





Biology of Invasive Plants 3. *Vincetoxicum nigrum* (L.) Moench and *Vincetoxicum rossicum* (Kleopow) Barbarich

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Biology of Invasive Plants

Cite this article: Westbrook AS, Milbrath LR, Weinberg J, and DiTommaso A (2023) Biology of Invasive Plants 3. *Vincetoxicum nigrum* (L.) Moench and *Vincetoxicum rossicum* (Kleopow) Barbarich. *Invasive Plant Sci. Manag* **16**: 3–26. doi: [10.1017/inp.2023.7](https://doi.org/10.1017/inp.2023.7)

Received: 16 September 2022

Revised: 14 January 2023

Accepted: 21 January 2023

First published online: 3 April 2023

Series Editors:

Darren J. Kriticos, Cervantes Agritech & David R. Clements, Trinity Western University

Keywords:

Cynanchum louisae; *Cynanchum rossicum*; dog-strangling vine; swallowwort; swallow-wort

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Scientific Classification

Domain: Eukaryota

Kingdom: Plantae

Phylum: Spermatophyta

Subphylum: Angiospermae

Class: Dicotyledonae

Order: Gentianales

Family: Apocynaceae

Subfamily: Asclepiadoideae

Tribe: Asclepiadeae

Subtribe: Tylophorinae

Genus: *Vincetoxicum* Wolf

Species 1: *nigrum* (L.) Moench

Synonyms: *Cynanchum louiseae* Kartesz & Gandhi, *Cynanchum nigrum* (L.) Pers.

EPO Code: CYKNI

Species 2: *rossicum* (Kleopow) Barbarich

Synonyms: *Cynanchum rossicum* Kleopow, *Cynanchum rossicum* (Kleopow) Borhidi, *Vincetoxicum officinale* var. *rossicum* (Kleopow) Grodz.

EPO Code: VNCRO

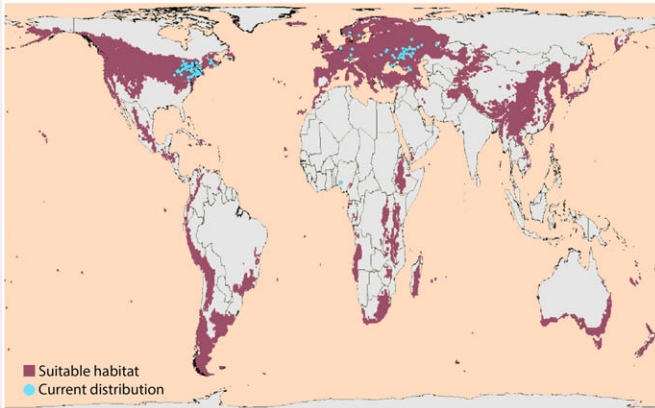
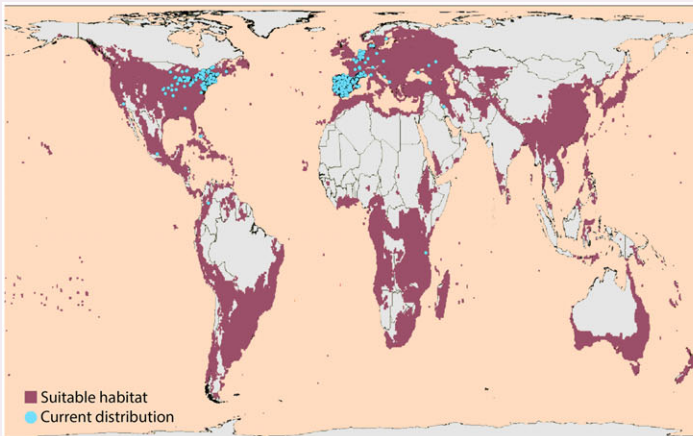
Name and Taxonomy

Vincetoxicum comes from the Latin *vinco* (to conquer or subdue) + *toxicum* (poison), for the supposed use of these plants as an antidote for poison (DiTommaso et al. 2005b). The specific epithet *rossicum* is a Latinized reference to the presumed origin of *V. rossicum* in Russia, whereas *nigrum* is Latin for “black” in reference to the flower color of *V. nigrum*. The identities of North American specimens of *V. nigrum* and *V. rossicum* were confirmed by Gaina Konechnaya and Nikolai Tsvelev, Institute of Botany, Russian Academy of Sciences, St Petersburg, Russia (personal communication). In addition to the two invasive *Vincetoxicum* species, a third species, *Vincetoxicum hirundinaria* Medik. [syn.: *Cynanchum vincetoxicum* (L.) Pers., *Vincetoxicum officinale* Moench], occupies a large native range in Eurasia but appears only to be a rare garden escape elsewhere, not showing invasive tendencies like *V. rossicum* and *V. nigrum*. Some workers have considered *V. rossicum* to be a dark-flowered form of the *V. hirundinaria* species complex (Gleason and Cronquist 1991; Lauvanger and Borgen 1998) as hybrids between the two are known (Markgraf 1971).

The common name pale swallowwort (or the more widely used hyphenated form “pale swallow-wort,” both used in the United States) for *V. rossicum* may be confusing because the pink or maroon flowers of *V. rossicum* are paler than the dark purple flowers of *V. nigrum*, but darker than the cream-colored flowers of *V. hirundinaria* (DiTommaso et al. 2005b). Alternate common names for *V. rossicum* include European swallowwort (for its region of origin), dog-strangling vine (for its ability to form dense mats, Canada), dompte-venin de Russie (Canada), and russesvalerot (Norway). Common names for *V. nigrum* include black swallowwort (or black swallow-wort, United States), Louise’s swallowwort (based on one of its synonyms), black dog-strangling vine (Canada), and dompte-venin noir (Canada). In addition to white swallowwort, common names for *V. hirundinaria* include German ipecac, poison-rope swallowwort (Canada), white dog-strangling vine (Canada), and common vince-toxicum (Belgium) (references in Global Biodiversity Information Facility 2021, 2022a, 2022b).

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Vincetoxicum nigrum* and *Vincetoxicum rossicum* at a glance . . .Vincetoxicum rossicum*, pale swallowwort*Vincetoxicum nigrum*, black swallowwort**Impacts**

- Grow in dense, near-monospecific stands in invaded North American range
- Reduce diversity at multiple trophic levels and alter ecosystem function
- Interfere with no-till crop production and other land use goals

**Dispersal**

- Seeds are dispersed by wind and sometimes by animals
- Anthropogenic pathways account for most long-distance transport

**Management**

- Belowground reserves enable recovery from aboveground damage
- Control typically requires intensive cultural tactics or repeated use of systemic herbicides
- Biological control efforts are in progress

**Biosecurity**

- Deliberately introduced to North America and parts of Europe as ornamental plants
- Propagation and transport are now prohibited across much of North America



The genus *Vincetoxicum* N.M. Wolf (1776) is placed within the subtribe Tylophorinae in the tribe Asclepiadeae in the subfamily Asclepiadoideae in the family Apocynaceae. The incorporation

of the former family Asclepiadaceae into the Apocynaceae was required to make the Apocynaceae monophyletic (Endress and Bruyns 2000). The family Asclepiadaceae was not reduced to a tribe

