

The Biology of Invasive Alien Plants in Canada. 2. *Cynanchum rossicum* (Kleopow) Borhidi [= *Vincetoxicum rossicum* (Kleopow) Barbar.] and *Cynanchum louiseae* (L.) Kartesz & Gandhi [= *Vincetoxicum nigrum* (L.) Moench]

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DiTommaso, A., Lawlor, F. M. and Darbyshire, S. J. 2005. **The Biology of Invasive Alien Plants in Canada. 2. *Cynanchum rossicum* (Kleopow) Borhidi [= *Vincetoxicum rossicum* (Kleopow) Barbar.] and *Cynanchum louiseae* (L.) Kartesz & Gandhi [= *Vincetoxicum nigrum* (L.) Moench].** Can. J. Plant Sci. **85**: 243–263. *Cynanchum rossicum* (dog-strangling vine) and *C. louiseae* (black dog-strangling vine) are introduced, perennial herbs or small twining vines in the Milkweed family (Asclepiadaceae). Generic placement of these two species has been problematic, but are here treated as members of *Cynanchum* subgenus *Vincetoxicum*. The species occur primarily in natural upland areas, including understories of woodlands, pastures, old fields, shores, flood plains and ruderal areas of southern Ontario and Quebec and the northeastern United States. Ecosystems on well-drained, stony soils are often densely colonized, but both species can tolerate a wide moisture regime. Plants establish in full sun or under forest canopies and may form monospecific stands in all light conditions. They often form dense colonies which smother other vegetation and reduce invertebrate and vertebrate biodiversity. Reproduction is by polyembryonic, wind-dispersed seeds. Effective control is primarily by herbicides, since mechanical control is difficult and no biological control agents have been developed. A third European species, *C. vincetoxicum*, has been reported as an occasional garden escape in southern Ontario and the northeastern United States, but has not yet become naturalized. Information on this species is included because of its close relationship with *C. rossicum* and its better known biology.

Key words: Dog-strangling vine, swallow-wort, *Cynanchum*, *Vincetoxicum*, CYKNI, invasive plant, weed biology

DiTommaso, A., Lawlor, F. M. et Darbyshire, S. J. 2005. **Biologie des plantes exotiques envahissantes au Canada. 2. *Cynanchum rossicum* (Kleopow) Borhidi [= *Vincetoxicum rossicum* (Kleopow) Barbar.] et *Cynanchum louiseae* (L.) Kartesz & Gandhi [= *Vincetoxicum nigrum* (L.) Moench].** Can. J. Plant Sci. **85**: 243–263. *Cynanchum rossicum* (cynanche) et *C. louiseae* (cynanche noir) sont des herbacées vivaces ou de petites vignes exotiques de la famille de l'asclépiade (Asclépiadacées). La détermination du genre des deux espèces s'est avérée difficile, mais on a convenu de les classer dans le sous-genre *Vincetoxicum* de *Cynanchum*. L'espèce affectionne surtout les plateaux naturels, y compris les sous-étages des boisés, des pâturages, des champs en friche, des rivages, des plaines inondables et des zones rudérales du sud de l'Ontario et du Québec ainsi que du nord-est des États-Unis. L'écosystème des sols rocaillieux bien drainés est souvent densément peuplé, mais les deux espèces tolèrent de fortes variations d'humidité. Elles s'établissent au soleil ou sous la canopée forestière, où elles constituent parfois des peuplements monospécifiques, peu importe la luminosité. Leurs denses colonies étouffent souvent les autres plantes et réduisent la biodiversité des invertébrés et des vertébrés. Les deux espèces se multiplient au moyen de semences à embryons multiples dispersées par le vent. On en vient surtout à bout avec des herbicides, car aucun agent de lutte biologique n'a été mis au point et le désherbage par des moyens mécaniques s'avère difficile. Une troisième espèce, d'origine européenne, *C. vincetoxicum*, a été signalée à l'occasion comme échappée de culture dans le sud de l'Ontario et le nord-est des États-Unis, mais elle ne s'est pas encore acclimatée. On la mentionne ici parce que sa biologie est mieux connue et parce qu'elle présente des liens étroits avec *C. rossicum*.

Mots clés: Cynanche, dompte-venin, *Cynanchum*, *Vincetoxicum*, CYKNI, plante envahissante, biologie des mauvaises herbes

1. Species Name and Taxonomic Relationships

I. *Cynanchum rossicum* (Kleopow) Borhidi — Synonyms: *Vincetoxicum rossicum* (Kleopow) Barbar.; *Cynanchum medium* misapplied, not R. Br.; *Vincetoxicum medium* misapplied, not (R. Br.) Dcne. — **dog-strangling vine** (Darbyshire et al. 2000); pale swallow-wort (swallowwort) and swallow-wort (Darbyshire 2003); European swallow-wort (Kartesz 1999), swallowwort (Christensen 1998); **dompte-venin de Russie** (Darbyshire et al. 2000).

II. *Cynanchum louiseae* Kartesz & Gandhi — Synonyms: *Cynanchum nigrum* (L.) Pers., not Cav.; *Vincetoxicum nigrum*

(L.) Moench – **black dog-strangling vine** (Darbyshire et al. 2000); black swallow-wort and black swallowwort, climbing poison, and Louise's swallow-wort (Darbyshire 2003); Louis' [sic] swallow-wort (United State Department of Agriculture 2000); **dompte-venin noir** (Darbyshire et al. 2000).

Asclepiadaceae, milkweed family, Asclépiadacées.

Cynanchum: Greek: *kyon* = dog + *anchein* = to strangle or poison; alluding to the supposed use of some European species for poisoning dogs and other vermin (Forster 1991). *Vincetoxicum*: Latin: *vinco* = to conquer, overcome, master, surpass or subdue + *toxicum* = poison; alluding to its supposed herbal attributes as an antidote for poisons.

The common name “swallow-wort”, and particularly “pale swallow-wort”, is probably best restricted to *Cynanchum vincetoxicum* (L.) Pers. (= *Vincetoxicum hirsutaria* Medik.). This widespread European species has pale cream-coloured (white, yellowish, greenish or rarely brownish) flowers. Although sometimes called “pale swallow-wort”, the flowers of *C. rossicum* (pink or maroon) are pale only in relation to the dark purple flowers of *C. louiseae*. Although *C. vincetoxicum* (sensu stricto) has not yet become established in North America, there are records of it growing spontaneously as a rare garden escape in Ontario and the northeastern US (e.g., Macoun 1906; Fernald 1950) and it may become a problem in the future.

The family Asclepiadaceae is generally recognized as a distinct unit of about 2000 species, in about 300 genera, based on the specialized floral characteristics associated with insect pollination (entomophily) (Cronquist 1988; Kunze 1991). The family is clearly derived from ancestors in, or close to, the less specialized Apocynaceae (Cronquist 1988). This phylogenetic relationship has led some authors to place the milkweed family within the family Apocynaceae as either a tribe, Asclepiadae, or a subfamily, Asclepiadoideae (e.g., Liede 1999).

There has long been considerable controversy over the taxonomic distinction of the genus *Vincetoxicum* from *Cynanchum* (e.g., Woodson 1941; El-Gazzar et al. 1974; Liede 1999). Some authors recognize the distinctiveness of *Vincetoxicum* (e.g., Bullock 1958; Markgraf 1972; Ali and Khatoun 1982; Liede 1996; Liede and Täuber 2002), while others (e.g., Woodson 1941; Forster 1991; Ping-tao et al. 1995; Kartesz 1999) lump it with *Cynanchum*. Forster (1991) considered it as a section [sect. *Vincetoxicum* (N. Wolf) Tsiang & Li] of *Cynanchum*, but others have treated it as a subgenus [subgenus *Vincetoxicum* (N. Wolf) Domin] (Domin 1928). All plant names in this account follow those of Darbyshire et al. (2000), as far as possible.

The application of the generic name *Vincetoxicum* has had a confusing history, being at one time applied to various native North American plants. It is now known that the name should be used for a number of temperate Old World species (Bullock 1958, 1967).

In Europe, Markgraf (1971, 1972) distinguished 11 species in *Vincetoxicum* which he recognized as a separate genus from *Cynanchum*. He considered *C. vincetoxicum* to be highly variable and recognized nine subspecies, all of which possess yellow-white flowers. The closely related dark-flowered forms, *C. fuscatum* (Hornem.) Link [= *V. fuscatum* (Hornem.) Reichenb.] and *C. rossicum*, were recognized as separate species. Lauvanger and Borgen (1998) examined the populations of *Cynanchum* in Norway. Their analysis of morphology and isoenzymes suggested that those with light-coloured flowers are conspecific with *C. rossicum* and the latter might best be considered as a subspecific taxon of *C. vincetoxicum*. The purported hybridization between these two taxa (Markgraf 1971), the production of light-coloured petals in *C. rossicum* under low light conditions, and the morphological and molecular evidence given by Lauvanger and Borgen (1998), all support the position of Gleason and Cronquist (1991) who treated them as a single species.

Since there is such a close relationship between *C. vincetoxicum* and *C. rossicum* that they are sometimes considered conspecific, and considerably more is known about *C. vincetoxicum*, information on this latter taxon is also provided with the assumption that it may apply to *C. rossicum* as well.

In extreme southwestern Ontario, *Cynanchum laeve* (Michx.) Pers. [= *Ampelamus laevis* (Michx.) Krings] has been reported as a rare garden escape (Newmaster et al. 1998). The species is native to the eastern United States and its relationship to the genus *Cynanchum* is uncertain (Liede and Täuber 2002).

2. Description and Account of Variation

(a) *Species description* — The descriptions are based primarily on measurements from North American populations and supplemented with additional data from the taxonomic literature. Measurements are given as the typical range with unusual extremes in parentheses. Terms in parentheses provide more specific descriptions.

I. *Cynanchum rossicum* (Figs. 1A, 1B, 2, 3A, 4A and 6). Perennial herb or small vine (Fig. 1A). A horizontal woody rootstalk forms a short rhizome (Fig. 2). The pale fibrous roots are somewhat thick and fleshy. The stems are 60–200 (250) cm long, more or less erect, twining, scrambling or climbing and pubescent (tomentose to villose) in longitudinal bands. The leaves are opposite, (6) 7–12 × (2.5) 5–7 cm, with the largest leaves in the middle of the stem and tending to be rounder and smaller basally and narrower and smaller apically. The leaves are ovate to elliptic, acute at the tip, have smooth (entire) margins, and are pubescent on the margins and major veins underneath (abaxially). The petioles are 5–20 mm long. The flower buds are ovoid to conoidal, with a pointed apex (Fig. 3A) and the unopen petals are twisted. Five to twenty flowers are produced in the axils of the leaves in umbelliform cymes. The peduncles of the inflorescences are more or less straight, (1) 1.5–4.5 (5) cm long and pubescent (tomentose to villose) in longitudinal bands (Fig. 3A). The pedicels of the flowers are more or less evenly pubescent. The flowers are 5–7 mm in diameter and 5-parted. The calyx segments are strap-like (subulate to lanceolate) and 1–1.5 mm long. The corolla is pink, red-brown or maroon. The scarcely fleshy petals are ovate-lanceolate to lanceolate in shape, (2.5) 3–5 mm long (about half as wide as long) and hairless. The petal margins are hyaline to translucent in a strip 0.05–0.15 mm wide. The fleshy corona (staminal crown) is distinctly 5-lobed with the lobes united only at the base. The corona is usually about the same colour as the corolla or a little darker, although it is sometimes a lighter pink, orange or yellow. The gynostegium (see Section 8a) is pale yellow or yellowish-green. Fruits (Fig. 1B) are slender (fusiform) follicles, smooth (glabrous), (2.8) 4–7 cm long and often 2 are formed per flower. The light to dark brown seeds (Fig. 4A) are obovate to oblong, 4–6.5 (7) × (1.9) 2.4–3.1 mm, flattened or concave on one side and convex on the other, with a membranous marginal wing up to 0.25 mm wide and an apical tuft of hairs (coma) 2–3 cm long.

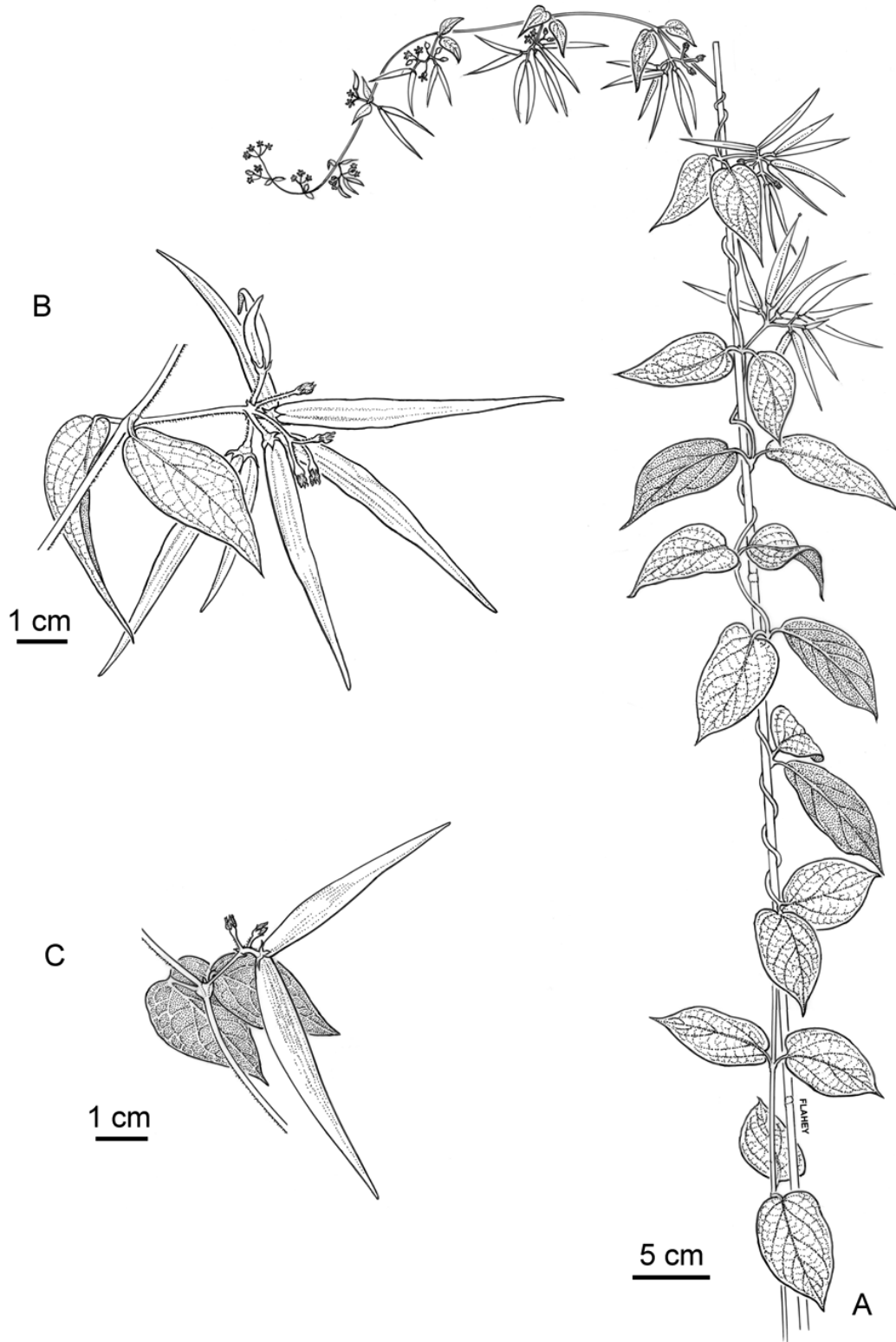


Fig. 1. *Cynanchum* A. habit of *C. rossicum* from plant grown in a greenhouse; B. axillary inflorescence showing fruits of *C. rossicum*; C. axillary inflorescence showing fruits of *C. louiseae*.



