leading to further spread through uncomposted stable refuse (Georgia 1942; Salisbury 1961; Mitich 2000). Up to 40% of the seeds passing through cattle, sheep, and other animals also may transport seeds in their feces or coats (Georgia 1942). However, Fischer et al. (1996) found very few L. vulgare seeds carried on sheep’s feces in Germany.

(c) Seed Banks, Seed Viability and Germination—L. vulgare seeds can remain viable for an extended period if conditions are not conducive to germination. Toole and Brown (1946) reported the results of a buried seed experiment in Virginia. Seeds were buried at 3 depths (20, 56 and 107 cm) in 1902 and germination was tested in subsequent years. Germination percentages remained high up until 10 yr when 39, 29 and 41% germination of seeds germinated from the three respective depths. The next two trials, at 16 and 21 yr, showed a decline in germination percentages by about half. Trials after 21 yr showed a dramatic reduction although some seeds (1%) were still viable at the end of the experiment after 39 yr after burial. Dore and Raymond (1942) estimated an average of 0.52 million viable seeds ha\(^{-1}\) in the surface soils of permanent pastures in southern Quebec. In the United Kingdom, Milton (1943) recorded seed populations as high as 6.6 million ha\(^{-1}\) in the top 18 cm of soil.

Disk and ray achenes are similar in terms of size, mass and general morphology, and germination tests on achenes from both sources at 20°C produced 90-95% germination after 4 d (Howarth and Williams 1968). The remaining seeds appeared to be dormant, and germinated after a much longer period. Although the ripening of L. vulgare seeds is not automatically followed by a period of dormancy, environmental conditions can sometimes induce seed dormancy (Howarth and Williams 1968).

Seeds may germinate as soon as they are shed because they have no innate dormancy mechanism (Povilaitytis 1956). If conditions are conducive, most seeds germinate in the fall of the year in which they are shed or in the following spring (Salisbury 1961). Thompson (1989) showed that germination of L. vulgare was inhibited in darkness but showed no response to differences in light intensity. Povilaitytis (1956) recorded that germination in darkness was generally low but was much higher at 20°C than at 30°C. A “prolonged” stratification (moist seeds at 1 to 7°C) reduced the sensitivity to light and the seeds were able to germinate “to a reasonable extent” in the dark. Keller and Kollmann (1999) tested germination response in seeds collected from four European sites and found that germination percentage was high between 5°C and 10°C with no further increase at higher temperatures. Geographic origin significantly affected germination response to temperature and day length. Rapid germination at relatively cool temperatures may be an adaptive advantage enabling seedlings to establish in a pasture situation where competitive shading may quickly develop.

When seeds were broadcast seeded and then lightly incorporated into fallow land, seedling establishment was only 5% from a seed lot that produced 75% germination in the laboratory (Cole and King, pers. obs.).

(d) Vegetative reproduction—Individual plants slowly spread laterally by rooting along the decumbent portions of the stem and lowest branches. The lower decumbent portion of the stem overwinters and expands to form a rootstock or short rhizome at or just below the soil surface. In following years, the rhizome expands and gives rise to roots and lateral as well as terminal stems. In dense populations, clumps will coalesce as they expand. Excised branches rooted successfully in a commercial soil mix in the greenhouse (Cole and King, unpublished data).

9. Hybrids

Although Howarth and Williams (1968) indicated that no spontaneous L. vulgare hybrids were confirmed in 1968,
Hornback (1982) described Shasta daisy as a “complex hybrid” developed from Luther Burbank’s artificial crossing of *L. vulgare* with the Portuguese daisy *L. maximum*, the European daisy *L. lacustre* and the Japanese daisy *L. nipponicum*. By listing Shasta daisy as *L. x superbum*, Hortus Third (L.H. Bailey Hortorium 1976) acknowledged it as a hybrid species.

The anomaly of discoid heads found infrequently in *L. vulgare* was described as an inheritable trait rather than hybridization between normal radiate and mutant discoid heads as found in *Bidens, Layia* or *Senecio* (Bogle 1983).

10. Population Dynamics

*L. vulgare* is adapted to take advantage of disturbance and removal of existing vegetation in pastures, rangeland, hay fields, abandoned croplands, roadsides, railway embankments and waste areas. A typical cycle, as observed in Alberta (Cole and King, pers. obs.), is as follows. The cycle begins with disturbance and overgrazing, which allows *L. vulgare* to become established in a pasture. The plants produce large numbers of seeds, and if tillage is used, dense stands of *L. vulgare* may develop. Often these *L. vulgare* populations eventually succumb to competition by grasses and other species, but a substantial seed bank of *L. vulgare* may remain in the soil, so that if disturbance and overgrazing recur, above-ground populations of *L. vulgare* would again increase.