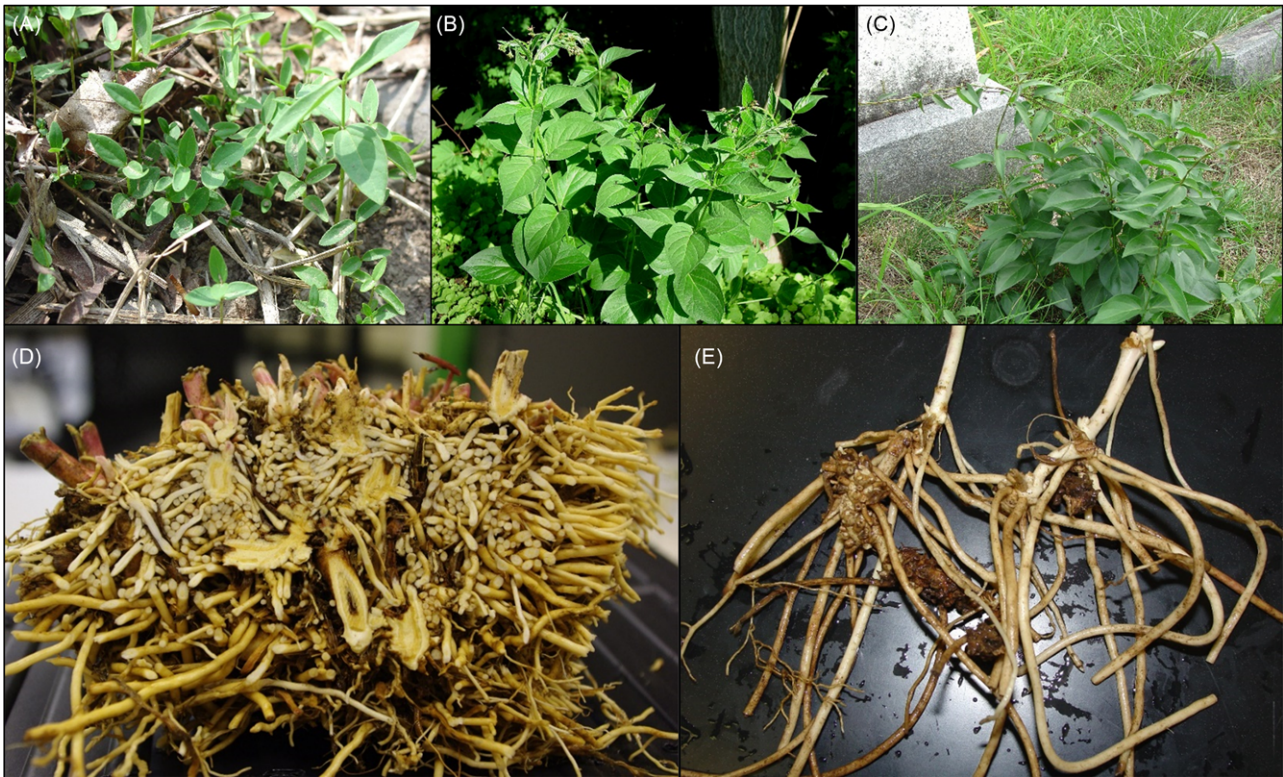


Figure 1. (A) Seedlings and small juveniles of *Vincetoxicum rossicum*. (B) Individual *Vincetoxicum rossicum* plant. (C) Individual *Vincetoxicum nigrum* plant. (D) Cross-section of a *Vincetoxicum rossicum* root system. (E) Two connected rootstocks of *Vincetoxicum nigrum* (southeastern New York, USA). (Photo credits: (A–C and E) Jeromy Biazzo; (D) Scott Morris.)

or subfamily, as erroneously reported (DiTommaso et al. 2005b). Instead, the five subfamilies in the revised family Apocynaceae include three subfamilies (Periplocoideae, Secamonoideae, and Asclepiadoideae) that were formerly included in the Asclepiadaceae and two subfamilies (Rauvolfioideae and Apocynoideae) that were already present in the Apocynaceae (Endress et al. 2007; Endress and Bruyns 2000). Within the Asclepiadoideae (tribe Asclepiadeae), the subtribe Tylophorinae is closely related to the subtribe Cynanchinae, which contains the genus *Cynanchum* L. (Fishbein et al. 2018). The relationship between *Vincetoxicum* and *Cynanchum* has historically elicited controversy (DiTommaso et al. 2005b; Liede 1996), but it is now clear that these two genera should be separated (Endress et al. 2007, 2014).

The subtribe Tylophorinae initially included several genera (Endress et al. 2007; Liede et al. 2002), most of which were subsequently merged with *Vincetoxicum* (Endress et al. 2014; Liede-Schumann and Meve 2018). The combined group, *Vincetoxicum* sensu lato, contains at least 140 species native to Africa, Asia, and Europe (Liede-Schumann et al. 2016; Liede-Schumann and Meve 2018). Over evolutionary time, the species *V. rossicum*, *V. nigrum*, and *V. hirundinaria* emerged from a clade (*Vincetoxicum* sensu stricto) that expanded northwest along the Asian mountain chains to Europe (Liede-Schumann et al. 2016).

The duplicate genus *Vincetoxicum* T. Walter (1788) (Bullock 1967) was erected for North American species, resulting in several illegitimate synonyms under the name *Vincetoxicum*. These species are properly placed in the genera *Matelea* Aubl. and *Gonolobus* Michx. within the subtribe Gonolobinae (Endress et al. 2014; USDA-NRCS 2021).

Description

Unless otherwise noted, the following information is drawn from the descriptions of North American *V. rossicum* and *V. nigrum* presented by DiTommaso et al. (2005b). These species are perennial herbs or small vines (Figure 1). Although not rhizomatous (Averill et al. 2011), they have short, horizontal, semi-woody rootstalks and slightly fleshy roots (Figure 1). Root-to-shoot ratios are often high, particularly in *V. rossicum* (Milbrath 2008). Stems are usually 60- to 200-cm long in *V. rossicum* and 40- to 200-cm long in *V. nigrum*, but occasionally longer (particularly when climbing up shrubs). Stems are pubescent with the hairs in longitudinal bands (especially in *V. rossicum*, which also has denser hairs on peduncles and pedicels). Leaves are largest in the middle of the stem, opposite, entire-margined, and pubescent on margins and major veins of the lower surface. Leaves of *V. rossicum* are ovate to elliptic, acute at the tip, and typically 7 to 12 by 5 to 7 cm with 5- to 20-mm petioles. Leaf bases are often truncate or slightly cuneate. Leaves of *V. nigrum* are oblong to ovate and typically 5 to 12 by 2 to 6.5 cm with 10- to 15-mm petioles. Leaf bases are often emarginate or cordate in *V. nigrum*.

Reproductive traits show much more interspecific variation than vegetative traits. *Vincetoxicum rossicum* flower buds are ovoid to conoidal with pointed apices, whereas *V. nigrum* flower buds are globose with rounded apices. Petals are twisted before opening in *V. rossicum*. Flowers are produced in umbelliform cymes in leaf axils, with 5 to 20 flowers in *V. rossicum* and 4 to 10 flowers in *V. nigrum*. Peduncles of the inflorescences are pubescent and longer (1.5 to 4.5 cm) in *V. rossicum* than in *V. nigrum* (0.5 to 1.5 cm). Flowers are five-parted with diameters

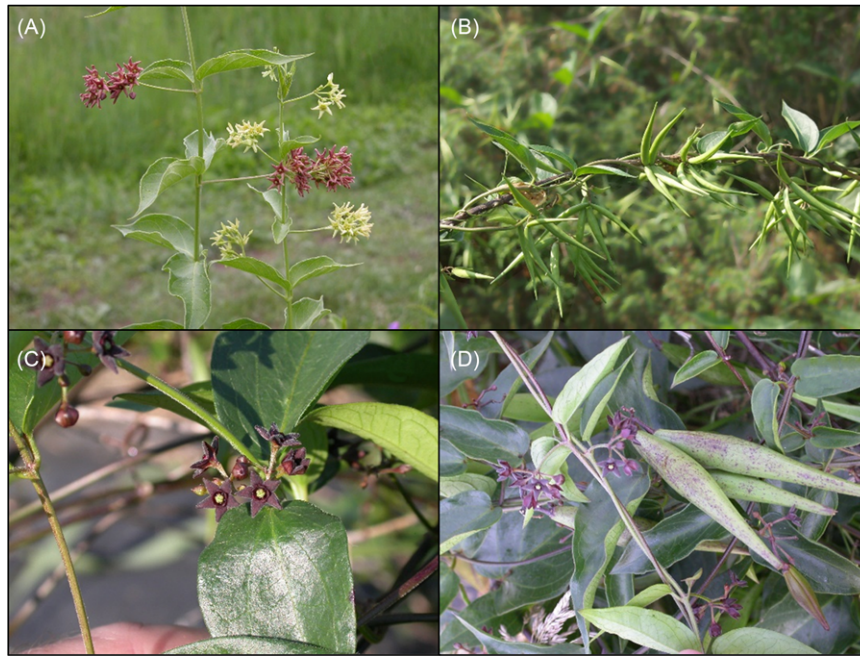


Figure 2. (A) *Vincetoxicum rossicum* typically has pink, red-brown, or maroon flowers but also occurs in a white-flowered mutant form. (B) *Vincetoxicum rossicum* follicles are slender. (C) *Vincetoxicum nigrum* flowers are dark purple to blackish. (D) *Vincetoxicum nigrum* follicles may be slender or plump. (Photo credits: (A) Stephen Darbyshire; (B) Larissa Smith; (C and D) Jeromy Biazzo.)