Fig. 2. Cross section through the woody rootstalk (rhizome) of *Cynanchum rossicum*.

II. *Cynanchum louiseae* (Figs. 1C, 3B and 4B). Perennial herb or small vine. A horizontal woody rootstalk forms a short rhizome (but not a creeping rhizome) similar to *C. rossicum* (see Fig. 2). The pale fibrous roots are somewhat thick and fleshy. The stems are 40–200 cm long, more or less erect, climbing, twining, or scrambling and pubescent (tomentose to villose) with the hairs often in longitudinal bands. The leaves are opposite, 5–12 × 2–6.5 cm, with the largest leaves in the middle of the stem and tending to be rounder and smaller basally and narrower and smaller apically. The leaves are oblong to ovate, acute to acuminate at the tip, have smooth (entire) margins, and are lightly pubescent on the margins and major veins underneath (abaxially). The petioles are 10–15 (20) mm long. The flower buds are globose, with a rounded apex (Fig. 3B) and the unopen petals are not twisted. Four to ten flowers are produced in the axils of the leaves in umbelliform cymes. The peduncles of the inflorescences are usually curved, 0.5–1.5 (2.8) cm long and pubescent (tomentose to villose) with the hairs in longitudinal bands or not. The pedicels of the flowers are more or less evenly pubescent. The flowers are 5–8 (9) mm in diameter and five-parted (Fig. 3B). The calyx segments are ovate to triangular and about 1–1.5 mm long. The corolla is dark purple to blackish. The fleshy petals are ovate to broadly deltoid in shape, (1) 1.5–3 mm long (about as wide as long) and finely hairy (hairs 0.1–0.2 mm long) on

the inner (adaxial) surface. The petal margins are hyaline to translucent in a strip less than 0.05 mm wide. The fleshy corona (staminal crown) is inconspicuously 5-lobed or undulating (crenulate). The corona is similar in colour to the corolla. The gynostegium is pale green or yellowish-green. Fruits are slender (fusiform) to plump follicles, smooth (glabrous), 4–8 cm long and only sometimes are two formed per flower (Fig. 1C). The dark brown seeds (Fig. 4B) are ovoid to obovoid, (5.5) 6–8 × 3–4.7 mm, flattened, with a narrow membranous marginal wing and an apical tuft of hairs (coma) 2–3 cm long.

The seedlings of both species are similar. The cotyledons and first leaves are ovate to elliptic with a somewhat pointed or rounded apex (Fig. 6).

Moore (1959) reported a chromosome count of $2n = 22$ for plants of *C. rossicum* (under the name *C. medium*) from Ottawa (ON). Chromosome numbers for *C. louiseae* in Spain have been reported as $n = 11$ (Diosdado et al. 1993) and $2n = 22$ (Aparicio and Silvestre 1985) and a count of $2n = 44$ is reported from Italy (Pardi 1933, in Moore 1959). As no chromosome counts are available for North American material of *C. louiseae*, it is unknown whether these populations are diploid or tetraploid.

(b) *Distinguishing features* — The two species of *Cynanchum* established in Canada are easily distinguished

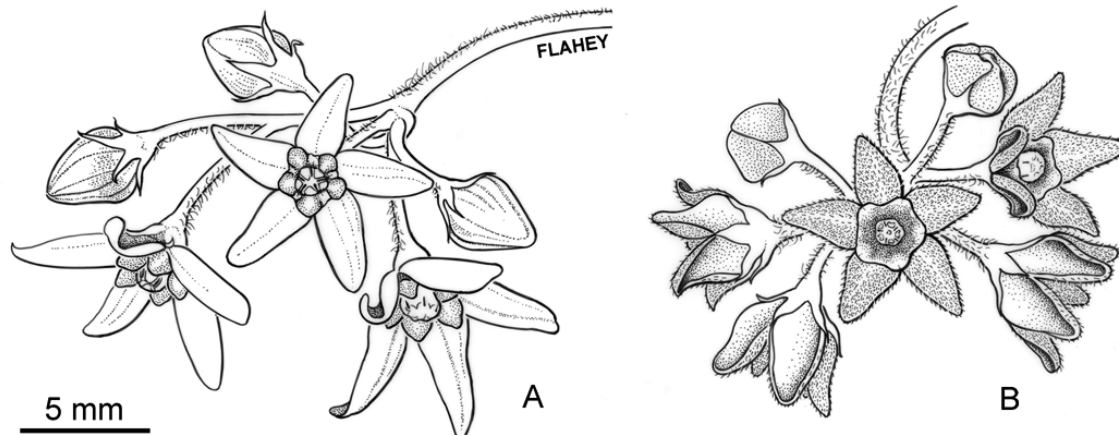


Fig. 3. Inflorescences of *Cynanchum* species showing buds and mature flowers A. *C. rossicum*; B. *C. louiseae*.

when in flower (Fig. 3). In *C. rossicum* flowers, the corona is distinctly lobed and the petals are light pink or brown to maroon, strap-like (much narrower at the base than they are long) and hairless on the inner surface, while in *C. louiseae* the corona is indistinctly lobed and the petals are dark purple or black, deltoid (about half as wide at the base as they are long) and pubescent on the inner surface. In addition, the flower buds of *C. rossicum* are pointed and conical, while in *C. louiseae* the buds are rounded and globose. When not in flower the two species are less easily distinguished, although there are a number of characteristics that can be helpful for identification. Peduncles of the inflorescences (particularly when plants are in fruit) are longer in *C. rossicum* than *C. louiseae*, usually 1.5–4.5 cm versus 0.5–1.5 cm, respectively (Fig. 1B and C). The leaf bases in *C. rossicum* tend to be truncate to slightly cuneate, while in *C. louiseae* they tend to be emarginate or slightly cordate, but rarely truncate. The hairs on the stems, peduncles and pedicels are denser and in more distinct bands in *C. rossicum* than *C. louiseae*. The seeds of *C. rossicum* tend to be about half as long as those of *C. louiseae* (Fig. 4). The variation of these non-floral characters is such that they are unreliable for positive identification.

Pringle (1973) stated that *Cynanchum louiseae* “has twice the chromosome number... [and] considerably larger guard cells than those of...” *C. rossicum*, without presenting any data. This statement was tested using stomatal guard cells on the lower (abaxial) epidermis of mature leaves from herbarium specimens. All specimens (60 *C. rossicum* and 18 *C. louiseae*) bore flowers to permit accurate identification and were collected from Canadian populations. While mean guard cell size was significantly different ($P < 0.0001$), 21.6 μm (SE = 0.1) versus 33.0 μm (SE = 0.3), respectively, there was considerable overlap in range values (Fig. 5). The smallest cell of *C. louiseae* approached the median of *C. rossicum* and the largest cell of *C. rossicum* was larger than the median for *C. louiseae*. Although the guard cell size data suggest that *C. louiseae* populations are tetraploid, this diagnostic approach must be used with caution until more is known about the chromosome races present in North America.

Key to the four species of *Cynanchum* and related genera in eastern Canada. All species produce seeds with a coma of silky hairs in pods.

1. Plants erect, not twining; sap a milky latex.....2
1. Plants erect to sprawling or climbing, the tips of the stems twining; sap not milky, clear and watery3
2. Corolla not bell-shaped, the segments spreading or reflexed and more or less obscuring the calyx; gynostegium present (anthers fused to stigma); pollinaria formed (pollen grains fused and pollen sacs from adjacent anthers joined by a yoke-like translator)*Asclepias* L.
2. Corolla bell-shaped, the segments erect and not obscuring the calyx; gynostegium not present (anthers not fused to stigma); pollinaria not formed (pollen grains separate and pollen sacs not joined)*Apocynum* L.
3. Flowers white or creamy yellow4
3. Flowers pink, maroon, purple or black, not white or creamy-yellow5
4. Leaves triangular or deltoid and deeply cordate, with the basal lobes broadly rounded; the corona lobes divided into 2 strap-like linear tips (appearing as 10 lobes) which greatly exceed the gynostegium; mature pods 10–15 cm long; occasional garden escape*Cynanchum laeve*
4. Leaves ovate and truncate to shallowly cordate; corona lobes not divided (appearing as 5) and about the same length as the gynostegium; mature pods less than 10 cm long; occasional garden escape*Cynanchum vincetoxicum*
5. Peduncles mostly more than 2 cm long; flower buds conic and pointed; corona distinctly lobed, usually contrasting in colour with the corolla; petals strap-like (about twice as long as broad), pink to maroon (sometimes quite dark), glabrous above; seeds 4–6.5 mm long*Cynanchum rossicum*
5. Peduncles mostly less than 2 cm long; flower buds globose and rounded; corona wavy but not distinctly lobed, similar in colour to the corolla; petals deltoid (up to twice as long as broad), purple to almost black, finely pubescent above; seeds usually 6–8 mm long*Cynanchum louiseae*

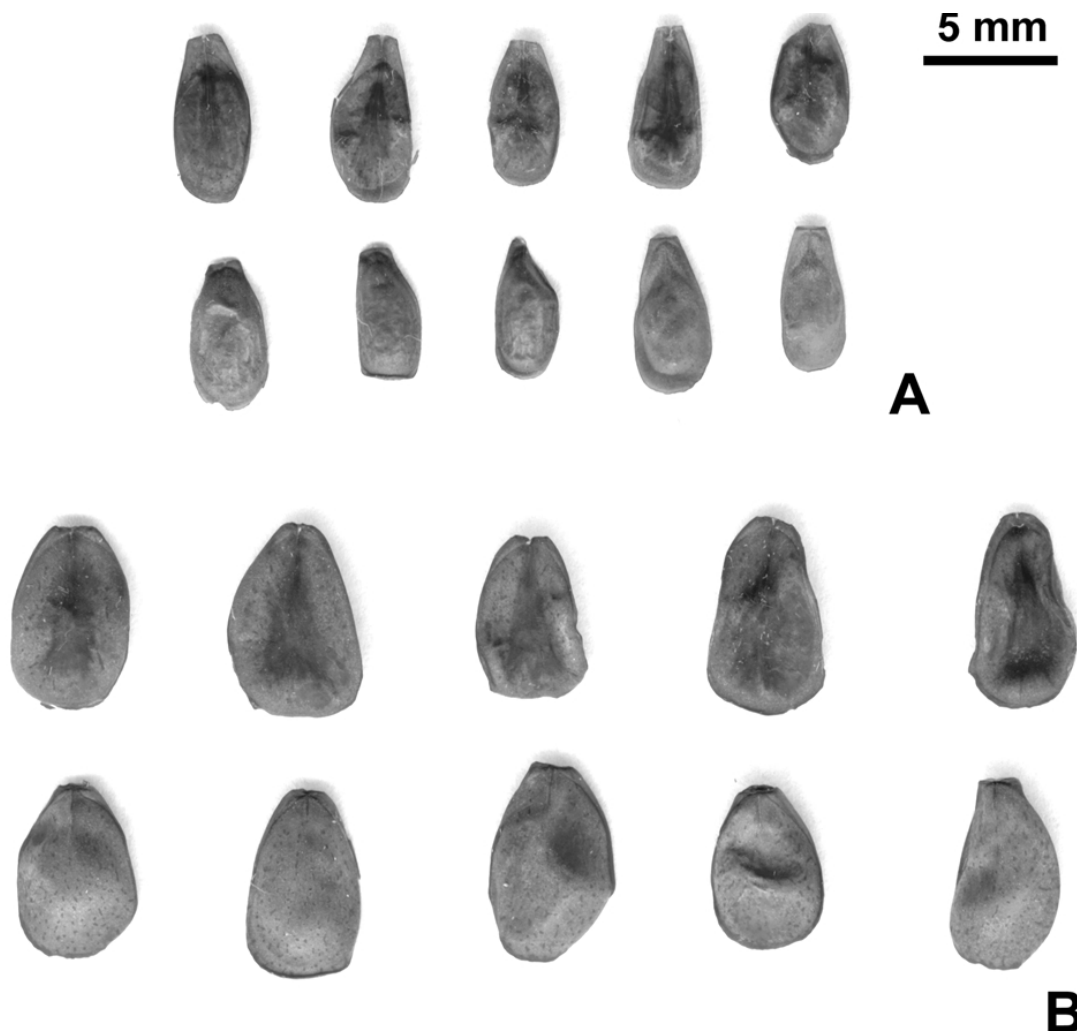


Fig. 4. Seeds of *Cynanchum* species with comas removed A. *C. rossicum* (DAO 145407); B. *C. louiseae* (DAO 788841).

(c) *Intraspecific variation* — Morphological and genetic (isozyme) variation in both *C. rossicum* and *C. louiseae* was examined by Lauvanger and Borgen (1998). Markgraf (1972) did not formally recognize any subspecific variants in either of these two taxa. Considerable intraspecific variation occurs in the *C. vincetoxicum* species complex (Markgraf 1971, 1972; Donadille 1965; Lauvanger and Borgen 1998), where many subspecific taxa have been described and with which *C. rossicum* is sometimes combined.

(d) *Illustrations* — Figure 1 illustrates *C. rossicum* habit (A) and fruits (B), and *C. louiseae* fruits (C). Figure 3 depicts buds and mature flowers of *C. rossicum* and *C. louiseae*. Seeds of *C. rossicum* and *C. louiseae* are depicted in Fig. 4. Figure 5 shows guard cell lengths of abaxial epidermis stomata for the two *Cynanchum* species. Figure 6 shows two seedlings of *C. rossicum*, about 2 wk after initial emergence, arising from a single polyembryonic seed (see Section 8c).

Detailed line drawings of the flower and pollinarium of *C. rossicum*, were published by St. Denis and Cappuccino

(2004). Colour photographs, particularly of *C. rossicum*, can be found at the web site <http://www.swallow-wort.com> (2 September 2004) and at the sites linked from there.

3. Economic Importance and Environmental Impact

(a) *Detrimental* — *Cynanchum rossicum* is more likely to be found away from sites of cultivation than *C. louiseae* (Sheeley 1992). Both are, however, of concern to managers of natural and semi-natural lands (Kirk 1985). Dense populations may cover substantial areas, out-competing other vegetation and reducing faunal and floral biodiversity. Both species may have deleterious effects on monarch butterfly (*Danaus plexippus* Linnaeus) populations (see Section 13c). They pose a low threat to monarch butterfly populations via displaced oviposition and larval mortality, although a greater potential threat may be the reduction of host plant availability through competitive displacement. They also serve as hosts for various insect pests of crops and as alternate hosts for *Cronartium* Fr. rusts attacking *Pinus* L. species (see Section 13).