Testing the invasiveness of weeds in a *Festuca ovina* L. dominated grassland in the United Kingdom, Burke and Grime (1996) found that disturbance of the indigenous *F. ovina* sward was an important factor in the establishment of *L. vulgaris* from sown seeds. The small-seeded *L. vulgare* proved more dependent on disturbance for establishment than some of the larger-seeded invaders sown. Olson and Wallander (1999) noted that bare soil was more prominent in areas with high densities of *L. vulgare*. Sanders (1993) found that, in general, *L. vulgare* is more prolific on poorer soils. This may not necessarily indicate a preference for or a tolerance of soils with low fertility, but more likely a competitive disadvantage on fertile soils (Olson and Wallander 1999). Grime et al. (1988) indicated that *L. vulgaris* is more common in open habitats where the growth of potential dominants is restricted by soil infertility and disturbance, such as cutting for hay and grazing. Olson et al. (1997) and Smith (1980) suggested that *L. vulgare* requires selective grazing of neighboring plants or a disturbance to establish. Once established, *L. vulgare* gains an advantage over more desirable forage plants in pastures because it is seldom grazed (Gilkey 1957). Howard and Williams (1968) noted that it was not abundant on lightly grazed grasslands in the British Isles.

Under favourable germination conditions and the absence of strong competitors, *L. vulgare* can produce dense stands of seedlings. The combination of prolific seed production by established plants and good conditions can result in a dense mat of rosettes (Olson and Wallander 1999). In Alberta, Cole et al. (1999) recorded an average population of 459 seedlings m⁻² in the spring after rototilling a *L. vulgare*-infested pasture the previous summer. Similarly, in the northeastern United States, *L. vulgare* became the dominant plant in a field after herbicides killed the existing plants and the field was plowed and disked (Marks and Mohler 1985).

*L. vulgare* can remain a dominant species in the plant community and exhibit “white as snow” fields for a number of years if the other vegetation does not grow to out-compete the daisies or is removed by grazing or mowing (Fig. 5). In Western Canada, in the first year of growth from seed the plant forms a vegetative rosette, with only about 1% of the rosettes producing flowering stems, flower heads and viable seeds. Flowers and seeds are generally produced in the second and subsequent years (Cole 1998). As mentioned previously, population densities may increase noticeably where cattle are grazing because they selectively avoid *L. vulgare* (Mitch 2000).

If other vegetation grows and shades *L. vulgare*, it becomes less dominant in the plant community. In newly established swards, *L. vulgare* had an average biomass of 2.5 g per plant 1 yr after seeding when growing with meadow bromegrass, compared to 21 grams per plant when growing with Kentucky bluegrass and 80 g per plant when growing alone on bare soil (Cole 1998). Cole (1998) found that using a vigorous forage species and/or fertilizer application to stimulate forage growth was an effective means of suppressing *L. vulgare*. The suppression was mainly a result of reduced light reaching the *L. vulgare* located lower in the canopy. Boutin and Morisset (1988, 1989) reported that *L. vulgare* growth and leaf survival was considerably reduced when light and nutrition levels were reduced by 70%, with plants showing less response to variations in soil fertility. Maintaining an adequate plant canopy of associated species ensures their competitiveness and minimizes light penetration to the seedlings, rosettes and basal leaves of flowering *L. vulgare* in lower canopy levels (Olson and Wallander 1999). A thick litter layer also impedes germination and establishment of *L. vulgare* (Povilaitis 1956).

Using microscale field mapping on reseeded former arable land in the United Kingdom, Spearman et al. (2000) found *L. vulgare* to have clumped patterns of distribution with little or no association between seedling “clumps” and mature plant “clumps”. In general, both seedling and mature plant densities declined over the growing season and over years, although not declining to extinction within clumps, suggesting that *L. vulgare* persists preferentially in patches of suitable habitat. The fact that the density, dispersion and persistence of *L. vulgare* varied among sites seeded with different ecotypes may indicate a difference in ecotype success (Spearman et al. 2000). Rich and Woodruff (1996) reported a significant decrease in the frequency of *L. vulgare* from 1930 to 1960 in unimproved grassland in Scotland. However, there is potential for future population growth from buried seed reserves. *L. vulgare* seeds in the soil can remain viable for many years (Section 8c) to germinate and re-invade the plant community when conditions become favorable for growth. This may occur when the land is rotated back into slow-to-establish forage species. Livingston and Allessio (1968) found that in Massachusetts ox-eye daisy invaded fields quickly after their abandonment and persisted for about 2 yr. Viable seeds were recorded in the
soils of these fields for up to seven additional years. Prince and Hodgdon (1946) observed viable ox-eye daisy seeds buried in old pasture soils of New Hampshire. Although ox-eye daisy was a common weed in the study area, they found germination rates of interred seeds to be very low. As detailed in Section 8c, Toole and Brown (1946) reported germination rates of interred seeds in Virginia, 39 yr after burial.