of 5 to 7 mm (*V. rossicum*) or 5 to 8 mm (*V. nigrum*). Calyx segments (1 to 1.5 mm) are more straplike in *V. rossicum* and closer to triangular in *V. nigrum*. *Vincetoxicum rossicum* and *V. nigrum* are usually easy to distinguish by corolla characteristics, especially color: pink, red-brown, or maroon in *V. rossicum* and dark purple to blackish in *V. nigrum* (Figure 2A and C). However, white-flowered individuals of *V. rossicum* are known from Ontario, Canada, and New York State, USA (S Darbyshire and L Milbrath, personal observation; Figure 2A). *Vincetoxicum rossicum* petals (3- to 5-mm long) are ovate-lanceolate to lanceolate, hairless, and only slightly fleshy. In contrast, *V. nigrum* petals (1.5- to 3-mm long) are ovate to deltoid, finely hairy on the inner surface, and fleshy. Both species have fleshy coronas that typically share the corolla color. The *V. rossicum* corona is more deeply lobed. The gynostegium (anthers fused with the stigmatic disk) is pale yellow to pale green. Fruits are smooth follicles, 4- to 7-cm long in *V. rossicum* and 4- to 8-cm long in *V. nigrum*. *Vincetoxicum rossicum* follicles are slender, and *V. nigrum* follicles may be slender or plump (Figure 2B and D). Two follicles may be formed per flower (more frequently in *V. rossicum*). The seeds of *V. rossicum* (4 to 6.5 by 2.4 to 3.1 mm) are light to dark brown, obovoid to oblong, and convex on one side. *Vincetoxicum nigrum* seeds are larger (6 to 8 by 3 to 4.7 mm), dark brown, ovoid to obovoid, and flattened on both sides. Seeds have membranous marginal wings (wider in *V. rossicum*, up to 0.25 mm) and a large coma (2 to 3 cm). Seedlings of *V. rossicum* and *V. nigrum* are not easily distinguishable. The cotyledons and first leaves are ovate to elliptic and may have slightly pointed apices. Cotyledons are not typically visible (Figure 3). Because *V. nigrum* has larger seeds, *V. nigrum* seedlings are initially larger than *V. rossicum* seedlings (Milbrath 2008).

Vincetoxicum hirundinaria, a widespread species in Eurasia and possible occasional garden escape in North America, is most easily distinguished from *V. rossicum* and *V. nigrum* by its white,



Figure 3. Cotyledons of *Vincetoxicum nigrum* (and *V. rossicum*) do not typically emerge from the seed. At the right, a seed has been manually dissected. (Photo credit: Scott Morris.)

yellow, or greenish-white flower petals (except in the case of white-flowered *V. rossicum* mutants). Petals may or may not be hairy (Cullen et al. 2011). Otherwise, *V. hirundinaria* appears similar to *V. rossicum* and *V. nigrum*, according to descriptions from Eurasia (Bojnanský and Fargašová 2007; Cullen et al. 2011). Disagreements arise as to what constitutes a species or subspecies within the highly variable and widespread *V. hirundinaria* complex (Markgraf 1972; Pobedimova 1952, 1978). As noted earlier



Figure 4. (A) Field infestation of *Vincetoxicum rossicum* in New York, USA. (B) Forest infestation of *Vincetoxicum rossicum* in New York, USA. (C) Emerging shoots of *Vincetoxicum nigrum* in New York, USA. (Photo credits: (A) Jeromy Biazzo; (B and C) Kristine Averill.)

(see “Name and Taxonomy”), *V. rossicum* has been included under the name *V. hirundinaria* (Gleason and Cronquist 1991; Lauvanger and Borgen 1998). These taxonomic disagreements, combined with the white-flowered mutant form of *V. rossicum*, have likely contributed to erroneous reports of invasive *V. hirundinaria* in North America.

In North America, *V. rossicum* is diploid ($2n = 2x = 22$) and *V. nigrum* is tetraploid ($2n = 4x = 44$) (Bon et al. 2013); hybridization between the two species in North America is therefore considered unlikely. *Vincetoxicum rossicum* is also reported to be diploid in its native range (Russia), and *V. nigrum* to be tetraploid in its native range (southern France; Bon et al. 2013). However, *V. nigrum* has been reported to be diploid in Spain (references in DiTommaso et al. 2005b). *Vincetoxicum hirundinaria* is diploid in its native range (Guermache et al. 2010). Genome sizes (mean $2C$ values \pm STD) are reported to be 0.71 ± 0.02 pg for *V. rossicum* and 1.44 ± 0.03 pg for *V. nigrum* and appear to be similar between the native and introduced ranges (Bon et al. 2013). For *V. rossicum* and *V. nigrum*, genetic diversity is much lower in North America than in Europe (Bon et al. 2010; Douglass 2008), with the majority of North American populations apparently derived from one major European genotype per species (Bon et al. 2010). The source population for *V. rossicum* has been identified in Ukraine (Sforza et al. 2013a).

Importance

Vincetoxicum rossicum and *V. nigrum* are listed as noxious or prohibited weeds across much of the northeastern United States and eastern Canada (Supplementary Table S1). In North America and other invaded regions, such as Norway, these weeds threaten both unmanaged and managed ecosystems by outcompeting resident and desirable species (Bjureke 2007; DiTommaso et al. 2005b). They can grow in dense near-monospecific stands (Figure 4), altering ecosystem structure and function (DiTommaso et al. 2005b; Douglass et al. 2009). In such stands, stem densities are often 100 to 200 stems m^{-2} (>10-cm tall) and >1,400 stems m^{-2} (<10 cm) under high light (Milbrath et al. 2018; Sheeley 1992; Smith et al. 2006). In southern Ontario, Livingstone et al. (2020a) found that invasion by *V. rossicum* significantly decreased plant community diversity. Invasion also increased total productivity; however, productivity tended to increase with the richness of the remaining resident community. Changes to species diversity are associated with changes to functional diversity (Livingstone et al. 2020a; Sodhi et al. 2019). *Vincetoxicum rossicum* reduces plant community diversity by limiting resource availability to all residents and severely restricting resource availability to residents in

particular niches (Sodhi et al. 2019). That is, *V. rossicum* acts as an ecological filter, causing the nonrandom exclusion of some resident species (Sodhi et al. 2019). In addition to competing with resident species, *V. rossicum* may drive plant diversity loss through ecosystem modification (such as changes to soil characteristics; Carboni et al. 2021). *Vincetoxicum* invasion is particularly concerning in rare habitats such as alvar ecosystems (Kricsfalusy and Miller 2010; O’Brien et al. 2010) and not necessarily prevented by high initial biodiversity in the invaded community (Kricsfalusy and Miller 2010). Dibble et al. (2007) included *V. nigrum* in the complex of introduced species that may enhance fire risks in forests and overgrown fields of the northeastern United States.

In addition to reshaping resident plant communities, *Vincetoxicum* invasion effects changes at other trophic levels. For example, *V. rossicum* can have significant impacts on soil fungal and bacterial communities (Bongard et al. 2013a; Bugiel et al. 2018; Greipsson and DiTommaso 2006). Malloch et al. (2020) reported interactive effects of *V. rossicum* invasion and urbanization on microarthropod communities in leaf litter. Ernst and Cappuccino (2005) reported reduced arthropod communities on invasive *V. rossicum* compared with native old-field plants and mixed grass communities, accounting for both stem- and ground-dwelling species of all feeding guilds. This finding is consistent with reports that *V. rossicum* and *V. nigrum* are seldom damaged by phytophagous arthropods in eastern North America (Carpenter and Cappuccino 2005; Milbrath 2010). Livingstone (2018) suggested that pollinator richness and abundance are lower in ecosystems highly invaded by *V. rossicum*. Because invasive *Vincetoxicum* harbor very few arthropods, they are unlikely to be a reservoir for arthropod crop pests. *Vincetoxicum* species may be more problematic as reservoirs for fungal pathogens. For example, research in northern and southern Europe has demonstrated that *V. nigrum* and *V. hirundinaria* can serve as alternate hosts for *Cronartium flaccidum* (Alb. & Schwein.) G. Winter, a rust fungus that causes disease in pines (*Pinus* spp.) (Bon and Guermache 2012; Kaitera et al. 2012, 2017). In an outdoor experiment in Switzerland, leaves of *V. rossicum* and *V. nigrum* became infected with the fungal pathogens *Ascochyta* sp. and *Cercospora* sp. (Ascomycota), respectively (Weed et al. 2011a). There is some evidence that the fungal communities associated with *V. rossicum* in North America could have positive effects on *V. rossicum* and negative effects on native plants (Day et al. 2016; Dickinson et al. 2021).