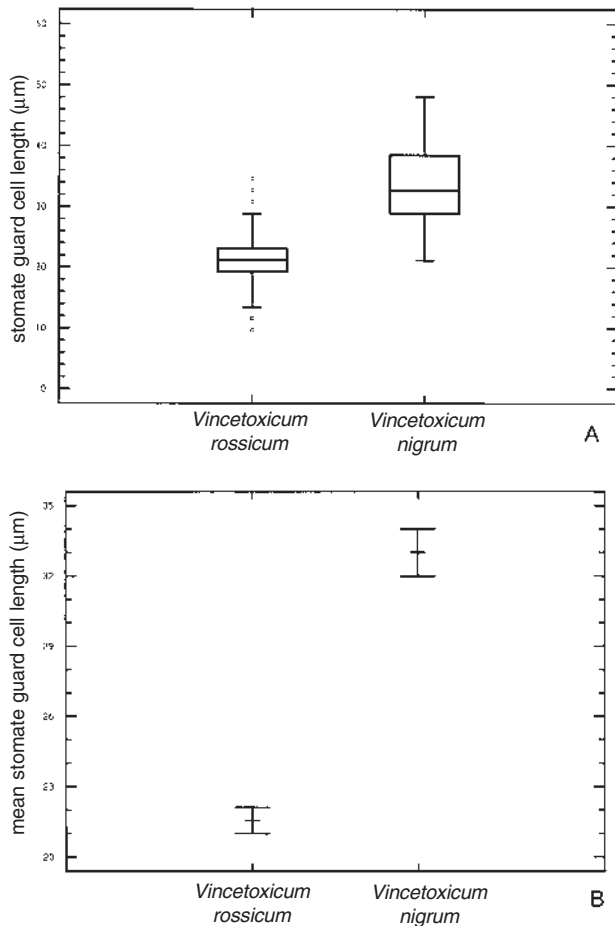


Fig. 5. Guard cell length from abaxial epidermis stomata in *Cynanchum* species A. Box-and-whisker plots (Tukey 1977) from all measurements of 20 cells from each of 60 *C. rossicum* specimens and 18 *C. louiseae* specimens. (The plot divides the data into four areas of equal frequency. The box encloses the middle 50% with the median as a vertical line inside the box. Vertical lines, whiskers, extend from each end of the box to the smallest and largest data points within 1.5 interquartile ranges from the first and third quartiles, respectively. Points beyond the whiskers are plotted separately.); B. An LSD means plot with 95% confidence interval ($P < 0.0001$), using the averages from the 20 cells from each of 78 samples.

The roots of the closely related *C. vincetoxicum* contain the haemolytic glycoside vincetoxin and are considered poisonous to humans and mammals (Haznagy and Toth 1971; Wiegrebe et al. 1970). The same is likely true for other species in subgenus *Vincetoxicum* (Alex 1992). I. *Cynanchum rossicum*. In Ontario, *C. rossicum* invades gardens, lawns, shrubberies, hedgerows, fencerows, shrubby thickets, a variety of deciduous and mixed forest types (including pine plantations), and pastures (herbarium specimen label data). Small trees in restoration sites in Ontario have been smothered by twining *Cynanchum* vines (Christensen 1998). Old-field sites colonized by *C. rossicum* near Ottawa (ON) have substantially lower diversity of arthropods than nearby old-field sites with largely native

vegetation (Ernst and Cappuccino 2004). The decline in arthropod diversity will likely continue if *C. rossicum* is successful at greater displacement of native old-field plants.

Christmas tree growers in central New York State report increased pressure by *C. rossicum* in plantations, especially in the past decade. Moreover, the New York State Forest Owners' Association has expressed concern that infestations of *C. rossicum* in central New York State may be negatively impacting forest regeneration. Although neither species is currently a serious problem in cultivated fields, *C. rossicum* has been recently observed in no-till corn and soybean fields in several central and western New York State counties and thus may pose a management problem in these cropping systems in the future (DiTommaso, personal observation). Some landowners in New York State have gone so far as to abandon their horse pastures after control efforts against *C. rossicum* over a 5–10 yr span were largely unsuccessful (landowner communication to Lawlor). However, this species does not appear to be a nuisance in cattle pastures, and some grazing by cattle has been observed in New York State (Lawlor, personal observation). These pastures are, however, quickly re-colonized within a few years of removing cattle, especially if populations are present on adjacent land.

Several Scandinavian grazing studies have confirmed that sheep avoid or rarely graze on *C. vincetoxicum*, and thus do not support earlier reports of sheep fatalities after ingestion of this species (Hægström 1990). A feeding trial (6.25, 7.8 and 6.25 g of plant material per kilogram of animal, on 3 consecutive days) using *C. rossicum* resulted in the death of a Spanish-type goat 4 d after the last dose (Kip Panter, personal communication). Blood serum chemistry was normal except for creatine kinase, which began to rise 24 h following the first dose (468 Units per litre, versus 143 U L⁻¹ for the control) and peaked (718 U L⁻¹) 30 hours after the first dose. Species of *Cynanchum*, like other milkweeds, are reported to contain cardenolides (Burrows and Tyrl 2001) and, although only a single goat was tested, the results suggest that sufficient amounts of toxin(s) are present to consider the plant dangerous for grazing livestock and wildlife, especially if other better quality forage is limited.

Natural area managers in both Ontario and New York State are greatly concerned about these species. In particular, *C. rossicum* is beginning to invade alvar communities in eastern Ontario and the rare alvar ecosystems of Jefferson County (NY) are under increasing competitive pressure from nearby large infestations of *C. rossicum*. Near-shore islands of eastern Lake Ontario, especially Grenadier Island (NY) and Galloo Island (NY), as well as Henderson (NY) on the mainland, support large, dense infestations. These sites are southwest and upwind of prevailing winds from the New York alvar systems. Habitats of the U.S.-federally-listed hart's tongue fern, *Phyllitis scolopendrium* var. *americana* Fernald in Onondaga County (NY) are also being invaded (Lawlor 2000).

Dense populations of *C. rossicum* discourage grassland birds from nesting in summer months and may provide protection to small rodents from raptor predation in winter (G. Smith, personal communication). A preliminary study of a habitat managed for grassland birds in Jefferson County,

NY, showed a significant negative correlation between *C. rossicum* cover and the number of breeding grassland birds. Twelve 200 m diameter plots were monitored during the 2004 breeding season. Non-parametric Spearman's rank correlations showed a decline in the abundance of savannah sparrow, *Passerculus sandwichensis* (J. F. Gmelin), ($Rho = -0.708$, $P = 0.01$); bobolink, *Dolichonyx oryzivorus* (Linnaeus), ($Rho = -0.951$, $P < 0.0001$); and, eastern meadowlark, *Sturnella magna* (Linnaeus), ($Rho = -0.793$, $P < 0.0021$), as *C. rossicum* cover increased. These birds were absent in pure stands of *C. rossicum* (Central and Western NY Chapter - The Nature Conservancy, unpublished data).

II. *Cynanchum louiseae*. Establishment of *C. louiseae* is threatening the endemic Jessop's milkvetch, *Astragalus robinsii* (Oakes) A. Gray at Windsor (VT) on ice-scoured banks of the Connecticut River (R. Popp, personal communication).

(b) *Beneficial* — I. *Cynanchum rossicum*. During World War II, the Canadian Department of Agriculture conducted studies searching for latex-producing plants as a substitute for *Hevea brasiliensis* (A. Juss.) Müll. Arg. in rubber production. Several species of subgenus *Vincetoxicum* were investigated, including *C. rossicum*, at the Central Experimental Farm, Ottawa, ON (McNeill 1981). Unfortunately, no published information is available from this research.

II. *Cynanchum louiseae*. Although species of the genus *Cynanchum* are described in Hortus Third (L. H. Bailey Hortorium 1976) as "weedy herbs", only *C. louiseae* is listed as a cultivated ornamental in the United States. It is likely that both *C. louiseae* and *C. rossicum* have been cultivated as ornamentals in Canada and the United States under the name "*Cynanchum nigrum*" (Monachino 1957; Pringle 1973).

Cynanchum vincetoxicum has been widely used in European traditional medicine as a laxative, diaphoretic, diuretic, emetic and anti-tumor agent (Uphof 1968; Nowak and Kisiel 2000; Duke et al. 2002). The "root" has been used in veterinary medicine to treat dropsy and other ailments (Uphof 1968). Phenanthroindolizidine alkaloids are characteristic constituents of some genera of Asclepiadaceae, including subgenus *Vincetoxicum* (Liede 1996; Staerk et al. 2000), and are strongly cytotoxic. Biochemical studies focusing specifically on *C. louiseae* and *C. rossicum* have not been done. In post World War I Germany, *C. vincetoxicum* was grown as a fiber plant (Hegi 1927), but no published information is available on the potential for using *C. rossicum* and *C. louiseae* as fiber crops.

(c) *Legislation* — Neither species is listed in any Canadian Federal or Provincial Noxious Weed or Seeds Acts, nor are they listed as noxious weeds in Federal or State Weed or Seed statutes in the United States. "Dog Strangling Vine" is, however, designated as a noxious weed under the Weed Control Act of Ontario in Blanchard Township, Perth County (M. Cowbrough, personal communication).



Fig. 6. Seedling of *Cynanchum rossicum* about two wk after initial emergence in the greenhouse. Note the two seedlings originating from a single seed via polyembryony.

4. Geographical Distribution

The present distribution of both species in Canada is in southern Ontario and southwestern Quebec (Fig. 7). *C. vincetoxicum* is an occasional garden escape, but has not naturalized (see above).

I. *Cynanchum rossicum*. The more common *C. rossicum* occurs mostly between London and Ottawa in southern Ontario, but it has been found at Montreal and has recently established in the Outaouais region of west Quebec (Fig. 7A). Although there is an old (1885) specimen of *C. rossicum* collected by James Fletcher from "cultivated ground" in Victoria (Moore 1959; Pringle 1973), this species has not become established in British Columbia (Douglas et al. 1998). *C. rossicum* is also widely distributed in central New York State. On the basis of US herbarium specimens, it occurs in Connecticut, Indiana, Massachusetts, Michigan, New Hampshire, New Jersey, New York, and Pennsylvania (Sheeley 1992; Sheeley and Raynal 1996) and in Missouri (Kartesz 1999).

Although widely grown in botanical gardens in Europe, there are few reports of *C. rossicum* escaping cultivation on that continent. It has been reported to have spread from cul-

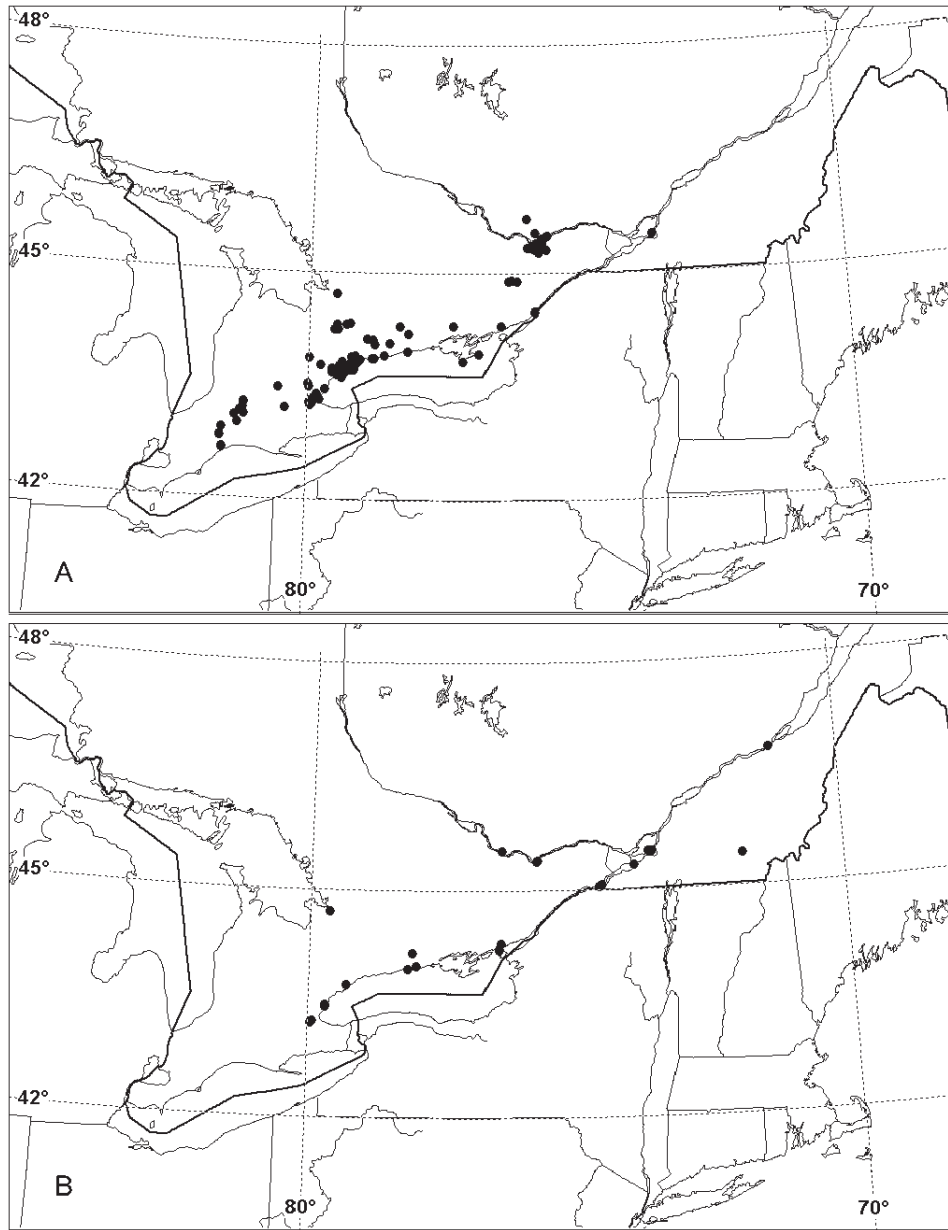


Fig. 7. Distribution of *Cynanchum* species in Canada plotted from specimens at CAN, DAO, HAM, MICH, MT, QFA, QUE, SFS, TRT, TRTE, UWO, WAT (herbarium acronyms after Holmgren et al. 1990) A. *C. rossicum* (207 specimens); B. *C. louiseae* (59 specimens).

tivation in Germany by Markgraf (1971). It has become highly invasive in Norway, where it was introduced prior to 1865 (Lauvanger and Borgen 1998).

The species was originally described from the Kharkov region (near Kiev) in the Ukraine and is apparently endemic to southwestern European Russia in regions north of the Black Sea and the Caucasus (Pobedimova 1952).