Rodent burrows in pastures and hay fields can also create areas where *L. vulgare* seeds are exposed to mineral soil and minimal competition (Olson and Wallander 1999).  

**11. Response to Herbicides and Other Chemicals**

Experimental results in Alberta indicated that *L. vulgare* sprayed with herbicides in May (Cole et al. 1994) did not exhibit new stem growth from the base of the plant, as was observed in plants sprayed in June (Maurice and Cole 1987). In May, when *L. vulgare* was mostly 3 cm in height and 20% of the plants were in the early bud stage, spraying metsulfuron (18 g a.i. ha\(^{-1}\)) and metsulfuron (18 g a.i. ha\(^{-1}\)) + 2,4-D ester (0.56 kg a.i. ha\(^{-1}\)) and picloram (0.54 kg a.i. ha\(^{-1}\)) provided almost complete control in the year of application at three different experimental sites in central Alberta (Cole et al. 1999). Dichlorprop (1.20 kg a.i. ha\(^{-1}\)) + 2,4-D ester (1.13 kg a.i. ha\(^{-1}\)), 2,4-D amine (1.68 kg a.i. ha\(^{-1}\)), 2,4-D ester (1.68 kg a.i. ha\(^{-1}\)), dicamba (1.0 kg a.i. ha\(^{-1}\)) + 2,4-D ester (1.0 kg a.i. ha\(^{-1}\)), thifensulfuron (0.04 kg a.i. ha\(^{-1}\)) + tribenuron (0.02 kg a.i. ha\(^{-1}\)), clopyralid (0.20 kg a.i. ha\(^{-1}\)), clopyralid (0.20 kg a.i. ha\(^{-1}\)) + 2,4-D ester (0.56 kg a.i. ha\(^{-1}\)), and mecoprop (0.26 kg a.i. ha\(^{-1}\)) + dicamba (0.35 kg a.i. ha\(^{-1}\)) + 2,4-D amine (0.95 kg a.i. ha\(^{-1}\)) all provided intermediate control. Triclopyr at 0.96 kg a.i. ha\(^{-1}\), MCPA at 1.68 kg a.i. ha\(^{-1}\), and metsulfuron at 18 kg a.i. ha\(^{-1}\) provided 100% control of *L. vulgare* (Derr 1993). Mecoprop and 2,4-D at 2.24 kg a.i. ha\(^{-1}\) stopped the growth of *L. vulgare* at a site in Europe and prevented flowering (Salisbury 1961). Isoxaaben (0.63 and 1.25 kg a.i. ha\(^{-1}\)) virtually eliminated *L. vulgare* from artificial seed banks in the United Kingdom. (Pywell et al. 1998).

Likewise, resistance to 2,4-D and also MCPA has been reported In New Zealand (Taylor 1981). Martin et al. (1990) reported poor control by either metsulfuron or picloram + 2,4-D when applied using a rotary weed wiper, although metsulfuron was the “more active” of the two. However, Sanders and Rahman (1994) reported effective control of *L. vulgare* obtained through spring applications with thifensulfuron (15 and 30 g a.i. ha\(^{-1}\)), 2,4-D (2.07 kg a.i. ha\(^{-1}\)) and 2,4-D (2.07 kg a.i. ha\(^{-1}\)) + clopyralid (30 g a.i. ha\(^{-1}\)) in New Zealand. Nicholson et al. (1993) found fall or spring spraying with these same herbicides provided comparable control in New Zealand. Fall spraying, however, caused more damage to *Trifolium repens*. All treatments delayed flowering of *L. vulgare* for 2 mo, with thifensulfuron controlling *L. vulgare* as well as 2,4-D + clopyralid but with significantly less damage to legumes. Also in New Zealand, Fellowes (1973) found that bentazon alone at 1.12, 2.24 and 3.36 kg a.i. ha\(^{-1}\) and with MCPB at 1.12 kg a.i. ha\(^{-1}\) substantially reduced the occurrence of *L. vulgare* without injuring *Lolium perenne* L. or *T. repens*.