Vincetoxicum infestations may harm monarch butterfly (*Danaus plexippus* L.) populations by acting as an oviposition sink or by competing with milkweeds. If *D. plexippus* females oviposit

on these plants rather than on milkweeds (*Asclepias* spp.), the larvae do not survive (Haribal and Renwick 1998). This mortality risk is reduced by the preference of *D. plexippus* females for *Asclepias* over *Vincetoxicum* hosts. Some experiments have shown a very strong preference for *Asclepias*, although this outcome may have resulted from using laboratory-reared insects (Alred et al. 2022a; DiTommaso and Losey 2003; Mattila and Otis 2003). Other work has shown some to substantial oviposition on *Vincetoxicum* plants under field conditions (Alred et al. 2022a; Casagrande and Dacey 2007; Milbrath 2010). If oviposition on *Vincetoxicum* occurs at a significant rate, this rate likely depends on the ratio of *Vincetoxicum* to *Asclepias* plants at a landscape level. It has been suggested that *Vincetoxicum* species may do more damage to *D. plexippus* populations by outcompeting desirable *Asclepias* hosts than by serving as oviposition sinks (DiTommaso et al. 2005b; DiTommaso and Losey 2003). As the two genera are related (in the same tribe, Asclepiadeae), and *Vincetoxicum* species tend to suppress native vegetation, the competitive effects of *Vincetoxicum* species on *Asclepias* species are likely to be substantial; however, these effects are difficult to measure in natural systems (MacIvor et al. 2017). Jackson and Amatangelo (2021) suggested that *V. rossicum* is a poor competitor against common milkweed (*Asclepias syriaca* L.) on an individual basis at low densities but gains a competitive advantage as its density increases (Allee effect). Because the effects of *Vincetoxicum* invasion on *D. plexippus* oviposition and *Asclepias* survival and performance appear to be context dependent, it is not entirely clear how the negative effects of *Vincetoxicum* species on *D. plexippus* compare with other threats to this species (Malcolm 2018; Wilcox et al. 2019).

Vincetoxicum rossicum and *V. nigrum* can be problematic in North American agricultural systems with low disturbance. For example, these species have been reported in no-till field crops and Christmas tree farms (DiTommaso et al. 2005b; Douglass et al. 2009; Lawlor 2003). Horse pasture owners have also reported severe infestations, sometimes leading to abandonment of the pasture (DiTommaso et al. 2005b; Douglass et al. 2009). In addition to competing with desirable species, *Vincetoxicum* plants may overgrow and thereby reduce the effectiveness of electric fences (Tewksbury et al. 2002). These species are thought to be toxic to mammals (DiTommaso et al. 2005b; Hess 2014; Weston et al. 2005), although grazing by cattle and sheep has been reported (DiTommaso et al. 2005b; Tewksbury et al. 2002). Because established *Vincetoxicum* populations are difficult to eradicate, severe infestations can decrease the land value of fields and pastures (AD, personal observation). *Vincetoxicum* infestations may also interfere with land use goals in areas managed for nonagricultural purposes. For example, vines of *V. rossicum* have been observed to weigh down small trees planted at restoration sites in Ontario (Christensen 1998). The number of breeding grassland birds decreased with increasing *V. rossicum* cover in a habitat managed for grassland birds in New York (DiTommaso et al. 2005b). The foliage of *Vincetoxicum* species is typically unpalatable to herbivores native to North America, such as white-tailed deer (*Odocoileus virginianus* Zimmermann) (Lawlor 2003). Most visitors to an urban park felt that a *V. rossicum* infestation detracted from the aesthetic value of the park (Livingstone et al. 2018). In its introduced North American range, *V. rossicum* colonizes a variety of habitats within the urban matrix, ranging from lawns and gardens to remnants of natural ecosystems (Cadotte et al. 2017; Potgieter and Cadotte 2020). Control of this aggressive weed is a major issue in Toronto, Ontario (Potgieter and Cadotte 2020; Potgieter et al. 2021).

Vincetoxicum plants offer some benefits. For example, they have traditionally been used for medicinal purposes in Europe. *Vincetoxicum hirundinaria* has been administered as an emetic, diuretic, or anti-tumor agent (Duke 2002, p. 325; Tanner and Wiegrebe 1993; Uphof 1968, p. 168). Extracts from *Vincetoxicum* species, including *V. hirundinaria*, exhibit antifeedant activity against the phytophagous larvae of the Colorado potato beetle (*Leptinotarsa decemlineata* Say) and Egyptian cotton leafworm (*Spodoptera littoralis* Boisduval) (Guzel et al. 2015; Pavela 2010). Despite these possible uses, *Vincetoxicum* invasion should generally be considered deleterious.

Distribution

Vincetoxicum rossicum is native to Ukraine and southwestern Russia (DiTommaso et al. 2005b; Figure 5A). This species has been anthropogenically introduced to other areas of Europe (see “Invasion History”; Markgraf 1971). It is naturalized in Norway (Bjureke 2007; Lauvanger and Borgen 1998). Introductions to Belgium, Denmark, Finland, Germany, the Netherlands, and Sweden have also been reported (Gassmann 2022b; Global Biodiversity Information Facility 2022b). In North America, *V. rossicum* has been reported in the U.S. states of Connecticut, Indiana, Massachusetts, Michigan, Missouri, New Hampshire, New Jersey, New York, and Pennsylvania (Gassmann 2022b; USDA-NRCS 2021). It has been reported in the Canadian provinces of British Columbia (but not persisting), Ontario, and Quebec (Gassmann 2022b; USDA-NRCS 2021). There has been one report of *V. rossicum* in Nigeria (Global Biodiversity Information Facility 2022b).

Vincetoxicum nigrum is native to southwestern Europe, including Portugal, Spain, France, and Italy (DiTommaso et al. 2005b; Figure 5B). Naturalized in the Netherlands (Markgraf 1972), this species is also present in Belgium (Gassmann 2022a; Global Biodiversity Information Facility 2022a). There are occasional reports from Albania, the Bahamas, Bulgaria, Colombia, Croatia, the Czech Republic, Denmark, Germany, Iran, Mexico, Norway, Russia, Sweden, Tanzania, Turkey, and Ukraine (Global Biodiversity Information Facility 2022a; Petrova 2010). In North America, *V. nigrum* has been reported in the U.S. states of California, Connecticut, Illinois, Indiana, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, and Wisconsin (Gassmann 2022a; USDA-NRCS 2021). The single population reported in California has apparently died out (Milbrath and Biazzo 2016), so the current distribution in the United States likely extends no farther west than Kansas and Nebraska. *Vincetoxicum nigrum* is present in the Canadian provinces of Ontario and Quebec (Gassmann 2022a; USDA-NRCS 2021).

Vincetoxicum hirundinaria is widespread in its native Eurasian range but not strongly invasive like *V. rossicum* and *V. nigrum*. Records of *V. hirundinaria* in North America are often misidentifications: many of these specimens are correctly identified as *V. rossicum*. The misidentifications reflect confusion over nomenclature or potentially the white-flowered mutant of *V. rossicum* (see “Name and Taxonomy”; “Description”). Although *V. hirundinaria* has been reported in New York and Michigan, USA, and Ontario, Canada (USDA-NRCS 2021), it is likely that most of these reports represent garden specimens with the exception of a 1904 collection involving a garden escape (Pringle 1973; Sheeley and Raynal 1996).