II. *Cynanchum louiseae*. Populations of *C. louiseae* are scattered in southern and eastern Ontario and in southern Quebec, mostly around Montreal (Fig. 7B). Based on US herbarium

specimens, *C. louiseae* is known from: Connecticut, Illinois, Indiana, Maine, Maryland, Massachusetts, Michigan, Missouri, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, and Wisconsin (Sheeley 1992; Sheeley and Raynal 1996). The species has also been reported from California, Kansas, Kentucky (probably in error), Minnesota, and Nebraska (Sanders 1996; Kartesz 1999; USDA 2000; Cholewa 2002).

It is endemic to southwestern Europe, primarily in the Iberian Peninsula, southern France and northern Italy (Pobedimova 1952; Markgraf 1972).

5. Habitat

Unless otherwise indicated, information provided in sections 5(b) and 5(c) is based on herbarium specimen label data and/or authors' personal observations.

(a) *Climatic requirements* — Both species grow in temperate climates in Eurasia and North America.

I. *Cynanchum rossicum*. In North America, the species is distributed in areas with mean January temperatures from 0.7°C (at New York, NY) to -10.8°C (at Ottawa, ON); mean July temperatures from 20.7°C (at Ottawa) to 26.4°C (at St. Louis, MO); and, mean annual precipitation from 776 mm (at Toronto, ON) to 1206 mm (at Boston, MA) (Court 1974, Hare and Hay 1974). The Canadian and US conditions are similar to that of its native range in the Ukraine (Lydolph 1977).

II. *Cynanchum louiseae*. Indigenous to southwestern Europe, *C. louiseae* has adapted to more rigorous conditions in North America. Within the North American range, mean January temperatures range from 0.7°C (at New York), to -11.5°C (at Quebec, QC); mean July temperatures from 19.3°C (at Quebec) to 26.4°C (at St. Louis); and, mean annual precipitation from 631 mm (at St. Paul, MN) to 1206 mm (at Boston) (Court 1974; Hare and Hay 1974). Climate in its North American range is generally cooler (or more extreme) and wetter than at Marseilles, in southern France, or Lisbon in Portugal, where mean January temperatures are 5.5°C and 10.8°C, mean July temperatures are 23.3°C and 22.2°C and mean annual precipitation is 546 mm and 707.5 mm, respectively (Arléry 1970; Escardó 1970). At least one North American population, Riverside, CA, occurs at a considerably warmer and drier site. Mean temperatures are 19.1°C and 34.3°C for January and July, respectively, and the annual precipitation is 255 mm (Western Regional Climate Center 2003).

(b) *Substratum* — Both *C. rossicum* and *C. louiseae* are upland species. Rivers and streams that experience spring flood scouring, such as flood plain ravines along Lake Ontario and the banks of the Connecticut River near Windsor (VT), have been extensively invaded. Habitats subject to hydrologic extremes such as the alvar communities, rocky outcrops and coastal areas are often colonized.

I. *Cynanchum rossicum*. The species is typically associated with calcareous soils. In Ontario and western Quebec, *C. rossicum* occurs primarily on shallow soils over limestone bedrock, silty and sandy loams, glacial till, deep loams of upland woods and rocky or clay loam based ravines. Western Quebec populations also occur on shallow mineral and sandy loam soils over limestone bedrock, and loamy soils over igneous bedrock. It often grows along open rocky or gravelly shores. In study sites near Toronto (ON), populations were found growing on sand loams and loamy sands overlying glacial till with carbonate deposits in the upper layers indicating a fluvial origin (Christensen 1997). In Ottawa, it is often abundant in sunny undisturbed old fields (Ernst and Cappuccino 2005) and along railway lines where

it forms dense stands in the well-drained ballast of the roadbeds and embankments.

In central New York State, *C. rossicum* populations are found on shallow soils over limestone bedrock to deep moderate or well-drained silt-loam soils in wooded ravines, calcareous cliff and talus slopes, alluvial woods, pastures and grasslands (Lawlor 2000). Sheeley (1992) found soil depths at his central New York State *C. rossicum* study sites to be variable, but having a mean soil depth of 9.5 cm. He found a mean soil pH of 6.7 at a shaded site and 7.0 at an open site. At other sites studied in central New York State, pH ranged from means of 5.9 to 7.2, and up to 8.0 at dredge fill sites (Lawlor 2000).

Cynanchum rossicum is tolerant of wide variations in moisture and exposure levels. Populations of *C. rossicum* at Great Gully Preserve (NY) colonize moist, well-drained alluvial soils in shaded riparian zones, while in Jefferson County (NY) populations growing on limestone bedrock sustain spring flooding and July drought (Lawlor, personal observation).

In the eastern Ukraine, *C. rossicum* grows on stony soil in meadow steppes and outcrops and is usually associated with calcium and carbonates (V. Onyschenko, personal communication).

II. *Cynanchum louiseae*. Roadside infestations are common in southern Ontario and Quebec, where soils are usually alkaline and often salinized from de-icing salts. Most populations occur in areas dominated by limestone bedrock, although it is sometimes found on igneous rock substrates (e.g., Mont Royal, QC) or sandy areas of low pH. In New England, it is reported to grow above the high tide mark on rocky coastal shores and is becoming an increasing concern on off-shore islands of coastal Maine (A. Haines, personal communication). Although most frequently found associated with calcareous or alkaline soils, some populations are found at sites in Rhode Island and parts of New England which have acidic soils (B. Brumback, personal communication).

In southern France, *C. louiseae* grows on slopes and stony, dry areas from sea level to 500 m in elevation in the lower Pyrenees (Fournier 1977).

(c) *Communities in which the species occurs* — In North America, both *C. rossicum* and *C. louiseae* are associated with disturbed and waste areas, such as transportation corridors, limestone quarries, abandoned pastures and old fields, Christmas tree plantations and other perennial cropping systems. The species are ecologically similar, flourishing in sunny open areas, shrubby habitats and hedges. Once established, they will readily move into nearby, less disturbed habitats. Both species may dominate in the herbaceous vegetation, however plant densities are usually considerably less in shaded habitats under forest canopies than in sunny locations.

I. *Cynanchum rossicum*. It has been reported on the edges of alluvial woods, railroad embankments, fencerows, woods (maple, beech, oak and ash) in Ontario and western Quebec, and gardens, grassy slopes, and streambanks in southern Ontario (Moore 1959; Kirk 1985). Colonized habitats also

include grasslands (verges, lawns, old fields, etc.), pastures, hedgerows, gardens, etc. In Ontario, *C. rossicum* often grows in the forest understory associated with trees, such as eastern red-cedar (*Juniperus virginiana* L.), northern white cedar (*Thuja occidentalis* L.), white ash (*Fraxinus americana* L.), prickly-ash (*Zanthoxylum americanum* Mill.), eastern hop hornbeam [*Ostrya virginiana* (Mill.) K. Koch], sugar maple (*Acer saccharum* Marsh.) and basswood (*Tilia americana* L.). Understory shrubs and herbaceous plant species often found growing with *C. rossicum* include Virginia creeper [*Parthenocissus quinquefolia* (L.) Planch.], poison-ivy [*Toxicodendron radicans* (L.) Kuntze], white snakeroot [*Ageratina altissima* (L.) King & H. Rob.], herb-Robert (*Geranium robertianum* L.), garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande], European buckthorn (*Rhamnus cathartica* L.), Jack-in-the-pulpit [*Arisaema triphyllum* (L.) Schott], May-apple (*Podophyllum peltatum* L.), grey twig dogwood (*Cornus foemina* Mill.) and Canada goldenrod (*Solidago canadensis* L.) (Lawlor 2000; herbarium specimen label data). Other vegetation present in the Highland Creek valley infestation of *C. rossicum* in Toronto include riverbank grape (*Vitis riparia* Michx.), wild red raspberry (*Rubus idaeus* L.), goldenrods (*Solidago* spp.), tufted vetch (*Vicia cracca* L.), grasses (*Agrostis*, *Bromus*, *Phleum*) and other herbaceous species as well as white spruce [*Picea glauca* (Moench) Voss], Scotch pine (*Pinus sylvestris* L.) and staghorn sumac [*Rhus hirta* (L.) Sudw.] (Christensen 1997). Common forbs found in several old field communities near Ottawa included tall goldenrod (*Solidago altissima* L.), common milkweed (*Asclepias syriaca* L.), New England aster (*Aster novae-angliae* L.), Canada thistle [*Cirsium arvense* (L.) Scop.], garlic mustard (*Alliaria petiolata*) and purple loosestrife (*Lythrum salicaria* L.) (Ernst and Cappuccino 2005).

In New York State, it occurs in habitats with a variety of plant communities including calcareous shoreline outcrops, calcareous cliff and talus slopes, successional old fields, successional shrublands and forest openings, calcareous pavement barrens and limestone woodlands, riverside sand/gravel bars, rich mesic maple-basswood forests, successional northern hardwoods, pastureland, conifer plantations, limestone quarries, dredge spoils, and brushy cleared land with a suite of non-native wasteland weeds (Reschke 1990; Sheeley 1992; Lawlor 2000).

The native habitat of *C. rossicum* is steppe, sandy hills and ravines (A. Gassmann and S. Y. Reznik, personal communication). In the Ukraine and southwestern Russia, it is found in forest-steppe and steppe zones (Visulina 1957; Pobedimova 1978; V. Onyschenko, personal communication), on slopes of ravines and scrub habitats (Pobedimova 1952).

II. *Cynanchum louiseae*. In Ontario and Quebec, *C. louiseae* has been found in grazed pasture, hedges, gardens, dry-mesic oak-maple forests, tree plantations, cedar woods, small woodlots and thickets, as well as various ruderal habitats such as ditches, fencerows, vacant lots and roadsides (Alex 1992; herbarium specimen label data). In North America, it is found in a wide range of upland habitats and is primarily a species of woods and moist sunny areas

(Gleason and Cronquist 1991), waste places and ruderal habitats (Britton and Brown 1913). Other habitats where it has been found in the United States include prairies, maple-beech woods and swampy meadows (Sheeley 1992). In southeastern Europe it is reported to occur in copses and bushy places (Polunin and Smythies 1973; Fournier 1977).

6. History

Detailed information on the early establishment and occurrence of *Cynanchum* species in Canada is given by Moore (1959) and Pringle (1973) and for the United States by Sheeley and Raynal (1996). Based on herbarium specimen label data, Sheeley (1992) determined that populations of *C. louiseae* at Peoria County (IL) and *C. rossicum* at Great Gully (NY) may have persisted 70 yr or more since establishment. Certainly the population of *C. rossicum* at Ottawa (ON) has been present for at least this length of time (see below).

I. *Cynanchum rossicum*. The earliest Canadian specimen of *C. rossicum* was collected in 1885 in Victoria (BC) and described as adventitious by Macoun (1897). The species has not persisted in British Columbia (Moore 1959; Douglas et al. 1998). Moore (1959) reported that the first collection in Ontario was in 1889 at Toronto Junction (but this specimen could not be located). The earliest collection seen was by W. Scott from Hamilton in 1900 (specimen at TRT). Information on the specimens is insufficient to determine whether these early Ontario records were of cultivated or adventitious plants. A collection from a naturalized population was made in Ottawa on the Central Experimental Farm in 1931 (specimen at DAO) which may have originated from ornamental planting as early as 1905 (Pringle 1973).

The first collections of *C. rossicum* in the northeastern United States were from Monroe and Nassau counties (NY) in 1897 (Sheeley and Raynal 1996). Herbarium specimens examined document the earliest State records as: Massachusetts, 1919; Pennsylvania, 1927; New Jersey, 1938; Connecticut, 1942; Indiana, 1961; New Hampshire, 1979; and, Michigan, 1985. It was, however, not until the papers of Monachino (1957) and Moore (1959) that *C. rossicum* was distinguished from *C. louiseae* in North America.

II. *Cynanchum louiseae*. The history of *C. louiseae* in Canada is obscured by its confusion with *C. rossicum*. Moore (1959) stated that *C. louiseae* was represented by only a single collection from Montreal (1949). Pringle (1973), however, noted collections of *C. louiseae* from Northumberland County (ON) in 1952 and 1956 and a separate introduction in 1955 at Hamilton (ON), where it escaped from cultivation at the Royal Botanical Gardens. A number of collections of *C. louiseae* were made in the Kingston (ON) area in the 1960s (Pringle 1973), which might trace to introduction from Cambridge (MA) to George Lawson's botanical garden prior to 1863 (Dore 1967; Pringle 1973). Another early report of *C. louiseae* as a garden weed was at Queen Victoria Niagara Falls Park (ON) (Cameron 1895), but no supporting specimen has been found, nor has its presence in the Niagara region been confirmed (Hamilton 1943; Yaki 1970).

The earliest North American herbarium specimen was collected in Ipswich, Essex County (MA) in 1854, but this collection bears little information. A subsequent collection from Essex County (MA) in 1864, states “escaping from the botanic garden where it is a weed and promising to become naturalized” and “Has become naturalized” (Sheeley 1992). The fifth edition of Gray’s *Manual of Botany* (Gray 1867) reported *C. louiseae* as a weed escaping from gardens in the Cambridge (MA) area.

7. Growth and Development

(a) *Morphology* — Both species produce a stout, rhizome at the root crown which gives rise to perennating buds. These rhizomes assist perennation, but do not seem to facilitate population spread. If the main aerial stem is damaged, buds on the rhizome readily sprout to produce multiple axillary shoots. A deep rhizome system and clonal growth was reported for *C. louiseae* by Lumer and Yost (1995), but this has not been confirmed by other workers. The fibrous root system is extensive and tenacious so that plants are not easily pulled from the ground. Species in the subgenus *Vincetoxicum* all have wind-borne, polyembryonic seeds facilitating long-distance dispersal and seedling establishment.

Sheeley (1992), studying plants in Onondaga Co. (NY), found that the mean stem length of shade-grown *C. rossicum* plants was significantly longer (136.3 cm, SD = 4.8) than that of plants in sunny locations (65.1 cm, SD = 3.6), but that the stem weights were not significantly different (1.33 g, SD = 0.07, versus 1.30 g, SD = 0.15, respectively). Production of longer stems by shaded plants may be adaptive in that it allows them to overtop shrubs and other competitive vegetation, thus capturing greater quantities of light as well as providing increased height for launch of wind-dispersed seeds.

(b) *Perennation* — Both introduced species are perennial, herbaceous vines. Overwintering is by seeds and the woody rhizomatous rootstock (Fig. 2). Culms senesce in late summer or early autumn, after seed dispersal. Dead stems usually persist through the winter and those twined around supportive vegetation will persist for a few seasons. At the beginning of the growing season one of the perennating buds on the root crown will sprout. If late frosts destroy the tender top growth, another bud will sprout (Lawlor, personal observation). In forested areas, non-reproductive plants may persist for decades until a gap-forming event provides favourable light conditions for successful reproduction (Sheeley 1992).