Unfortunately, most of the herbicides that control *L. vulgare* also remove or suppress any legumes and other desirable broad-leaved plants growing in pasture, rangeland or hay land (Cole et al. 1999). A valuable component of the forage stand is removed and at the same time there is less competition for the *L. vulgare*. In two field experiments in central Alberta, the removal of the legume and broad-leaved plant component of the forage stand with metsulfuron at 18 kg a.i. ha\(^{-1}\) resulted in significantly more *L. vulgare* plants the year after spraying than in the untreated control (Cole et al. 1999). The use of herbicides alone may not be the best method of obtaining long-term management of *L. vulgare*, especially if legumes and other susceptible broad-leaved plants make up a significant proportion of the stand.

**12. Response to Other Human Manupulations**

Three direct methods of non-chemical control of ox-eye daisy are hand pulling, cultivation and mowing. These three methods will be discussed below, followed by discussion of five general management strategies: grazing management, consideration of relative competitive ability, fertilizer application, fertilizers in conjunction with other factors, and additional preventative strategies.

Hand pulling and removing new, small infestations of flowering plants will help prevent spread by seeds, but the entire rootstock can be difficult to remove from the ground (Cole et al. 1999). Cultivation will control *L. vulgare* and Muenscher (1955) recommended a short rotation, including a cultivated crop at least once every 3 yr. Cultivation is not always possible in many pastures, rangelands and roadside areas (Olson and Wallander 1999) and cultivation may also stimulate seed germination. At an eastern US site, Marks and Mohler...
(1985) found *L. vulgare* to be the dominant plant species in a field 14 mo after being sprayed with herbicides, followed by plowing and disking to kill existing plants. 

Howarth and Williams (1968) reported that *L. vulgare* abundance appears to be related to the cut-ting or grazing intensity and that it "resists" cutting. Although timely mowing will prevent or reduce *L. vulgare* seed production, it may also increase *L. vulgare* stand density by removing competitive forage growth, especially after several mowings. Four mowing experiments in pasture and hay fields in central Alberta showed increased ox-eye daisy numbers with additional mowings (Cole et al. 1999). At one site, the number of plants the year following different mowing regimes was 393 m⁻² with three mowings, 350 plants m⁻² with two mowings, 235 plants m⁻² after one mowing and 156 plants m⁻² in the unmown control. The increase in plant numbers was mainly in flowering plants and not rosettes or seedlings. Olson and Wallander (1999) acknowledged that mowing may stimulate rosette production (and thus flowering plants the following year).

The direct non-chemical manipulations discussed above have had limited success. To address a *L. vulgare* infestation in pasture, it is important to ensure that the pasture is not overgrazed (Holm et al. 1997), especially under dry conditions. In the United Kingdom, population increases were much smaller with intensive rotational grazing by cattle and intensive rotational and season-long grazing by sheep, while lenient cattle grazing did not affect population levels (Norman 1957; Pilkington et al. 2000). Olson et al. (1997) provided information that 2 yr of short-duration (5.5 to 9 d per season) intensive cattle grazing in the Northwestern US reduced *L. vulgare* seedling and rosette densities with minimal impact on the grasses (*Phleum pratense L.*, *Bromus inermis Leyss.*, *Poa pratensis L.* and *Dactylis glomerata L.* present in the pasture. After short-duration intensive grazing to trample and "force" cattle to eat *L. vulgare*, a long rest period allowed the forage to recover and become competitive with *L. vulgare* (Olson and Wallander 1999). Olson and Wallander (1999) also speculated that sheep and goats would probably have a more significant impact on *L. vulgare* than cattle, as sheep and goats readily graze it (Olson and Lacey 1994). By reducing seed production, they would reduce spread and, potentially, the competitiveness of the species. Grazing by cattle and other ungulates may also spread *L. vulgare* seed via their feces (Howarth and Williams 1968) as Olson and Wallander (1999) found that cattle did not completely avoid the plant. 