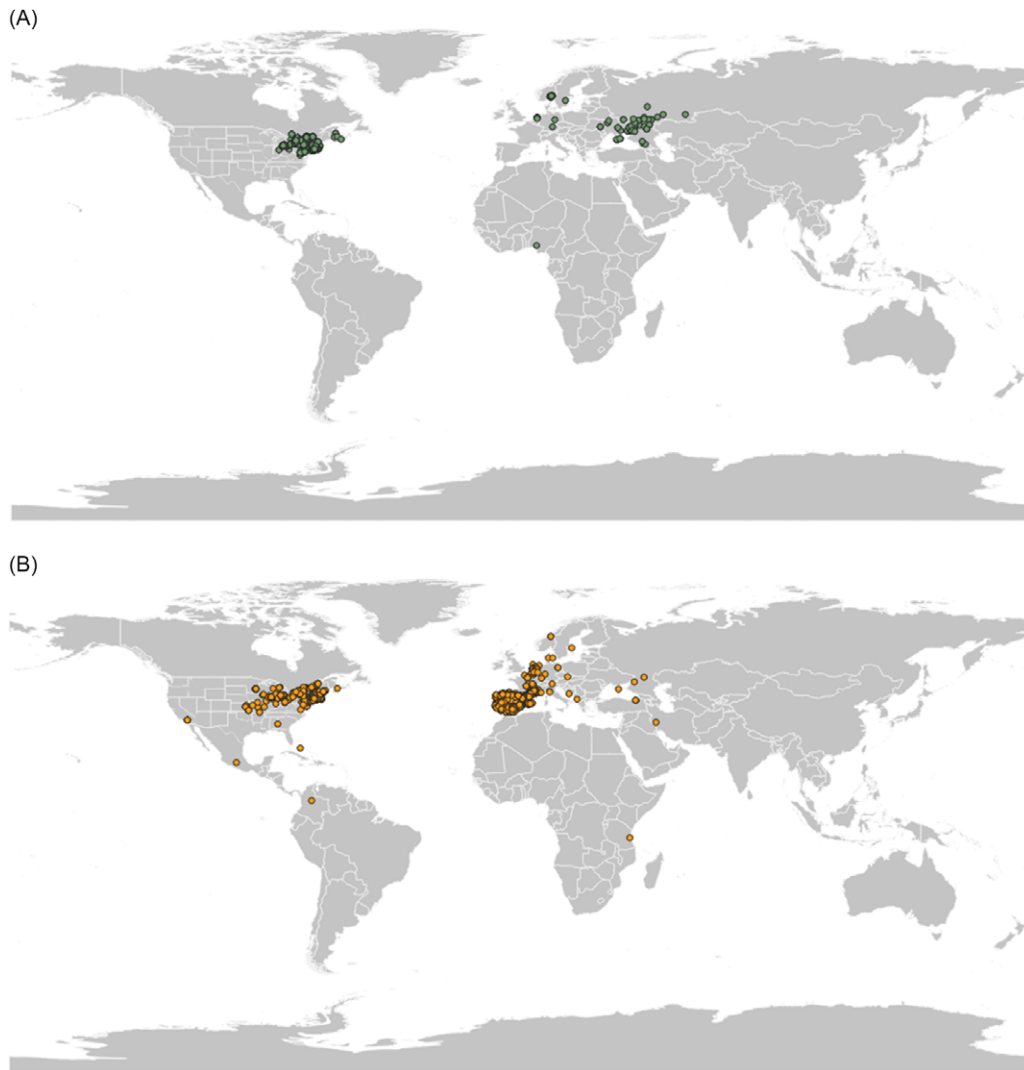


Figure 5. Current distributions of (A) *Vincetoxicum rossicum* and (B) *Vincetoxicum nigrum*. Data source: Global Biodiversity Information Facility (2022a, 2022b).

Habitat

According to the Köppen-Geiger classification, *V. rossicum* most frequently inhabits Dfa (cold, no dry season, hot summer) and Dfb (cold, no dry season, warm summer) climate types (Supplementary Figure S1A). *Vincetoxicum nigrum* most frequently inhabits BSk (arid, steppe, cold), Csa (temperate, dry summer, hot summer), Csb (temperate, dry summer, warm summer), Cfa (temperate, no dry season, hot summer), Cfb (temperate, no dry season, warm summer), Dfa, and Dfb climate types (Supplementary Figure S1B).

In their introduced North American ranges, *V. rossicum* and *V. nigrum* behave as generalists with respect to climate and habitat type. Kricsfalusy and Miller (2010) characterized *V. rossicum*'s North American range as similar in temperature but wetter than its native range in Ukraine and Russia. In both ranges, *V. rossicum* tends to inhabit semi-open scrub or woodland habitats on calcareous soils (Kricsfalusy and Miller 2010). However, *V. rossicum* populations in North America occupy a wider variety of light environments and soil types (Kricsfalusy and Miller 2010). *Vincetoxicum nigrum* may inhabit cooler and wetter habitats in North America than in southwestern Europe (DiTommaso et al.

2005b). In both species, cold temperatures are tolerated well but typically associated with phenological delays (see “Growth and Development: Stress Tolerance”; “Growth and Development: Phenology”). *Vincetoxicum* species tolerate a wide range of moisture levels, but permanently waterlogged soils are not suitable (see “Growth and Development: Stress Tolerance”). These species primarily inhabit upland habitats, including exposed habitats with highly variable water availability (DiTommaso et al. 2005b). Based on a survey of *V. rossicum* populations in Ontario, Dickinson et al. (2021) reported that aboveground biomass production was positively correlated with precipitation but not strongly associated with habitat type or abiotic soil variables.

Vincetoxicum rossicum is often found on calcareous soils, including shallow soils over limestone bedrock as well as deeper soils (DiTommaso et al. 2005b; Kricsfalusy and Miller 2010; Weston et al. 2005). In New York, Douglass (2008) reported that soils colonized by *V. rossicum* (pH 5.2 to 7.6) had higher levels of calcium (Ca) and aluminum (Al) than soils colonized by *V. nigrum* (pH 5.2 to 7.2). Soils colonized by *V. rossicum* had a slightly higher average pH compared with *V. nigrum* (6.8 relative to 6.0). In a study combining soil measurements with data retrieved from the Soil Survey Geographic Database, Magidow et al. (2022) found

that *V. rossicum* colonized soils with higher mean pH than soils colonized by *V. nigrum* in the northeastern United States and southeastern Canada. However, soil characteristics (pH, fertility, texture, and taxonomy) varied widely across the ranges of both species (Magidow et al. 2022). Common garden and growth chamber experiments have provided only weak support for the hypothesis that *V. rossicum* and *V. nigrum* perform best on different soils (Magidow et al. 2013). Soil factors do not appear to limit range expansion in *V. rossicum* (Sanderson et al. 2015).

At smaller spatial scales, light and disturbance are important influences on species distributions. *Vincetoxicum rossicum* and *V. nigrum* both inhabit high-light environments, including fields, habitat edges, and waste areas (DiTommaso et al. 2005b). *Vincetoxicum rossicum* is also frequently found in forest understoreys, whereas *V. nigrum* is less common in understory habitats (Alred et al. 2022b; Averill et al. 2011; Milbrath et al. 2017), even though both species have the photosynthetic capacity to tolerate low light (Averill et al. 2016). *Vincetoxicum nigrum* often occupies shaded environments in its native European range (Averill et al. 2011). In both species, light limitation can reduce establishment, growth, and reproductive potential (see “Growth and Development: Ecophysiology”). *Vincetoxicum* species are not problematic in highly disturbed habitats like tilled crop fields (DiTommaso et al. 2005b). *Vincetoxicum* populations cannot survive under frequent, extreme disturbance because these perennials may remain vegetative for several years before flowering (see “Life-Form and Life History”). Averill et al. (2010) tested *V. rossicum* establishment and growth in two old fields under strong disturbance treatments (herbicide or herbicide plus tillage) or weak disturbance treatments (mowing or no disturbance). At one site, establishment was increased under weak disturbance relative to strong disturbance. However, total biomass at both sites was increased under strong disturbance relative to weak disturbance. These data suggest a possible trade-off between initial establishment and subsequent growth, in addition to illustrating the effects of small-scale habitat characteristics on *Vincetoxicum* competitiveness within the introduced range.

Invasion History

Vincetoxicum nigrum, *V. rossicum*, and *V. hirundinaria* are all native to Europe, with the native distribution of *V. hirundinaria* also including parts of Asia and Africa (see “Distribution”; Royal Botanic Gardens, Kew 2021). In addition, *V. nigrum* and *V. rossicum* have invaded areas of Europe to which they are not native (see “Distribution”). For example, a population of *V. nigrum* (native to southwestern Europe) was found to be established in Bulgaria in 2009 (Petrova 2010). It is naturalized in the Netherlands and is considered a garden escape in Belgium (Global Biodiversity Information Facility 2022a; Markgraf 1972; Ronse 2013). Markgraf (1971) noted that *V. rossicum* has been grown in gardens in Central and Western Europe since at least the 1800s, with some escapes reported. *Vincetoxicum rossicum* was anthropogenically introduced to Norway before 1865, although misidentified as *V. hirundinaria*, and is now considered invasive there (Bjureke 2007; Lauvanger and Borgén 1998).