(c) *Physiological data* — In the sun, mean xylem water potentials of *C. rossicum* plants were -0.062 mPa at mid-day and -0.079 mPa at pre-dawn compared with -1.6 mPa and -0.12 mPa, respectively for a *Solidago* sp. (Sheeley 1992). Mean xylem water potentials of *C. rossicum* in the shade were -0.430 mPa and -0.233 mPa during mid-day and pre-dawn, respectively. The low water tensions for *C. rossicum* suggest good drought tolerance (Sheeley 1992).

In a study of *C. vincetoxicum* in Hungary, Nemeth (1974) found that the foliage area capable of assimilating photo-

synthates peaked in late June at the same time that peak shoot dry weight was reached. The relative moisture content of rhizomes and roots also peaked about 2 wk before peak shoot weight. The dry matter shoot-to-root ratio was found to be highest at the end of the growing season.

(d) *Phenology* — Seed germination and seedling emergence occurs in early autumn (September–October), as well as in the spring (May) in both species. In eastern Canada and the northeastern United States, shoots of both species typically emerge in late April to early May. Stems are approximately 5 cm long before leaves begin to enlarge and unfurl (Sheeley 1992). Flowering appears to be indeterminate with flower and fruit development occurring simultaneously.

I. *Cynanchum rossicum*. In a 1997 study by Christensen (1998), marked plants of *C. rossicum* populations in open and in semi-shaded locations in the lower Don River Valley (ON) emerged in mid-May and showed rapid stem elongation until mid-June. Inflorescences were usually visible among the top leaves before the elongating stems began to twine. Stem growth tapered off in early July, and most flowering occurred from mid-June to early July, with some flowering continuing through to mid-August. Fruit development began around the third week of June and continued until mid-August, when most pods were fully enlarged and seed dispersal began. All marked plants had senesced and fruits dehisced by the end of September. The time of fruit dehiscence was similar in an Ottawa (ON) population studied by St. Denis and Cappuccino (2004) in the 2001 season, where fruits began to dehisce from 10th–17th August. Flowering of *C. rossicum* in central New York State began around mid-May, when stems were about seven or eight nodes in length and peaks about 5 wk after stem emergence during the first week of June (Sheeley 1992). Immature fruits were apparent by the first week of June. Similar patterns were observed at several central and northern New York State sites, but flowering was delayed about 10 d at the most northern site (Lawlor 2000; Smith et al. 2004). Fruits began to enlarge within 4–5 wk of flowering, although development appeared to be somewhat delayed in more northerly sites. Fruit dehiscence began by the third week of July in sunny sites at all locations (Lawlor 2000). In shaded sites, it is not unusual to see axillary shoots of *C. rossicum* in August bearing mature fruits and flowers simultaneously.

II. *Cynanchum louiseae*. Lumer and Yost (1995) observed populations of *C. louiseae* in sunny locations in the Hudson Highlands (NY) over two seasons where flowering began in late May, peaked in mid-June and ended in mid-July. In more southerly sites along the Hudson River, flowering began 2 wk earlier and in shaded sites continued into mid-August. Flowers began to open just after sunrise and took 20–30 min to fully open. They reported that individual flowers remained open for 6 to 8 d and were shed 1 to 2 d after closing. Fruit pods began to dehisce and release seed in mid-August and continued through to early October. In southern New York State, *C. louiseae* began to flower in late May, peaked in mid-June and ended by mid-July or mid-August

in shadier locations. Fruit ripening and first seed release began mid-August and continued to mid-October.

(e) *Mycorrhiza* — Plants of *C. rossicum* from open sunny sites and forested sites in central New York State readily established symbiotic associations with native arbuscular mycorrhizal fungal (AMF) populations (Greipsson and DiTommaso 2002; L. Smith, personal communication). Moreover, at each of the sites, soils from areas invaded by *C. rossicum* had greater mycorrhizal inoculum potentials (MIP) than soils from adjacent areas where *C. rossicum* was absent. If the plant has an effect on the composition of the soil microbial community this might well contribute to the displacement of the resident vegetation. Ongoing research by A. DiTommaso, S. Greipsson and L. Smith is focusing on the role that AMF play in mediating the invasion of different habitats by this aggressive weed.

8. Reproduction

(a) *Floral biology* — Both species are self-compatible and either insect-pollinated or self-pollinated (Lumer and Yost 1995; St. Denis and Cappuccino 2004). At least some populations of *C. vincetoxicum* are also known to be self-compatible (Leimu 2004). The complex insect pollination system in *Cynanchum*, and *Asclepiadaceae* in general, is described in detail by Knuth (1909), Müller (1883) and Kunze (1991). A structure, known as a pollinarium, serves as the pollen dispersal unit. Pollen grains in each anther theca are grouped together in a glutinous or waxy sac-shaped pollinium and the neighbouring pollinia from adjacent anthers become joined by a yoke-like structure called a translator. The translator consists of two arms attached to the respective pollinia and centrally joined at a notched corpusculum (Woodson 1941; Kunze 1991). The anthers are fused with the stigmatic disk into a specialized structure referred to as the gynostegium. The presence of nectaries opposite the corpuscula and angled under the gynostegium results in the pollinaria attaching to bristles on the visitors' probosci (or legs) as they are withdrawn from the nectaries.

In the glasshouse, in situ pollen germination of *C. rossicum* occurs within a day after anthesis (St. Denis and Cappuccino 2004), with pollen tubes eventually reaching the stigmatic surface to effect self-fertilization (autogamy). The lengthening pollen tubes make it increasingly difficult for insects to extract older pollinia. Woodson (1941) has observed a few cases of *Asclepiadaceae* flowers where one pollinium was attached to the stigmatic surface and the other pollinium was still in its anther sac, suggesting that extracted pollinaria attached to stigmatic surfaces may not always represent cross-pollination events. In situ pollen germination in various *Asclepiadaceae* may be stimulated by the moistening of pollinia by nectar secretions or rain (Kunze 1991).

Pollination syndromes found in many species of subgenus *Vincetoxicum* include sapromyophily, the presence of fetid odours and dark brown-purple flower colouration (which attracts insects such as carrion and dung flies) and myophily, the presence of light or dull flower colours, little odour and easily accessible nectar (Lumer and Yost 1995). The depressed number of flowers produced and seed set of these

species in shaded locations may be partly due to different resource allocation within the plants and partly to smaller populations of suitable pollinators in such canopied habitats.

I. *Cynanchum rossicum*. In a greenhouse study, St. Denis and Cappuccino (2004) found no differences in the initiation of fruit development between self- and cross-pollinated *C. rossicum* plants and Lawlor (unpublished data) confirmed self-fertilization in *C. rossicum* in the field. Both Christensen (1998), in Ontario, and Lawlor (unpublished data), in New York State, observed insect visitors on *C. rossicum* including: flies (*Anthomyiidae*, *Calliphoridae*, *Sarcophagidae*, *Syrphidae* and *Trixoscedididae*), ants (*Formicidae* and *Myrmicinae*), bees and wasps (*Vespidae* and *Halictidae*), and beetles (*Curculionidae* and *Carabidae*).

In a study of an old-field population at Ottawa (ON) in 2001, ants were the only diurnal floral visitors observed that were likely to effect pollination (St. Denis and Cappuccino 2004). The authors speculated that since *C. rossicum* flowers have a somewhat sweet odour (at least during the day), they may also be visited by nocturnal pollinators. Flowers on scattered (more isolated) plants were found to have more insect visitors than those of plants in dense adjacent monocultures, as estimated by the absence of pollinaria (St. Denis and Cappuccino 2004). This might be due to an influence on pollinator habitat in dense populations, a dilution effect of high numbers of flowers and/or shifts in pollinator foraging behavior in habitats with patchy resources.

II. *Cynanchum louiseae*. Self- and cross-pollination have been confirmed in *C. louiseae* with only flies identified as carriers of pollinaria, largely via the proboscis (Lumer and Yost 1995). Of the flies collected from target plants, six species from four families were identified as probable effective pollinators, including *Pollenia rudis* Fabricius and *Phaenicia sericata* Meigen (*Calliphoridae*, blow flies), *Sarcophaga* spp. (*Sarcophagidae*, flesh flies), and unidentified members of the *Anthomyiidae* and *Tachinidae*. No egg laying by flies was observed (Lumer and Yost 1995). Only 4.2% of bagged flowers produced mature fruits with viable seeds, compared with 11.1% of open-pollinated flowers (Lumer and Yost 1995).

(b) *Seed production and dispersal* — Both *C. rossicum* and *C. louiseae* produce seeds bearing a coma of long hairs which facilitates their dispersal by wind. While most seeds fall close to the parent plant (Cappuccino et al. 2002), long distance dispersal is possible.

I. *Cynanchum rossicum*. In a field experiment at Ottawa in 2001 by St. Denis and Cappuccino (2004), fruit set occurred in 25% of flowers produced by plants transplanted and grown in pots (originating from the same population). Insect visitation of flowers (i.e., pollinarium removal) increased the likelihood of fruit-set and increased incidence of seed polyembryony (see Section 8c). An experiment was conducted on plants from the same population grown in a greenhouse to examine the effect of pollinaria removal on fertility (St. Denis and Cappuccino 2004). Pollinaria were

either removed and placed on the stigmatic disk of the same flower (self-pollinated) or on flowers of other plants (cross-pollinated), with control flowers being un-manipulated. Flowers in all treatments showed 75% fruit-set and there was no significant difference between cross-pollinated versus self-pollinated flowers for fruit-set, number of seeds per pod, mean seed weight or polyembryony. These results are similar to those reported for greenhouse experiments on plants of *C. vincetoxicum* from isolated island populations in Finland by Leimu (2004).

Seed production in *C. rossicum* is affected by the amount of light received. Ramets in a shaded site in New York were found to be less fecund than those at a sunny site; they produced more cymes but fewer and lighter follicles having fewer seeds (Sheeley 1992). Plants in heavily shaded forest understories produced very few flowers and generally did not produce seeds, but may persist for years exploiting any canopy disturbance that may occur. At an open sunny site, ramets produced an average of 6 cymes and 33 flowers resulting in 8 mature follicles containing 10 seeds, with an average weight of 5.2 mg per seed. Total seed production at this site was estimated at 2090 seeds m^{-2} . In a partially shaded site, ramets produced an average of 3 cymes and 25 flowers resulting in 2 mature follicles each containing 7 seeds, with an average weight of 63.3 mg per seed. Total seed production in this site was estimated at 1330 seeds m^{-2} .

Lighter seeds of *C. rossicum* generally disperse over longer distances ($r^2 = 0.151$; $P = 0.0001$), but are less likely to germinate in a grass stand than heavier seeds (Cappuccino et al. 2002). At an average wind speed of 11.2 km h^{-1} , seeds traveled up to 18 m from their release point, with 50% of the seeds falling within 2.5 m of the release point.

(c) *Seed banks, seed viability and germination* — In North America, newly matured seed of both species of *Cynanchum* are usually dormant, although both produce some seeds which lack dormancy and will germinate without stratification. Greater germination (49%) occurs when seeds overwinter in the field than when not provided a cold treatment (28%) (Lumer and Yost 1995). The mechanisms that control seed dormancy in *Cynanchum* are not known.

I. *Cynanchum rossicum*. In a greenhouse study, Cappuccino et al. (2002) observed a total germination of 44.6% for November-collected seeds of *C. rossicum* from plants growing along the edge a mowed field in Ottawa when provided a 14 h photoperiod and no cold treatment. Larger seeds germinated later. In a parallel study, 34.5% of 142 *C. rossicum* seeds subjected to a 3-mo stratification period at 4°C and planted in trays containing a mixture of grasses germinated over the 57-d duration of the study, whereas 44.5% of 142 seeds germinated in trays without the grass mixture (Cappuccino et al. 2002). Germination continued for 47 d from the start of the trial with 50% of seeds germinating within a 3-d period (days 11–13 following planting). This corroborates Sheeley's (1992) work in New York State that found most germination of *C. rossicum* seeds collected in October and stored at 4.5°C for 1 or 6 mo occurred between 8 to 17 d, but continued for up to 40 d. In general, heavier

seeds were found to germinate later than lighter seeds especially for seeds producing either one or two seedlings. Seeds of *C. rossicum* freshly collected in late summer and early autumn from a heavily shaded forest site in central New York State were larger (5.3 mg, SE = 0.04) and more dormant (19.9% germination after 4 wk) than seeds from an adjacent open field site (3.8 mg, SE = 0.04; 48.0% germination) when subjected to controlled growing conditions of 25–17°C day-night temperatures and a 14 h photoperiod (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (DiTommaso et al. 2005). Moreover, for all sites combined, 90% of seeds weighed between 2.3 and 7.7 mg. Non-stratified seeds, from Onondaga Co. (NY), which were kept in storage for 4–5 wk with no light and subjected to a 21–13°C (14–10 h) cycle during the first flush of germination followed by a 27–20°C cycle, yielded 36% germination. Whereas, those exposed to the same temperature conditions with a 14 h photoperiod during storage yielded 46% germination (Sheeley 1992). Seeds from the same source stored for approximately 7 mo and started in a greenhouse on May 15, had a 22.5% germination rate under 31–25°C (day-night) and ambient light (Sheeley 1992). Germination began approximately 8 d after the start of trials, irrespective of treatment. Following 18 wk of dry storage at 4°C, seeds of *C. rossicum* collected in early November from three central New York State sites showed significantly greater total germination (27%) after 4 wk at 25–17°C day-night temperature and a 14 h photoperiod (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in a growth chamber than seeds from the same populations collected in late August at 13% germination (DiTommaso et al. 2005).

The seeds of many species in subgenus *Vincetoxicum* are polyembryonic, giving rise to varying numbers of plantlets (Fig. 6). The supernumerary embryos in *C. rossicum* and *C. louiseae* were observed by von Hausner (1976) to arise from nucellar cells in the micopylar region of the seed coat (i.e., adventitious polyembryony). In an earlier study, however, Seefeldner (1912) reported that cleavage was the cause of polyembryony in *C. vincetoxicum*. The common occurrence of polyembryony in these species may be an adaptation to conditions limiting successful pollination. The staggered emergence of seedlings may also be adaptive in environments with large temporal variability in climatic conditions and predation, especially for single seeds which have been dispersed over a great distance and are founders of new populations.

Cappuccino et al. (2002), studying material from Ottawa, found that of 112 *C. rossicum* seeds that germinated under greenhouse conditions (natural light supplemented with artificial light, 14–10 h), 44.7% produced a single seedling, 45.5% produced two seedlings and 9.8% produced three seedlings. They also found that seed size was not related to polyembryony. Polyembryony had a significant effect on seedling weight in a no competition study, with the combined weight of double seedlings almost 50% greater than that of single seedlings. In both greenhouse and field experiments at Ottawa in 2001, over half of the seeds produced were polyembryonic, with two to four embryos per seed (St. Denis and Cappuccino 2004). Sheeley (1992) observed multiple radicles protruding from seed coats of germinated *C. rossicum* seeds collected from central New York State

sites. Most germinated seeds produced two (34.7%) or three (40.3%) seedlings, while single seedlings occurred in 22.2% and four seedlings occurred in 2.8% of germinated seeds. Peak germination levels occurred between 8 and 17 d for all embryonic classes. Embryo vigour was variable, with some seeds producing multiple seedlings of equal size and vigour, while other seeds produced a combination of large vigorous seedlings as well as smaller less vigorous seedlings or seedlings which germinate at different times (Fig. 6; St. Denis and Cappuccino 2004). The polyembryonic status of *C. rossicum* seeds collected from two open-field and one forest understory sites in central New York State was not correlated with seed weight for two of the three sites. In the forest understory site, the likelihood of more than one embryo germinating from a seed increased with seed weight (DiTommaso et al. 2005). Polyembryony rates in Ukrainian material of *C. rossicum* were: one embryo, 13.2%; two embryos, 39.4%; three embryos, 34.6%; four embryos, 7.6%; five embryos, 5.2% (von Hausner 1976).