Pasture management may also involve planting competitive forages. Cole et al. (1999) seeded *Phleum pratense*, *Bromus inermis*, *Bromus riparius* (= *biebersteini* Roem. & Schult.), *Dactylis glomerata*, *Festuca rubra* L., *Poa pratensis*, *Medicago sativa* L., *Trifolium hybridum* L. and *Hordeum vulgare* L. into pasture heavily infested by *L. vulgare* that was rottotilled to stimulate germination of *L. vulgare* seeds. In the newly established sward, *L. vulgare* had an average biomass of 124 g m⁻² 1 yr after seeding when growing with *P. pratense* (similar biomass when growing with the other perennial grasses) compared to 34 g m⁻² when growing with *T. hybridum*, 13 g m⁻² when growing with *M. sativa* and 0.2 g m⁻² when growing with *H. vulgare*. When establishing a forage stand in a field infested by *L. vulgare* seeds, a suitable legume component may aid the new stand in outcompeting the *L. vulgare* in a shorter time, but would limit herbicide options as compared to establishing a grass-only forage stand. Using tillage and an annual crop such as *H. vulgare* may reduce *L. vulgare* but a sizeable seed bank might still be present. 

*L. vulgare* may be managed quite effectively by fertilizer applications. *L. vulgare* was outcompeted by the sown forage species when fertilizer was spring-applied to hay land for 2 consecutive years at four different experimental sites in central Alberta (Cole et al. 1999). At one site, *L. vulgare* was reduced from 218 plants m⁻² to 0 plants m⁻² within 2 yr. The application of fertilizer at soil-test recommendation rates in the early spring over several years, maintained suppression of existing plants and prevented the establishment of new plants from seed. Annual fertilizer application appeared to be particularly important in years of high moisture levels since the increased moisture resulted in a larger response by the forage species to fertilizer application. Olson and Wallander (1999) reported that fertilizer application alone over several years was almost as effective at reducing growth as applying the herbicides, 2,4-D (2.24 kg a.i. ha⁻¹) and picloram (0.14 kg a.i. ha⁻¹) in a trial conducted in eastern Washington. Ninety kg ha⁻¹ of N was the most cost-effective treatment after 7 yr, with grass yields increasing by 500% in higher-level N treatments. Maintaining an adequate plant canopy ensures a competitive stand that minimizes light penetration to seedlings and rosettes of *L. vulgare* (Olson and Wallander 1999).

Greenhouse studies demonstrated that under low light conditions, *L. vulgare* was unable to respond to increased levels of soil nutrients (Cole 1998). When artificially shaded, *L. vulgare* biomass decreased linearly with decreasing light intensity. An 85% reduction in light intensity reduced rosette biomass by 70% and seedling biomass by 92%. An integrated approach with an effective herbicide and fertilizer applied at 100 kg N ha⁻¹ and P, K and S to soil test recommendations as a surface application in April or May, increased the level of control compared with either treatment alone (Cole et al. 1999). In grass-only stands, herbicide and fertilizer treatments complemented each other more than in grass-legume stands. Similarly, Olson and Wallander (1999) reported considerable success at managing *L. vulgare* with herbicides and fertilizers, as the herbicide provided at least top-growth control of the plant, while the fertilizer stimulated growth of accompanying grasses. Fertilizer application and sheep or goat grazing may also be considered for an integrated-management approach to control, as long as the animals preferentially graze *L. vulgare* over the forage species (Olson and Wallander 1999).

Preventative measures can be used to avert new *L. vulgare* infestations by limiting intentional and unintentional spread of seeds (Olson and Wallander 1999). Public awareness, prohibiting *L. vulgare* in wild-flower seed mixes, checking crop seed
certificates for weed seed content, hay-certification programs, restricting livestock movement after they have been in L. vulgare-infested pastures (Georgia 1942) and sanitizing harvesting, tillage and other equipment before moving any of it to uninfested areas are measures that can be used to help prevent the spread of this weed. In the United States, L. vulgare seeds are an impurity of nearly all grass-seed commodities and fruiting plants are often cut with hay, baled and shipped widely throughout the country (Forcella 1985; Mitich 2000).

13. Response to Herbivory, Disease and Higher Plant Parasites

Herbivory

(a) Mammals—Some ungulates, such as goats, horses and sheep feed on L. vulgare, but others, such as cattle and pigs, avoid it (Howarth and Williams 1968; Olson 1999; Olson and Wallander 1999). Clear-Hill and Silvertown (1997) found that winter grazing by sheep reduced L. vulgare seedling emergence in the United Kingdom. In Montana, 2 yr of intensive grazing by cattle reduced densities of L. vulgare seedlings and rosettes and the number of seeds in the soil seed bank, but did not change densities of mature stems. Much of the impact of cattle was due to trampling and removing stems rather than to actual grazing.