The early history of *Vincetoxicum* in North America is obscured by inconsistent nomenclature and the fact that escapes did not immediately lead to explosive population growth. *Vincetoxicum nigrum* appears to have been introduced first, with most early herbarium specimens (beginning in Massachusetts, USA, in 1854) collected in or near gardens (Sheeley and Raynal 1996). The fifth

edition of *Gray’s Manual of Botany* (Gray 1868, p. 399) described *V. nigrum* as “a weed escaping from gardens” around Cambridge, MA. It may have been brought into Ontario as early as 1861 from the Botanic Garden at Cambridge, MA (Pringle 1973). Early herbarium records and descriptions of *V. rossicum* (mistakenly labeled *Cynanchum medium* R. Br. in early years) (Sheeley and Raynal 1996) suggest a similar invasion pathway. These records include the Canadian provinces of British Columbia in 1885 (which did not persist) and Ontario in 1889, and New York, USA, in 1897 (Moore 1959; Sheeley and Raynal 1996). Reports of *V. rossicum* in Canada and the northeastern United States remained sporadic until the second half of the 20th century (Sheeley and Raynal 1996). The third species, *V. hirundinaria*, has generated fewer records in North America. The seventh edition of *Gray’s Manual of Botany* (Gray 1908, p. 667) reported that this species [as *Cynanchum vincetoxicum* (L.) Pers.] had escaped from cultivation in southern Ontario, although it apparently has not persisted (Pringle 1973). The earliest herbarium specimen found by Sheeley and Raynal (1996) was collected in New York in 1916.

Following their initial introductions, *V. rossicum* and *V. nigrum* did not become major problems in North America for many decades. This long lag phase has been followed by a period of rapid expansion. Kricsfalussy and Miller (2008) formalized these observations for *V. rossicum* in the Toronto, Ontario, area. They found that the lag phase lasted nearly a century and that *V. rossicum* invasion followed an exponential trajectory from 2000 to 2005. More qualitative observations of larger-scale trends indicate that *V. rossicum* and *V. nigrum* were well established in some areas (but not particularly common) by the mid-20th century (Sheeley and Raynal 1996). These species became increasingly prevalent in subsequent decades, especially at the end of the 20th century and in the 21st century (DiTommaso et al. 2005b; Douglass et al. 2009). Several factors may have contributed to increasing range and population expansion rates. Positive associations between population size and expansion rate (e.g., larger populations produce more seeds) should occur when resources are available and environmental conditions are suitable. During the lag phase, *Vincetoxicum* species may have increased their ability to compete for resources and thrive under North American environmental conditions. This process may have involved evolutionary changes to the genotypes introduced from Europe (Douglass et al. 2009). Adaptive evolution could help explain the wide climatic ranges occupied by *Vincetoxicum* species in North America (see “Habitat”). Because *V. rossicum* and *V. nigrum* were already well established in North America by the time that their rapid expansion began attracting major concern, research and management efforts have focused on limiting environmental and economic injury rather than pursuing eradication, except in Minnesota, USA (Minnesota Department of Agriculture 2021).

Life-Form and Life History

Vincetoxicum species are herbaceous perennial vines that reproduce by seed (Figure 6). Based on North American studies, single-stemmed seedlings typically emerge in spring, although autumn germination can also occur from the seedbank (DiTommaso et al. 2005b; Milbrath et al. 2017). Survival rates for seedlings (and older plants) may be high, especially outside of heavily shaded forest habitats (Milbrath et al. 2017). High survival rates may be facilitated by resource allocation strategies that initially emphasize resource acquisition and storage. Although it is possible for flowering and follicle production to occur in the first or second years under semi-natural conditions (Averill et al. 2010; Magidow et al. 2013),

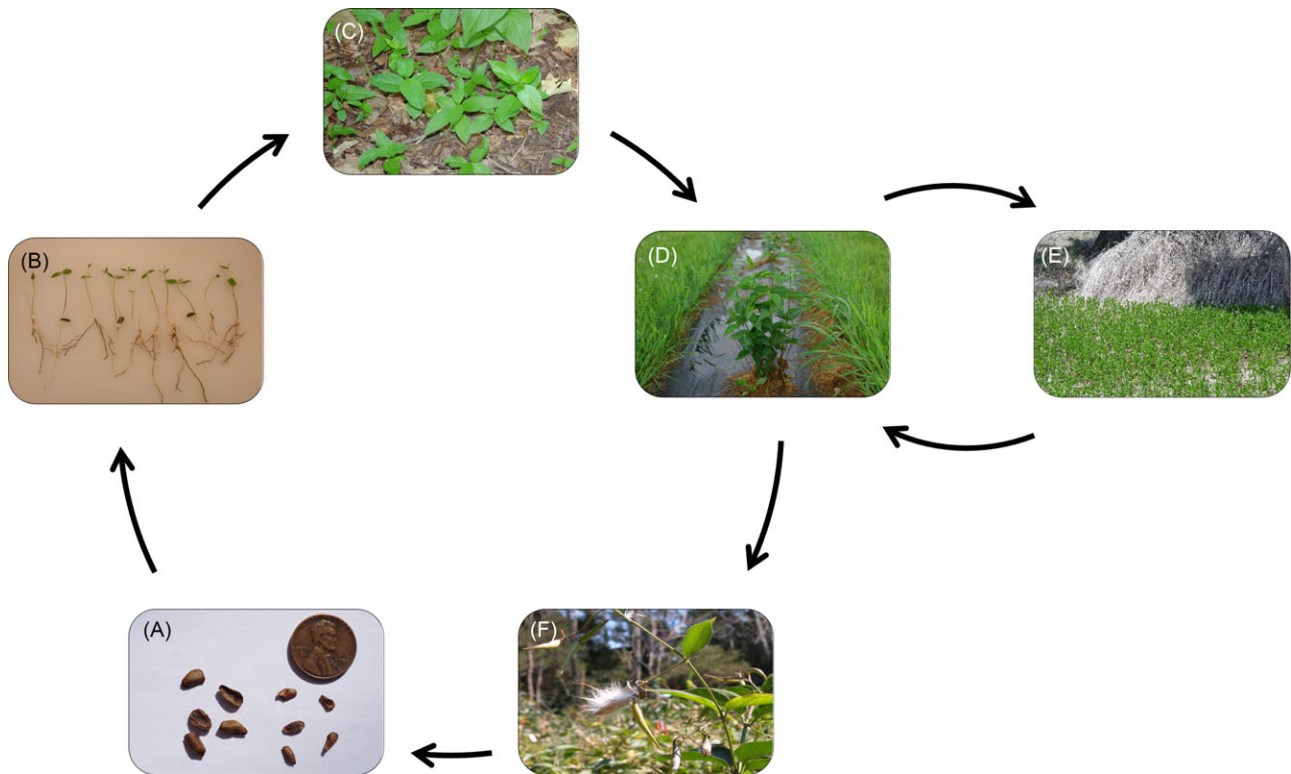


Figure 6. (A) Seeds of *Vincetoxicum nigrum* (left) and *Vincetoxicum rossicum* (right). (B) Seedlings (with seed coats) and older vegetative juveniles of *V. rossicum*. (C) Vegetative juveniles of *Vincetoxicum rossicum*. (D) Individual *Vincetoxicum rossicum* plant with multiple stems. (E) Senesced *Vincetoxicum rossicum* stems and spring regrowth. (F) Follicle dehiscence in *Vincetoxicum rossicum*. (Photo credits: (A and D) Scott Morris; (B) Kristine Averill; (C and E) Jeromy Biazzo; (F) Larissa Smith.)

flowering typically does not occur for several years (see “Reproduction: Population Dynamics”; Milbrath et al. 2017). During the pre-flowering juvenile period, *V. rossicum* plants grow slowly and store resources belowground (Averill et al. 2010; McKague and Cappuccino 2005; Milbrath et al. 2017). Gradual resource accumulation may be particularly important in shaded or otherwise low-resource environments, but the long juvenile period is not unique to a particular habitat type (Averill et al. 2010). In any competitive environment, *V. rossicum* may benefit from delaying reproduction until energy reserves are sufficient. Prolonged juvenile periods also occur in *V. nigrum*, although young *V. nigrum* plants are more likely to flower and produce follicles than young *V. rossicum* plants (Magidow et al. 2013; Milbrath 2008; Milbrath et al. 2017). The interspecific difference in time to flowering appears to be associated with increased root allocation in *V. rossicum* relative to *V. nigrum* (Milbrath et al. 2017). Once a plant begins flowering, it may continue for many years. Individual plants are long-lived (life span unknown; Milbrath et al. 2017), and populations may persist indefinitely (>70 yr; Sheeley and Raynal 1996).