Given the polyembryonic nature of *C. rossicum* seeds, the number of embryos produced per unit area may be a better measure of reproductive potential in this species than seed production alone. Hence, in the sites studied by Sheeley (1992), seed production of about 2090 seeds m⁻² in open sites and 1330 seeds m⁻² in partially shaded sites, may yield approximately 4680 embryos m⁻² and 2980 embryos m⁻², respectively.

Seedling biomass of *C. rossicum* in Ottawa populations was affected by competition with grasses (Cappuccino et al. 2002). Regression of seedling weight on germination date found negative residuals for 98% of seedlings in competition with grasses compared with positive residuals for 90% of seedlings growing without competition ($r^2 = 0.203$; $P < 0.0001$). Negative residuals indicate that seedlings in a given treatment were smaller than expected based on the length of time they were grown. Although seed size did not affect germination in the presence of competition with grasses, seedlings from larger *C. rossicum* seeds were heavier than seedlings from smaller seeds (Cappuccino et al. 2002).

II. *Cynanchum louiseae*. Of seeds collected from newly opened pods in early September in Dutchess County (NY) and placed in petri dishes with moistened filter paper 2 d later in direct light and at room temperature (approximately 22°C), 28% germinated that same autumn, while 49% of seeds germinated the next spring after the overwintering period (Lumer and Yost 1995). Under the same conditions, seeds produced by self-fertilization (bagged flowers) were found to have a similar germination (40%) to that of open-pollinated flowers (49%).

Polyembryony rates in European material of *C. louiseae* were reported by von Hausner (1976) as: one embryo, 61.5%; two embryos, 31.1%; three embryos, 4.9%; four embryos, 1.9%; five embryos, 0.6%.

(d) *Vegetative reproduction* — Both species have woody rootstocks which form short, more or less horizontal, underground stems (rhizomes). Buds form along the rootstock, as well as lower stem nodes, which give rise to aerial stems. Separate

plants are formed when the rootstock is mechanically fragmented. Spread of plants via rootstalk growth is not a significant factor in the population expansion of either species.

I. *Cynanchum rossicum*. Spreading rhizomes have not been detected in this species (Fig. 2; Sheeley and Raynal 1996; authors' personal observations). Colony expansion and reproduction occurs primarily via seed (Sheeley 1992; Christensen 1998; Lawlor 2000). Vegetative reproduction is possible when root crowns are divided into multiple sections with axillary buds. Root crowns of sexually mature plants from New York that had been dug, divided and tossed onto a bare soil surface during a dry July were able to establish, continue growing and reproduce the following season (Lawlor, personal observation).

II. *Cynanchum louiseae*. Rhizomatous connections have been reported between plants of *C. louiseae* by Lumer and Yost (1995) and these authors suggested that typical stands are likely comprised of only one to three different genets. However, such rhizome connections have not been observed by other researchers.

9. Hybrids

Although hybridization is rare in the Asclepiadaceae (Woodson 1941), *C. rossicum* has been purported to hybridize with *C. vincetoxicum* (Markgraf 1971; Lauvanger and Borgen 1998). Hybridization is unlikely in North America since *C. vincetoxicum* is rarely cultivated and occasional escapes are not known to persist (Pringle 1973; Sheeley 1992).

10. Population Dynamics

The climbing habit of these two species implies that they are strong competitors for light, often substantially reducing light availability for supporting forbs, shrubs and saplings. Ongoing experiments by Cappuccino (unpublished data) have shown that extracts of *C. rossicum* roots inhibit germination of radish (*Raphanus sativa* L.) seedlings. The extracts also show broad-spectrum antifungal activity (M. Smith and J.T. Arnason, unpublished data). No information is available on the allelopathic properties of *C. louiseae*.

I. *Cynanchum rossicum*. In preliminary research by Cappuccino (personal communication), *C. rossicum* seeds were collected in Ottawa (ON) and scattered on the soil surface in small plots in both old fields and woodlots near Ottawa where the species did not occur. She observed 30% germination and 85–90% seedling survival during the first year. Using a transition-matrix model, Cappuccino determined that an increase in the rate at which non-flowering individuals became reproductively mature would have the greatest effect on the population growth rate in *C. rossicum*.

In a transplant experiment conducted in 2001–2002, in an old-field in Ottawa (ON), Cappuccino (2004) reported greater biomass and seed set per individual for *C. rossicum* plants that were transplanted into experimental patches with densities of 81 plants m⁻², compared with patch densities of 1 or 9 plants m⁻². The observed Allee effect (i.e., low rate of

increase of small populations relative to large populations) was suggested to be one possible mechanism contributing to the latency period in this invasive species. Moreover, increased reproduction in high-density patches was due to a greater competitive ability of *C. rossicum* plants relative to the resident grasses and herbs rather than to differences in pollinator visitation rates.

Plant densities of *C. rossicum* are affected by light availability. In a study at Onondaga Co. (NY) in early spring 1991, Sheeley (1992) reported mean densities at open and shaded sites at 1922 and 780 stems m^{-2} , respectively. By mid-July, densities had increased to 2019 stems m^{-2} in the open site, but substantially declined to 270 stems m^{-2} in shaded site. This large decrease in density at shaded sites was largely due to a significant decline in the density of stems less than 10 cm long (634 to 122 stems m^{-2}). The density of reproductive ramets at the open site (21.8 stems m^{-2}) was only 25% of that of the shaded site (80.7 stems m^{-2}) (Sheeley 1992). Reproductive stem densities increased slightly during the growing season at both sites with 24.7 stems m^{-2} in the open site, and 86.2 stems m^{-2} in the shaded site at the end of the growing season.

In a 2-yr study site in New York State conducted in 1998–1999, Lawlor (2000) observed that seedling densities varied widely between study plots. In established populations growing under forest canopies only a few seedlings per m^{-2} were found, while in plots with rapidly expanding populations in open-canopy sites (e.g., Henderson), seedling densities varied from a few hundred to approximately 2500 seedlings m^{-2} . She also found that the density of stems greater than 25 cm long was relatively uniform within the habitat type. Regression of density of stems greater than 25 cm high against irradiance showed a positive relationship of stem densities to light levels ($r^2 = 0.63$; $P = 0.0001$). Densities of stems greater than 25 cm long were relatively low (35 to 61 stems m^{-2}) under a forest canopy (33 $\mu\text{mol m}^{-2} \text{s}^{-1}$) compared with 171–185 stems m^{-2} in fully irradiated plots (1555 $\mu\text{mol m}^{-2} \text{s}^{-1}$) where the species was the dominant ground cover. In a different open-canopy site in Henderson (NY), Smith et al. (2004) observed an average 4800 *C. rossicum* seedlings m^{-2} in late June with densities decreasing to 1000 seedlings m^{-2} by early August. It is not clear why seedling densities declined so dramatically over the 2-mo period or whether this is a common occurrence on these sites.

At Henderson (NY), the density and percentage cover of *C. rossicum* stems more than 25 cm in length in May 1998 was 198 stems m^{-2} and 95%, respectively (Lawlor 2000). In May 1999, 17 d after a frost event, the density of stems greater than 25 cm in length was 269 stems m^{-2} and cover was 75%. The lower cover estimate obtained after frost in 1999 was likely due to the cool spring weather delaying growth, as well as young stem death. The increase in stem density between the 2 yr was likely due to greater axillary bud production on the stem and initiation of dormant buds on the root crown. By the end of the 1999 season, stem densities had decreased to 195 stems m^{-2} , whereas cover had increased to 98%, compared with stem densities of 170 stems m^{-2} and 90% cover at the end of the 1998 season (Lawlor 2000).

Within its native range in the Ukraine and southern Russia *C. rossicum* is considered to be of infrequent occurrence (V. Onyschenko, personal communication).

II. *Cynanchum louiseae*. No data are available for North American populations of *C. louiseae*. The species is reported as infrequent in its native range (de Ruffray et al. 2002; V. Onyschenko, personal communication). A field collection trip in 2000 to southern France (Lawlor, unpublished) confirmed this as few populations were found, and these consisted of scattered plants or small patches of 3–15 stems and none exhibited the vigour and competitiveness of North American populations.

More research is required to determine the factors that affect the population dynamics of both species within their native regions.

11. Response to Herbicides and Other Chemicals

Repeated applications of 5% glyphosate to plants with a mean height of 51 cm were necessary to limit regrowth of *C. rossicum* the following year in a population near Toronto, ON (Christensen 1997). One to three applications were made in mid-June, early August, late August and/or in early September. Only those plots receiving applications in June plus early or late August, or in June plus early August and early September, had a reduction in cover greater than 90% the following year. Single applications of glyphosate did not provide satisfactory control. Lawlor and Raynal (2002) compared the effectiveness of two non-selective herbicides, glyphosate and triclopyr, to suppress *C. rossicum* populations in central New York State, when applied either as foliar sprays or to cut stems. Foliar-spray applications were more effective than cut-stem applications in reducing cover and biomass. Mean cover was 77.4% in the control plots versus 28.2%, 20.6% and 20.7% in plots treated with glyphosate (4.1 kg a.i. ha^{-1} , 10.4 kg a.i. ha^{-1}) and triclopyr (2.6 kg a.i. ha^{-1}), respectively. Mean above-ground biomass was 84.2 g m^{-2} in the control versus 15.1, 13.6 and 14.1 g m^{-2} in plots treated with glyphosate (4.1 kg a.i. ha^{-1} , 10.4 kg a.i. ha^{-1}) and triclopyr (2.6 kg a.i. ha^{-1}), respectively. The glyphosate foliar spray treatments were applied at the early flowering stage and the triclopyr foliar-spray was applied at early fruit formation. There were no significant differences in reduction of measured plant parameters among the foliar-spray treatments and effective control using either of these herbicides at recommended field rates required repeated applications. Cut-stem applications of glyphosate (4.1 kg a.i. ha^{-1} and 8.3 kg a.i. ha^{-1}) were found to be significantly more effective than similar treatments with triclopyr (1.9 kg a.i. ha^{-1} , 3.9 kg a.i. ha^{-1} and 7.8 kg a.i. ha^{-1}) at all concentrations tested (Lawlor and Raynal 2002).

In a study on Grenadier Island, NY, glyphosate (1.79 kg a.i. ha^{-1}) was found to be more effective than triclopyr (2.24 kg a.i. ha^{-1}). Both were significantly more effective than a mix of triclopyr and 2,4-D (1.12 : 2.24 kg a.i. ha^{-1}) and a mix of dicamba and 2,4-D (1.12 : 1.07 kg a.i. ha^{-1}). Dicamba (2.24 kg a.i. ha^{-1}) and two levels of 2,4-D (2.13 or 3.19 kg a.i. ha^{-1}) alone were not significantly different from the untreated control. Treatments were applied in late June 2003. Mean *C. rossicum* cover in late May 2004 was 96% in the control and 23, 45, 63, 73, 84, 83 and 89%, respectively, for the above herbicide treatments (Lawlor, unpublished).

In the study sites used by Christensen (personal communication) in Ontario and Lawlor (2000) in New York State,

the presence of both native and introduced herbaceous species increased substantially following herbicide applications. More disturbed sites, however, tended to be colonized to a greater extent by non-native species.

12. Response to Other Human Manipulations

I. *Cynanchum rossicum*. In Ontario repeated mowing reduced average stem height in *C. rossicum* plants, but had no effect on cover (Christensen 1998). Black plastic ground cover suppressed growth while it was intact, but animals repeatedly tore the cover in test plots before the trial could be completed (Christensen 1998).

Cultivation may not kill plants as root crown fragments left on the soil can root even under dry, mid-summer conditions (see Section 8d).

Grazing and trampling can stimulate sprouting from both stem leaf axils and perennating buds on the root crown. In a preliminary comparative study evaluating the efficacy of digging, pulling, and glyphosate application on *C. rossicum* growth at Great Gully Preserve (NY), digging was more effective at controlling *C. rossicum* than herbicide application, and considerably more effective than pulling (S.E. Bonanno, personal communication). Manual removal of fruits from plants is an additional control strategy sometimes employed at sites where digging and spraying cannot be used, such as with plants growing in bedrock crevices of the alvar ecosystems and the Niagara escarpment of Clark Reservation and Split Rock Gulf (NY), as well as rock rubble on and below cliffs on the escarpment (Lawlor, personal observation). This tactic greatly reduces seed pressure within the growing season, but because of the twining growth form of *C. rossicum* plants, mature pods are easily overlooked. To be effective, fruit removal must be repeated through the later part of the growing season as pods continue to mature and dehisce from late July through September. Additionally, cutting or mowing of plants, if properly timed, will prevent both seed production as well as successful re-growth and reproduction within a growing season.

II. *Cynanchum louiseae*. Studies on the control of this species have not been found.

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) Herbivory

(i) *Mammals, including both domestic and wild animals* — No conclusive evidence of the impact on *C. rossicum* by deer has been found in an enclosure study within Ontario and New York alvar systems, although plants likely grazed by deer based on incisor pattern have occasionally been observed (Lawlor, personal observation).

(ii) *Birds and other vertebrates* — There is no information on the consumption of *C. rossicum* or *C. louiseae* by birds. The silky seed comas have been observed incorporated into the nests of some bird species in Ottawa (C. Hanrahan, personal communication).

(iii) *Insects* — There is no information on insect herbivores on Canadian populations of *C. rossicum* and *C. louiseae*,

although herbaria specimens sometimes show limited insect predation. I. *Cynanchum rossicum*. In field surveys near Ottawa, ON, Ernst and Cappuccino (2005) reported that *C. rossicum* stands supported lower numbers of stem- and ground-dwelling arthropods, as well as lower numbers of individuals in most phytophagous feeding guilds, compared with stands of *Asclepias syriaca*, *Solidago altissima* or mixed graminoids. Moreover, *C. rossicum* stands were completely devoid of gall-makers and miners.