(a) Birds—No information found.

(c) Insects—Relatively few insects have been recorded feeding on L. vulgare in North America. These include the aphids Macrosiphoniella leucanthemi Ferrari and Macrosiphoniella sanborni (Gillette) (Miller and Stoetzel 1997; Stoetzel and Miller 1999) and the lygus bug, Lygus rubrosignatus Knight (Schwartz and Footitt 1992). L. vulgare contains acetylenes and thiophenes, which induce phototoxicity against phytophagous insects, although insects such as the lepidopteran Argyrotaenia velutinana (a) and the moths Macrosiphoniella trimaculata (a) Birds-No information found.

(d) Other invertebrates—Ox-eye daisy was observed to support moderate populations of the northern root-knot nematode Meloidogyne hapla Chitwood in Quebec (Belair and Benoit 1996) and Ontario (Townshend and Davidson 1962). Townsend and Davidson (1960), surveying plants around areas of strawberry cultivation affected with root rot in southern Ontario, found that the nematode Pratylenchus penetrans (Cobb) Chitwood & Oteifa formed orange to brown lesions in the roots of ox-eye daisy. The low infection rates observed were attributed to the unfavourable hardness of ox-eye daisy roots. Mauch and Ferraz (1996) found that L. vulgare supported high levels of reproduction of the southern root knot nematode Meloidogyne incognita (Kotold & White) Chitwood race 3 in Brazil. Although it cannot endure freezing soil temperatures, M. incognita did attack ox-eye daisy in the greenhouse experiments of Davidson and Townshend (1967). Both species of Meloidogyne form root galls on many species of plants. Howarth and Williams (1968) mention Aphiaphaneleoides fragariae Christie, A. hiraeosoboi Schwartz, and Ditylenchus dipsaci (Kun) Filipjev, as feeding on L. vulgare.

The slugs Deroceras reticulatum Muller and Arion lunatianus Mabbile feed on L. vulgare in Switzerland (Keller et al. 1999). Clear-Hill and Silvertown (1997) observed that D. reticulatum reduced seedling emergence of L. vulgare in the United Kingdom. The gall mite Epitricheris alinae Lino has been recorded feeding on L. vulgare in Finland (Davis et al. 1982).

Diseases

(a) Fungi—Fungi reported on ox-eye daisy in Canada include Ceratobasidium aniceps (Bres. & Syd.) Jackson (Conners 1967) and Ophiobolus mathiei (Westend.) Sacc. (Gins 1986). The following fungi were recorded as associated with L. vulgare in Europe: Deuteromycetes Septoria cerosporoides, S. chrysanthemi Allecher, S. leucanthemi Sacc. Spec. (Br. Rust F.), S. exigua Pass.; Ascomycetes Pseudopezicula leucanthemi Magnus; and Basidiomycetes Puccinia leucanthemi Pass., Botrytis cinerea Fr., Oidium chrysanthemi Rabenh., and Verticillium alboetrum Reinke & Berth. (Howarth and Williams 1968). The fungi Peronospora radii de Bary, Puccinia cinici-oleracii Pers. ex Desm., Septoria chrysanthemi Allecher, Septoria leucanthemi Sacc. & Speg. and Septoria socia Pass. were reported on L. vulgare by Ellis and Ellis (1985).

Phytophthora tentaculata Kröber and Marwitz was described from L. vulgare plants affected by a root and...
stem base rot in greenhouses in Germany (Krober and Marwitz 1993).

(b) Bacteria—Howarth and Williams (1968) list Corynebacterium fascians (Tiff.) Dowson as parasitic on L. vulgare. Erwinia chrysanthemi pv. chrysanthemi causes a bacterial blight on related chrysanthemums including L. maximum (Burkholder et al. 1953), and is also reported from L. vulgare (Instituto Colombiano Agropecuario 2002). The aphid-vectored aster yellows phytoplasma (previously considered a virus) was reported on L. vulgare in P.E.I. (Conners and Saville 1944). It has also been reported on L. vulgare in Italy (as the Italian clover phyllody), causing yellowing, virescence, and phyllody (Firrao et al. 1996).

(c) Viruses—Potato yellow dwarf virus was reported on L. vulgare in North America (Youngkin 1942). Tomato spotted wilt virus (Howarth and Williams 1968; Oliveira and Kitajima 1989; Rutter and Gitaitis 1993) is known to infect L. vulgare throughout the world, including North America, South America and Europe.

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