Each year, *Vincetoxicum* stems senesce in late summer or early autumn (DiTommaso et al. 2005b). Belowground organs overwinter. In the next growing season, one to several new stems sprout from buds on the root crown (DiTommaso et al. 2005b; Milbrath et al. 2017). In productive environments, older plants produce more stems than young plants (Milbrath et al. 2017). Averill et al. (2011) demonstrated this phenomenon in both *V. rossicum* and *V. nigrum* clumps (i.e., single genets or multiple genets in the case of polyembryony; see “Reproduction: Seed Production and Dispersal”). Stem numbers increased more quickly in old fields (-0.02 to 2.1 stems clump $^{-1}$ yr $^{-1}$ for *V. rossicum* and -0.01 to

4.6 stems clump $^{-1}$ yr $^{-1}$ for *V. nigrum*) than in forests (-0.01 to 0.8 stems clump $^{-1}$ yr $^{-1}$ for *V. rossicum*). Older plants may have up to 25 stems (Milbrath et al. 2016, 2017). However, under high densities, individual plants may only possess a single stem (LRM, unpublished data). Increases in stem number can facilitate proportional increases in per-plant biomass or seed production (Averill et al. 2011), or these trends can be decoupled (e.g., under disturbance; Milbrath et al. 2016). Depending on their length and the availability of supports, *Vincetoxicum* stems may be erect or scrambling, twining, or climbing (DiTommaso et al. 2005b). In hedgerow and woodland-edge habitats, *V. rossicum* can reportedly climb to heights of 2 to 3 m (Cappuccino et al. 2002). The climbing habit aids seed dispersal and increases the competitive (i.e., shading) and physical effects of vines on support plants.

Invasive *Vincetoxicum* species are effective competitors and tolerant of interspecific competition. Their life cycles are relatively slow. They tolerate only moderate disturbance and stress. For these reasons, they are best classified as Competitors in the C-S-R (Competitor, Stress tolerator, Ruderal) framework (Averill et al. 2010; Grime 1977).

Dispersal and Establishment

Vincetoxicum rossicum and *V. nigrum* reproduce exclusively by producing seeds, which are primarily wind dispersed. Wind-dispersed seeds typically travel short to moderate distances. Cappuccino et al. (2002) found that *V. rossicum* seeds traveled up to 18 m, with 50% of seeds traveling less than 2.5 m from the release point (release height: 1.5 m; windspeed: 11.2 km h $^{-1}$). Seed weight was negatively associated with dispersal distance.

Large seeds sometime achieved better germination and growth than small seeds; however, the relationships between seed weight and dispersibility or quality are weak enough that any trade-off between dispersibility and quality is probably unimportant at the local scale (Ladd and Cappuccino 2005). Release height is a more important influence on dispersal distance. Seeds released from 0.75 m landed 4.4 ± 3.3 m (mean \pm SD) from the release point in *V. nigrum* and 4.7 ± 3.5 m from the release point in *V. rossicum*, whereas seeds released from 2 m landed an average of 12.6 ± 9.6 m and 17.1 ± 12.1 m from the release point, respectively (DiTommaso et al. 2018). The maximum dispersal distances (2-m release height) were 72.1 m for *V. nigrum* and 79.6 m for *V. rossicum*. This interspecific difference reflected the fact that *V. nigrum* seeds are heavier. Long-distance wind dispersal of *V. nigrum* seeds could require the combination of a high release point and a strong wind (DiTommaso et al. 2018). Other seed-dispersal mechanisms are less common than wind dispersal. There are many anecdotal reports of animal dispersal, including dispersal by white-tailed deer (*O. virginianus*; DiTommaso et al. 2018) and dispersal along hiking trails (Sandilands 2013). Longer-distance transport is mostly anthropogenic. *Vincetoxicum* species have historically been transported deliberately as ornamentals and presumably continue to be transported inadvertently (see “Invasion Pathways”).

Within their bioclimatic envelopes (see “Habitat”), *V. rossicum* and *V. nigrum* are limited by competition from resident plant species. Greenhouse and growth chamber experiments have shown that competition against *A. syriaca*, Canada goldenrod (*Solidago canadensis* L.), and quackgrass [*Elymus repens* (L.) Gould] can substantially reduce *Vincetoxicum* performance (Blanchard et al. 2010; Jackson and Amatangelo 2021; Milbrath et al. 2019a; Sanderson and Antunes 2013). Research on *V. nigrum* has demonstrated that competitive responses are shaped by competitive environments over evolutionary time (Atwood and Meyerson 2011). Competitive environments also matter at smaller, more ecological spatiotemporal scales: in general, plant community invasibility depends on numerous determinants of resource supply and demand (Davis et al. 2000). However, some habitats invaded by *V. rossicum* and *V. nigrum* lack characteristics likely to promote resource surpluses, such as high disturbance levels (Averill et al. 2010; DiTommaso et al. 2005b).

Several factors may be helpful in explaining why *V. rossicum* and *V. nigrum* are so invasive. First, these species can survive and reproduce in low-resource environments (see “Life-Form and Life History”; “Growth and Development: Ecophysiology”). Second, positive density-dependent effects (e.g., plants twining together into a light-extinguishing mat) may help suppress allospecific competitors (see “Reproduction: Population Dynamics”). Third, their fitness is typically not limited by herbivores or pathogens in North America (enemy release; see “Management Options: Biological”). *Vincetoxicum* species contain phenanthroindolizidine alkaloids, notably (–)-antofine, in their seeds, leaves/stems, and roots (Capo and Saa 1989; Gibson et al. 2011, 2015; Mogg et al. 2008; Stærk et al. 2000). *Vincetoxicum rossicum* contains higher concentrations of (–)-antofine than *V. nigrum*; roots have higher concentrations than stems; and seeds, seedlings, and young plants of *V. rossicum* contain higher concentrations than adult plant roots (Gibson et al. 2011, 2015). These compounds are highly cytotoxic, as demonstrated in experiments with human cancer cells (Stærk et al. 2000, 2002; Tanner and Wiegrebe 1993). Phenanthroindolizidine alkaloids, which appear to be rare in the Asclepiadoideae, could contribute to invasiveness by reducing

palatability to herbivores in the introduced range (Liede-Schumann et al. 2016). Mogg et al. (2008) and Gibson et al. (2011) found that (–)-antofine from *V. rossicum* extracts exhibited antibacterial and especially antifungal activity. Mogg et al. (2008) also reported insect antifeedant activity, which was not attributable to (–)-antofine. Similarly, other *Vincetoxicum* species contain alkaloids that deter feeding by nonspecialist insects (Kathuria and Kaushik 2005; Verma et al. 1986).

Allelopathy has been proposed as a fourth explanation for successful *Vincetoxicum* invasion of occupied niches. Cappuccino (2004) indicated that *V. rossicum* extracts inhibited radish (*Raphanus sativus* L.) seed germination in addition to exhibiting antifungal activity. Such data suggest that tissue leachates or root exudates from *Vincetoxicum* invaders could affect native plants both directly (inhibition) and indirectly (altered rhizosphere communities). The cytotoxic alkaloids may act as “novel weapons” (sensu Callaway and Ridenour 2004), promoting invasiveness. Similarly, Douglass et al. (2011) found that *V. rossicum* and *V. nigrum* root exudates could reduce the germination and growth of some indicator species in laboratory tests (in one case, root exudates increased growth). *Vincetoxicum* tissue leachates had inhibitory, neutral, or stimulatory effects, depending on the indicator species (Douglass et al. 2011). Gibson et al. (2011) found that native Apocynaceae were more sensitive to (–)-antofine than *V. rossicum* and *V. nigrum*. However, Gibson et al. (2015) reported that (–)-antofine degrades rapidly under ambient conditions and its allelopathic activity is greatly reduced in nonsterile soil. In addition, the concentrations of (–)-antofine in *V. rossicum* and *V. nigrum* root exudates were too low for significant biological activity, although the authors did not rule out (–)-antofine accumulation in the rhizosphere (Gibson et al. 2015). While high concentrations of (–)-antofine in seeds and seedlings might contribute to establishment, it is not clear that allelopathy plays a role in *Vincetoxicum* invasions.