II. *Cynanchum louiseae*. In a laboratory study, where monarch butterfly adults were offered *C. louiseae* and common milkweed (*Asclepias syriaca*) in choice tests, adults that fed on *C. louiseae* laid some eggs, but none of the first larval instars survived (Haribal and Renwick 1998). In contrast, adults feeding on common milkweed, the preferred food source, produced healthy first instar larvae. In monarchs, five instar larval stages are generally required before reaching pupation. Field and laboratory studies by Casagrande and Dacy (2001) in Rhode Island with *C. louiseae*, and by DiTommaso and Losey (2003) in New York using both *Cynanchum* species, have been equivocal. Casagrande and Dacy (2001) reported that 21.7% of monarch butterflies oviposited on *C. louiseae* plants in laboratory choice tests, that also included test plants of *A. syriaca*, Oriental lilies (*Lilium speciosum* Thunb.), and common beans (*Phaseolus vulgaris* L.). In a similar study using outdoor cages, 24.5% of monarch butterflies were observed to oviposit on *C. louiseae* (Casagrande and Dacy 2001). In a greenhouse study, DiTommaso and Losey (2003) reported no oviposition by mated monarchs on either *Cynanchum* species in caged choice tests with *A. syriaca*. Larval feeding tests showed a significantly lower proportion of first instar larvae survival on *C. rossicum* (0.44 ± 0.05) and *C. louiseae* (0.14 ± 0.08) than on *A. syriaca* (1.0 ± 0.00) after 48 h (DiTommaso and Losey 2003). Larval weight was significantly lower for larvae fed *C. rossicum* (0.52 ± 0.04 mg) and *C. louiseae* (0.59 ± 0.12 mg), than larvae fed *A. syriaca* (2.57 ± 0.18 mg). The mean proportion of leaf consumed indicated a significant non-preference by monarch larvae for *C. rossicum* (0.03 ± 0.01) and *C. louiseae* (0.02 ± 0.01) over *A. syriaca* (0.51 ± 0.07) (DiTommaso and Losey 2003).

In greenhouse choice experiments by Mattila and Otis (2003), adult monarch butterflies laid an average of 80.7 eggs on *A. syriaca* compared with 0.4 eggs laid on *C. rossicum* over a 48 h period. They also found that 92% of larvae moved to *A. syriaca* leaves and consumed 3.94 cm² of leaf material compared with only 2% of larvae moving to *C. rossicum* and consumption of negligible amounts of leaf material (0.01 cm²). Moreover, larvae feeding on *C. rossicum* did not develop beyond the first instar, and died within 96 h.

Since *C. vincetoxicum* is the most common and widespread of the European Asclepiadaceae, most associated insects have been reported on this species (A. Gassmann, personal communication; Tewksbury et al. 2002). Because of its poisonous properties, herbivores are mainly specialized on this species (Leimu 2004). Specialized insect species include: the leaf eating Chrysomelidae, *Chrysochus asclepiadeus* Pallas and *Chrysomela aurichalcea* ssp. *bohemica* Mann; the weevil

Otiorynchus pinastris Herbst (Curculionidae); and, three dipteran species *Euphranta connexa* Fabricius (Tephritidae), *Contarinia vincetoxici* Kieffer and *Contarinia asclepiadis* Schniffermiller (Noctuidae) feeding on reproductive plant parts. Polyphagous species recorded on species of subgenus *Vincetoxicum* include: the leaf beetle, *Exosoma lusitanica* L. (Chrysomelidae); a spittle bug, *Philaenus spumarius* L. (Cercopidae); and, a few moths, such as *Scopula umbelaria* Hübner (Geometridae), *Sparganothis pillerians* Schiff. (Tortricidae), and *Nothris congressariella* Bruand (Gelechiidae), the last in association with *C. louiseae*.

In Sweden, the moth, *Abrostola asclepiadis* Schniffermiller (Noctuidae) was found to be monophagous on *C. vincetoxicum* (Förare 1995). Seldom more than 1% of available foliage was consumed with the exception of occasional, very local defoliation in patches or on isolated plants (Förare 1995), and the impact of this insect on its host in Europe is considered minimal (Solbreck and Sillén-Tullberg 1986).

The lygus bugs, *Lygaeus equestris* (L.) and *Tropidothorax leucopterus* Goeze (Lygaeinae), are reported to feed on seeds of *C. vincetoxicum* (Kugelberg 1973; Solbreck et al. 1989; Tullberg et al. 2000). The effect of *Lygaeus equestris* on seed production is relatively minimal, given that this insect is primarily a post-dispersal seed predator (Solbreck and Sillén-Tullberg 1986). Although neither insect has been tested on *C. rossicum* or *C. louiseae*, the potential of using these insects as biological control agents is rather limited given their polyphagous feeding behaviour.

The tephritid fly *Euphranta connexa* Fabricius is a pre-dispersal seed predator whose larva live in developing fruits of *C. vincetoxicum*, feeding on the immature seeds (Solbreck and Sillén-Tullberg 1986). Literature records outside of Sweden mention *C. vincetoxicum* or *Cynanchum* spp. as host plants for this fly (Solbreck and Sillén-Tullberg 1986). In general, populations of the fly are affected more by *C. vincetoxicum* pod production, than plant populations are affected by the seed predation of this fly (Solbreck and Sillén-Tullberg 1986). The potential of this fly to limit seed production in *C. louiseae*, and especially in *C. rossicum*, has not been investigated and needs further attention.

(iv) *Nematodes and/or other non-vertebrates* — No information was located.

(b) Diseases

(i) *Fungi* — Species of *Cynanchum*, especially *C. vincetoxicum*, are important alternate hosts for the widespread European rust fungus, *Cronartium flaccidum* (Alb. & Schwein.) G. Winter, the cause of cronartium rust and resin-top on various species in the genus *Pinus* (Moriondo 1980). In Italy, high inoculum concentrations (1×10^6 acidiospores mm^{-1} , or more) of this rust caused significant reductions in foliar biomass of *C. vincetoxicum* in both field and growth chamber studies (Ragazzi et al. 1986). *Cronartium asclepiadeum* (Wildenow) Fries is also known to infest *Cynanchum vincetoxicum* in Europe (A. Gassmann, personal communication).

I. *Cynanchum rossicum*. The susceptibility of *C. rossicum* to rust pathogens has not been determined to date, although

Kaitera (1999) suggested that various species in the *C. vincetoxicum* species complex may be susceptible to *Cronartium flaccidum*.

II. *Cynanchum louiseae*. Infection of *C. louiseae* plants by *Cronartium flaccidum* has been demonstrated under greenhouse conditions, where it is slightly to moderately susceptible (Kaitera et al. 1999). Infection and susceptibility are not known under field conditions. *Cronartium asclepiadeum* is also known to infect *C. louiseae* in Europe (A. Gassmann, personal communication).

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

(iii) *Viruses* — No information was located.

(c) *Higher plant parasites* — No information was located.

14. Prognosis

Both *C. rossicum* and *C. louiseae* were introduced to Canada and the United States from Europe over a century ago as horticultural plants, or perhaps additionally as contaminants in the nursery trade. While *C. rossicum* is documented to have been established (and probably naturalized) in Canada for over a century, *C. louiseae* has been naturalized for at least 50 yr and possibly much longer.

Both species form dense populations in many types of open and semi-open habitats. Their twinning and sprawling habit contributes to their effective competition with pre-existing vegetation, and frequently results in large monocultures. The heavy rootstocks provide an energy and water storage mechanism, which facilitates rapid early season growth and allows for survival in habitats with wide seasonal cycles of water availability. Large quantities of wind-borne seeds are produced, which may be widely dispersed. Polyembryony and facultative self-fertilization are characteristics which facilitate the establishment of populations from a single seed.

Field observations, herbarium specimen data, and distribution patterns (Fig. 7) suggest that *C. rossicum* is both more effective at dispersal and more competitive with pre-existing vegetation in a variety of habitats. While *C. louiseae* forms dense colonies over a wide region in southern Ontario and Quebec, it is more scattered in occurrence and generally has fewer outlying plants around any infestation area. Both species presently appear to be rapidly expanding their range in Canada (and North America), and there is no evidence that they are near to reaching their maximum geographic or ecological distribution. Spread of these two *Cynanchum* species is expected to increase exponentially as more colonies establish, coalesce and become seed sources. Various types of open and semi-open habitats are at risk to future invasion, including prairies, alvars, shores, forest edges, and open forests. In addition to the loss of floral and faunal biodiversity in native and semi-native communities, various perennial cropping systems are also at risk from the increased costs associated with control. Agroecosystems, such as pastures, perennial forage crops, tree nurseries, sugar maple woodlots (used for sap production), vineyards and orchards, are likely to be vulnerable.

Although herbicides have been shown to provide some control of mature plants, they are expensive and impractical to use over large areas, especially where selective management in a diverse plant community is required. Unfortunately, there is little information on the seed biology of either species, but anecdotal observations suggest that large seed banks may be formed in established colonies, which would greatly affect herbicide management techniques and costs. Although some of the indigenous insect fauna on native Asclepiadaceae have been observed to attack the introduced *Cynanchum* species (Section 13), the extent of herbivory is insufficient to provide significant control. Given the difficulties of control, perhaps the most effective single means of slowing spread and reducing competitive abilities of the *Cynanchum* species will be through the development of a biological control program with multiple agents.

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Alex, J. F. 1992. Ontario weeds. Descriptions, illustrations and keys to their identification. 2nd ed. Ontario Ministry of Agriculture and Food, Toronto, ON. 304 pp.

Ali, S. I. and Khatoun, S. 1982. Genus *Vincetoxicum* von Wolf (Asclepiadaceae) in Pakistan. *Pak. J. Bot.* **14**: 61–68.

Aparicio, A. and Silvestre, S. 1985. Números cromosómicos para la flora Española 422–434. *Lagascalia* **13**: 318–323.

Arléry, R. 1970. The climate of France, Belgium, The Netherlands and Luxembourg. Pages 135–193 in C. C. Wallén, ed. *World survey of climatology, Volume 5. Climates of Northern and Western Europe.* Elsevier Publishing Co., Amsterdam, The Netherlands.

Britton, N. L. and Brown, A. 1913. An illustrated flora of the Northern United States, Canada and the British possessions. Volume 3. Gentianaceae to Compositae. Charles Scribner's and Sons, New York, NY. 637 pp.

Bullock, A. A. 1958. Nomenclatural notes: X. On the application of the name *Vincetoxicum*. *Kew Bull.* **13**: 302.

Bullock, A. A. 1967. Nomenclatural notes: XVII. *Vincetoxicum* again. *Kew Bull.* **21**: 351–352.

Burrows, G. E. and Tyril, R. J. 2001. Toxic plants of North America. Iowa State University Press, Ames, IA. pp. 125, 140.

Cameron, R. 1895. Catalogue of plants which have been found growing without cultivation in the park and its outlying territories. Collected, mounted and catalogued for the Park Herbarium in the superintendent's office at Niagara Falls, Ontario. Appendix, Pages 1–46 in Ninth Annual Report of the Commissioners for the Queen Victoria Niagara Falls Park, being for the year 1894. Ontario Government Publication, Toronto, ON.

Cappuccino, N. 2004. Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae). *Oikos* **106**: 3–8.

Cappuccino, N., MacKay, R. and Eisner, C. 2002. Spread of the invasive alien *Vincetoxicum rossicum*: tradeoffs between seed dispersability and seed quality. *Am. Mid. Nat.* **148**: 263–270.

Casagrande, R. A. and Dacy, J. 2001. Monarch butterfly (*Danaus plexippus*) oviposition on black swallowwort (*Vincetoxicum nigrum*). *Rhode Island Nat. Hist. Surv.* **8**: 2–3.

Christensen, T. 1997. Chemical and mechanical control of pale swallow-wort (*Cynanchum rossicum* (Kleopov) Borh.): First year study results. Unpublished report, Urban Forest Associates, Toronto, ON. 11 pp.

Christensen, T. 1998. Swallowworts: The ecology and control of *Vincetoxicum* spp. *Wildflower: North America's magazine of wild flora* **14**: 21–25.

Cholewa, A. F. 2002. Checklist of the flora of Minnesota. [Online] Available: <http://www.cbs.umn.edu/herbarium/checklis2.htm> [2004 Sep. 02].

Court, A. 1974. The climate of the conterminous United States. Pages 193–343 in R. A. Bryson and F. K. Hare, eds. *World Survey of Climatology Volume 11. Climates of North America.* Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.

Cronquist, A. 1988. The evolution and classification of flowering plants. 2nd ed. New York Botanical Garden, Bronx, NY. 555 pp.

Darbyshire, S. J. 2003. Inventory of Canadian agricultural weeds. Agriculture and Agri-Food Canada, Ottawa. [Online] Available: http://res2.agr.ca/ecorc/weeds/herbes/title-titre_e.htm [2004 Sep. 02].

Darbyshire, S. J., Favreau, M. and Murray, M. 2000. Common and scientific names of weeds in Canada / Noms populaires et scientifiques des plantes nuisibles du Canada. Agriculture and Agri-Food Canada Publication / Agriculture et Agroalimentaire Canada Publication 1397. 132 pp.

de Ruffray, P., Brisse, H. and Grandjouan, G. 2002. SOPHY: Banque de données Botaniques et Ecologiques. Association d'Informatique appliquée à la Botanique. Université de Provence Aix Marseille, France. [Online] Available: <http://sophy.u-3mrs.fr/> [2004 Sep. 02].

Diosdado, J. C., Ojeda, F. and Pastor, J. 1993. In C. A. Stace, ed. *IOPB chromosome data 5.* Newsletter Intl. Organization Pl. Biosystematists **20**: 6–7.

DiTommaso, A., Brainard, D. C. and Webster, B. R. 2005. Seed characteristics of the invasive alien vine *Vincetoxicum rossicum* are affected by site, harvest date, and storage duration. *Can. J. Bot.* **83**: 102–110.

DiTommaso, A. and Losey, J. E. 2003. Oviposition preference and larval performance of monarch butterflies (*Danaus plexippus*) on two invasive swallow-wort species. *Entomol. Exp. Appl.* **108**: 205–209.

Domin, K. 1928. Beiträge zur Flora und Pflanzengeographie Australiens. *Bibliotheca Botanica* 22(89^b): 1033–1128.

Donadille, P. 1965. Contribution à l'étude du *Vincetoxicum officinale* Moench et des ses « variétés » dans le sud-est Français. *Nat. Monspel. Sér. Bot.* **16**: 17–40.

Dore, W. G. 1967. Canada's first botanic garden. *Greenhouse-Garden-Grass* **6(2)**: 6–14.

- Douglas, G. W., Straley, G. B., Meidlinger, D. and Pojar, J. 1998.** Illustrated flora of British Columbia. Volume 1. Gymnosperms and Dicotyledons (Aceraceae through Asteraceae). British Columbia Ministry of the Environment, Lands and Parks and Ministry of Forests, Victoria, BC. 436 pp.
- Duke, J. A., Bogenschutz-Godwin, M. J., duCellier, J. and Duke, P.-A. K. 2002.** Handbook of medicinal herbs. 2nd ed. CRC Press, Boca Raton, FL. 870 pp.
- El-Gazzar, A., Hamza, M. K. and Badawi, A. A. 1974.** Pollen morphology and taxonomy of Asclepiadaceae. *Pollen Spores* **16**: 227–238.
- Ernst, C. M. and Cappuccino, N. 2005.** The effect of an invasive alien vine, *Vincetoxicum rossicum* (Asclepiadaceae), on arthropod populations in Ontario old fields. *Biol. Invas.* (in press).
- Escardó, A. L. 1970.** The climate of the Iberian peninsula. Pages 195–239 in C. C. Wallén, ed. *World survey of climatology*, Volume 5. Climates of Northern and Western Europe. Elsevier Publishing Co., Amsterdam, The Netherlands.
- Fernald, M. L. 1950.** Gray's manual of botany. 8th ed. American Book Co., New York, NY. 1532 pp.
- Förare, J. 1995.** The biology of the noctuid moth *Abrostola asclepiadis* Schiff. (Lepidoptera, Noctuidae) in Sweden. *Ent. Tidskr.* **116**: 179–186.
- Forster, P. I. 1991.** A taxonomic revision of *Cynanchum* L. (Asclepiadaceae: Asclepiadoideae) in Australia. *Austrobaileya* **3**: 443–466.
- Fournier, P. 1977.** Les quatre fleurs de la France. Volume 1. 2nd ed. Édition Lechevalier S.A.R.L., Paris, France. xlviii + 1106 pp.
- Gleason, H. A. and Cronquist, A. 1991.** Manual of vascular plants of the northeastern United States and adjacent Canada, 2nd ed. The New York Botanical Garden, Bronx, NY. lxxv + 910 pp.
- Gray, A. 1867.** Manual of botany of the Northern United States. Including the district east of the Mississippi and north of North Carolina and Tennessee. 5th ed. Ivison, Blakeman, Taylor & Co., New York, NY. 703 pp. + 20 pl.
- Greipsson, S. and DiTommaso, A. 2002.** Impact of the invasive plant *Vincetoxicum rossicum* on activity of arbuscular mycorrhizal fungal populations. *Ecological Society of America Meeting Abstracts* **87**: 358.
- Hæggeström, C.-A. 1990.** The influence of sheep and cattle grazing on wooded meadows in Cland, SW Finland. *Acta Bot. Fenn.* **141**: 1–28.
- Hamilton, G. H. 1943.** Plants of the Niagara Parks System of Ontario. The Ryerson Press, Toronto, ON. xii + 233 pp.
- Hare, F. K. and Hay, J. E. 1974.** The climate of Canada and Alaska. Pages 49–192 in R. A. Bryson and F. K. Hare, eds. *World survey of climatology*. Volume 11. Climates of North America. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.
- Haribal, M. and Renwick, J. A. A. 1998.** Identification and distribution of oviposition stimulants for Monarch butterflies in hosts and nonhosts. *J. Chem. Ecol.* **24**: 891–904.
- Haznag, A. and Toth, L. 1971.** Aromatische stoffe aus *Cynanchum vincetoxicum*. *Planta Med.* **20**: 136–141.
- Hegi, G. 1927.** Illustrierte flora von Mittle-Europa. Volume 5, No. 3. J. F. Lehmann, Munich, Germany. pp. 1567–2250.
- Holmgren, P. K., Holmgren, N. H. and Barnett, L. C. 1990.** Index Herbariorum. Part I: The herbaria of the world. 8th ed. New York Botanical Garden, Bronx, NY. x + 693 pp.
- Kaitera, J. 1999.** *Cronartium flaccidum* fruitbody production on *Melampyrum* spp. and some important alternate hosts to pine. *Eur. J. For. Pathol.* **29**: 391–398.
- Kaitera, J., Seitamäki, L., Hantula, J., Jalkanen, R. and Kurkela, T. 1999.** Inoculation of known and potential alternate hosts with *Peridermium pini* and *Cronartium flaccidum* aeciospores. *Mycol. Res.* **103**: 235–241.
- Kartesz, J. T. 1999.** A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. 1st ed. in J. T. Kartesz and C. A. Meacham. *Synthesis of the North American Flora*, Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC. CD-ROM.
- Kirk, M. 1985.** *Vincetoxicum* spp. (Dog-strangling vines): Alien invaders of natural ecosystems in southern Ontario. *Plant Press (Mississauga)* **3**: 130–131.
- Knuth, P. 1909.** Handbook of flower pollination. Volume 3. Translation by J. R. A. Davis. Clarendon Press, Oxford, UK. 644 pp.
- Kugelberg, O. 1973.** Larval development of *Lygaeus equestris* (Heteroptera, Lygaeidae) on different natural foods. *Entomol. Exp. Appl.* **16**: 165–177.
- Kunze, H. 1991.** Structure and function in asclepiad pollination. *Plant Syst. Evol.* **176**: 227–253.
- Lauvanger, E. G. and Borgen, L. 1998.** The identity of *Vincetoxicum* in Norway. *Nord. J. Bot.* **18**: 353–364.
- Lawlor, F. 2000.** Herbicidal treatment of the invasive plant *Cynanchum rossicum* and experimental post control restoration of infested sites. M.Sc. Thesis, State University of New York College of Environmental Science and Forestry, Syracuse, NY. 77 pp.
- Lawlor, F. and Raynal, D. J. 2002.** Response of swallow-wort to herbicides. *Weed Sci.* **50**: 179–185.
- Leimu, R. 2004.** Variation in the mating system of *Vincetoxicum hirundinaria* (Asclepiadaceae) in peripheral island populations. *Ann. Bot. (Lond)* **93**: 107–113.
- L. H. Bailey Hortorium. 1976.** Hortus third: A concise dictionary of plants cultivated in the United States & Canada. Macmillan, New York, NY. 1290 pp.
- Liede, S. 1996.** *Cynanchum - Rhodostegiella - Vincetoxicum - Tylophora* (Asclepiadaceae): new considerations on an old problem. *Taxon* **45**: 193–211.
- Liede, S. 1999.** The genera *Cynanchum* and *Vincetoxicum* (Apocynaceae - Asclepiadoideae) in Malesia. *Blumea* **44**: 471–495.
- Liede, S. and Täuber, A. 2002.** Circumscription of the genus *Cynanchum* (Apocynaceae - Asclepiadoideae). *Syst. Bot.* **27**: 789–800.
- Lumer, C. and Yost, S. E. 1995.** The reproductive biology of *Vincetoxicum nigrum* (L.) Moench (Asclepiadaceae), a Mediterranean weed in New York State. *Bull. Torrey Bot. Club* **122**: 15–23.
- Lydolph, P. E. 1977.** World survey of climatology. Volume 7. Climates of the Soviet Union. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands. 443 pp.
- Macoun, J. M. 1897.** Contributions to Canadian Botany. X. *Canadian Record of Science* **1897**: 267–286.
- Macoun, J. M. 1906.** Contributions to Canadian Botany. XVIII. *The Ottawa Naturalist* **20**: 162–171.
- Markgraf, F. 1971.** Beobachtungen an den europäischen Arten der Gattung *Vincetoxicum*. *Bot. Linn. Soc.* **64**: 370–376.
- Markgraf, F. 1972.** *Vincetoxicum* N. M. Wolf. Pages 71–73 in T. G. Tutin, V. H. Heywood, N. A. Burgess, D. H. Valentine, S. M. Walters, and D. A. Webb, eds. *Flora Europaea*. Volume 3. Diapensiaceae to Myoporaceae. Cambridge University Press, Cambridge, UK.
- Mattila, R. and Otis, G. W. 2003.** A comparison of the host preference of monarch butterflies (*Danaus plexippus*) for milkweed (*Asclepias syriaca*) over dog-strangler vine (*Vincetoxicum rossicum*). *Entomol. Exp. Appl.* **107**: 193–199.
- McNeill, J. 1981.** Taxonomic, nomenclatural and distributional notes of Canadian weeds and aliens. *Nat. Can. (Qué)* **108**: 237–244.
- Monachino, J. 1957.** *Cynanchum* in the New York area. *Bull. Torrey Bot. Club* **84**: 47–48.
- Moore, R. J. 1959.** The dog-strangling vine *Cynanchum medium*, its chromosome number and its occurrence in Canada. *Can. Field-Nat.* **73**: 144–147.

- Moriondo, F. 1980.** Features of *Cronartium flaccidum* and its hosts in Italy. *Phytopathol. Mediterr.* **19**: 35–43.
- Müller, H. 1883.** The fertilisation of flowers. Translation by D. W. Thompson. Macmillan and Co., London, UK. 699 pp.
- Nemeth, F. 1974.** Growth analysis on a wild population of *Cynanchum vincetoxicum* L. *Agrobotanika* **16**: 165–176 [in Hungarian with English abstract and captions].
- Newmaster, S. G., Lehela, A., Uhlig, P. W. C., McMurray, S. and Oldham, M. J. 1998.** Ontario Plant List. Forest Research Information Paper 123. Ontario Forest Research Institute, Ontario Ministry of Natural Resources, Sault Ste. Marie, ON.
- Nowak, R. and Kisiel, W. 2000.** Hancokinol from *Vincetoxicum officinale*. *Fitoterapia* **71**: 584–586.
- Ping-tao, L., Gilbert, M. G. and Stevens, W. D. 1995.** Asclepiadaceae. Pages 189–270 in P. H. Raven and Z. Y. Wu, eds. *Flora of China*. Volume 16. Sciences Press, Beijing and Missouri Botanical Garden Press, St. Louis, MO.
- Pobedimova, E. G. 1952.** Family CXXXIII Asclepiadaceae Lindl. Pages 487–527 in B. K. Shishkin and E. G. Bobrov, eds. *Flora of the U.S.S.R.* Volume 18. Metachlamydeae. [Translation by N. Landau, 1967, Israel Program for Scientific Translation, Jerusalem, for The Smithsonian Institution and The National Science Foundation, Washington, DC.]
- Pobedimova, E. G. 1978.** Family 132. Asclepiadaceae R. Br. Pages 50–57 in A. A. Fedorov, ed. *Flora partis Europaeae URSS*. Volume 3. Nauka Press, Leningrad, Russia. [in Russian].
- Polunin, O. and Smythies, B. E. 1973.** Flowers of south-west Europe. A field guide. Oxford University Press, London, UK. xv + 480 pp.
- Pringle, J. S. 1973.** The spread of *Vincetoxicum* species (Asclepiadaceae) in Ontario. *Can. Field-Nat.* **87**: 27–33.
- Ragazzi, A., Fedi, I. D. and Mesturino, L. 1986.** Relation between inoculum concentration of *Cronartium flaccidum* aecidiospores and uredia and telia production on *Vincetoxicum hirundinaria* leaves. *Riv. Patol. Veg., Serie IV*, **22**: 87–92.
- Reschke, C. 1990.** Ecological Communities of New York State. New York Natural Heritage Program, New York State Dept. Env. Cons., Latham, New York, NY. Pages 41–66.
- Sanders, A. C. 1996.** Noteworthy Collections. *California Madroño* **43**: 523–532.
- Seefeldner, C. 1912.** Die Polyembryonie bei *Cynanchum vincetoxicum* (L.) Pers. *Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl., Abt. I*. **121**: 273–296.
- Sheeley, S. 1992.** The distribution and life history characteristics of Swallow-wort (*Vincetoxicum rossicum*). M.Sc. Thesis, State University of New York College of Environmental Science and Forestry, Syracuse, NY. 126 pp.
- Sheeley, S. E. and Raynal, D. J. 1996.** The distribution and status of species of *Vincetoxicum* in eastern North America. *Bull. Torrey Bot. Club* **123**: 148–156.
- Smith, L. L., DiTommaso, A., Lehmann, J. and Greipsson, S. 2004.** Biology of the invasive plant pale swallow-wort. *Proc. Northeastern Weed Science Society* **58**: 96 (Abstr.).
- Solbreck, C. and Sillén-Tullberg, B. 1986.** Seed production and seed predation in a patchy and time-varying environment. Dynamics of a milkweed - tephritid fly system. *Oecologia* **71**: 51–58.
- Solbreck, C., Olsson, R., Anderson, D. B. and Förare, J. 1989.** Size, life history and responses to food shortage in two geographical strains of a seed bug *Lygaeus equestris*. *Oikos* **55**: 387–396.
- Staerk, D., Christensen, J., Lemmich, E., Duus, J., Olsen, C. and Jaroszewski, J. 2000.** Cytotoxic activity of some phenanthroindolizidine *N*-Oxide alkaloids from *Cynanchum vincetoxicum*. *J. Nat. Prod.* **63**: 1584–1586.
- St. Denis, M. and Cappuccino, N. 2004.** Reproductive biology of *Vincetoxicum rossicum* (Kle.) Barb. (Asclepiadaceae), an invasive alien in Ontario. *J. Torrey Bot. Soc.* **131**: 8–15.
- Tewksbury, L., Casagrande, R. and Gassmann, A. 2002.** 16. Swallow-Worts. Pages 209–216. in R. Van Driesche, S. Lyon, B. Blossey, M. Hoddle, and R. Reardon, eds. *Biological Control of Invasive Plants in the Eastern United States*. U.S. Dep. Agric. For. Serv. Pub. FHTET–2002–04.
- Tukey, J. W. 1977.** Explanatory Data Analysis. Addison-Wesley, Reading, MA. xvi + 688 pp.
- Tullberg, B. S., Gamberale-Stille, G. and Solbreck, C. 2000.** Effects of food plant and group size on predator defense: differences between two co-occurring aposematic Lygaeinae bugs. *Ecol. Entomol.* **25**: 220–225.
- Uphof, J. C. Th. 1968.** Dictionary of Economic Plants. 2nd ed. J. Cramer, Lehre, Germany. 591 pp.
- United State Department of Agriculture. 2000.** Natural Resources Conservation Service Plants Profile. [Online] Available: <http://plants.usda.gov/> [2004 Sep 02].
- Visulina, O. D. 1957.** Family CXVII. Asclepiadaceae Lindl. Pages 270–287 in M. I. Kotov and A. I. Varvarich, eds. *Flora of the Ukrainian SSR*. Volume 8. Academy of Sciences of the Ukrainian SSR., Kyiv, Ukraine. [in Ukrainian].
- von Hausner, G. 1976.** Embryogenese und nucellar-polyembryonie bei *Cynanchum- Vincetoxicum*-Arten. *Beitr. Biol. Pflanz.* **52**: 101–126.
- Western Regional Climate Center. 2003.** Riverside Citrus Exp. St., California. [Online] Available: <http://www.wrcc.dri.edu/CLI-MATEDATA.html> [2004 Sep. 02].
- Wiegreb, W., Budzikiewicz, H. and Farber, L. 1970.** Alkaloide aus *Cynanchum vincetoxicum* (L.) Pers. 3. Mitt.: 14-hydroxy-2,3,6-trimethoxy-9,11,12,13,13a,14-hexahydro-dibenzo(f,h)-pyrrolo(1,2-b)-isochinolin. *Arch. Pharm.(Weinheim)* **303**: 1009–1012.
- Woodson, R. E., Jr. 1941.** The North American Asclepiadaceae I: Perspectives of the genera. *Ann. Missouri Bot. Gard.* **28**: 193–244.
- Yaki, G. J. 1970.** Plants of the Niagara Peninsula. Niagara Falls Nature Club Special Publication No. 2. 44 pp.