Invasion Risk

Foster et al. (2022) developed MaxEnt and spatial dispersal models for *V. rossicum* across its invasion history in North America (10-yr intervals, 1890 to 2020). This analysis suggested that the North American distribution of *V. rossicum* was largely a function of dispersal in the early stages of invasion. Environmental constraints played a more important role in later stages. Foster et al. (2022) concluded that *V. rossicum* may have reached environmental equilibrium and that its geographic distribution may be stabilizing, but noted caveats related to the period of reference, spatial scale, and potential for dispersal limitation or local adaptation.

To our knowledge, potential distributions of *V. rossicum* and *V. nigrum* have not previously been modeled at a global scale. We developed CLIMEX models to identify regions of the world that are potentially suitable for *V. rossicum* and *V. nigrum* persistence under current climate. CLIMEX software (v. 4, Hearne Software, Melbourne, Australia) determines potential species distributions based on model parameters that describe how the species respond to climate. Model parameters reflect experimental data (when available) and species occurrence records. Our models were based on responses to temperature and precipitation; we did not explicitly account for factors such as land use or biotic constraints. Modeling methods are described in Supplementary Appendix S1, and model parameters are given in Supplementary Tables S2 and S3.

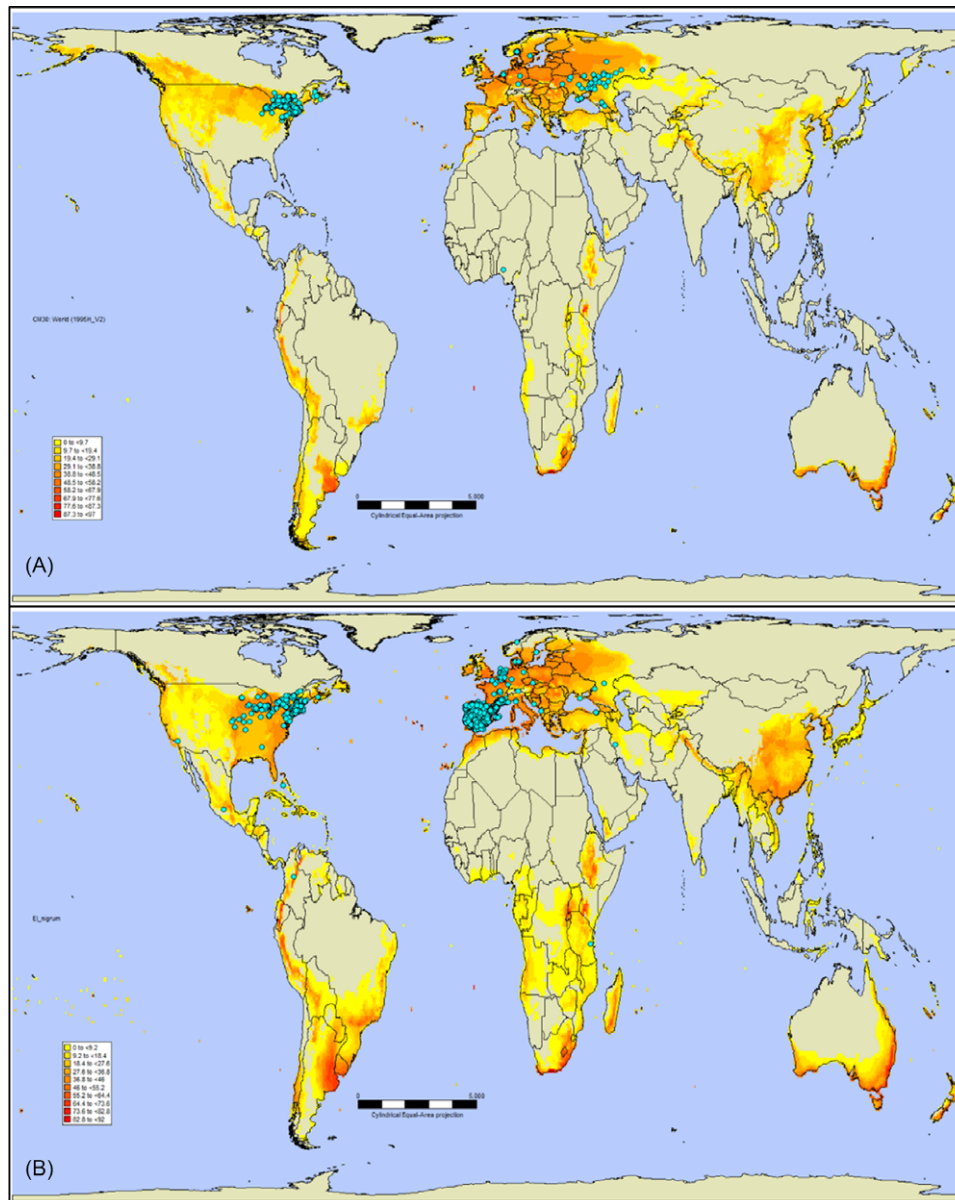


Figure 7. Climatic suitability for (A) *Vincetoxicum rossicum* and (B) *Vincetoxicum nigrum*. CLIMEX models were based on temperature and precipitation (see Supplementary Appendix S1). According to these models, unshaded areas are not suitable for *Vincetoxicum* population growth, yellow areas are somewhat suitable, and red areas are highly suitable. Current species distributions are also shown with blue dots (Global Biodiversity Information Facility 2022a, 2022b).

The CLIMEX models showed that the potential distributions of *V. rossicum* and *V. nigrum* are much larger than their current distributions (Figure 7). For example, the projected distribution of *V. rossicum* includes the northern half of the continental United States, and the projected distribution of *V. nigrum* includes most of the continental United States. Most areas of Europe are potentially suitable for both species. These results suggest that substantial range expansions are possible for both species.

Any discrepancies between our conclusions and those of Foster et al. (2022) could reflect the different goals, methods, and spatio-temporal scales of the two analyses. As different approaches provide different insights, it is useful to construct diverse models to develop a consensus picture of invasion risk. Further modeling efforts should also seek to develop high-resolution maps that account for additional influences on distribution (e.g., biotic constraints) and future climate change.

Invasion Pathways

Many reported introductions of *V. rossicum*, *V. nigrum*, and *V. hirsundinaria* to new continents and regions have been deliberate (see “Invasion History”). These species were primarily introduced to North America as ornamental plants that escaped from gardens repeatedly and in multiple locations (Sheeley and Raynal 1996). Cultivation is now uncommon and sometimes prohibited in North America (Supplementary Table S1). Garden escapes have occurred to a lesser extent in Europe (Lauvanger and Borgen 1998; Ronse 2013), where *Vincetoxicum* species are less likely to have large advantages over competitors. Long-distance *Vincetoxicum* transport may also occur inadvertently. Contamination in the nursery trade is one possibility (DiTommaso et al. 2005b). This mode of transport could easily bridge continents, although frequent intercontinental transport

seems unlikely to have occurred given the reduced genetic diversity of *V. rossicum* and *V. nigrum* in North America relative to Europe (Bon et al. 2010). Other plausible vectors for seed transport include vehicles, machinery, and hay (Cadotte et al. 2017; Plant Conservation Alliance's Alien Plant Working Group 2006). Although non-anthropogenic mechanisms like wind dispersal usually operate over short or medium distances (see "Dispersal and Establishment"), they could allow infrequent long-distance transport. Seeds of horseweed [*Conyza canadensis* (L.) Cronquist] may travel very long distances by entering the planetary boundary layer (Shields et al. 2006). Seeds of *V. rossicum* and *V. nigrum* might likewise achieve occasional long-distance transport when release height and wind speed are high (DiTommaso et al. 2018). Given that *V. rossicum* is considered rare and even endangered in some parts of its native range, it is unlikely that the Russia–Ukraine conflict will affect its invasiveness in the region.

Growth and Development

Morphology

The competitiveness of *Vincetoxicum* species is influenced by resource allocation patterns. Both *V. rossicum* and *V. nigrum* rely on root reserves for overwintering and recovery from damage (DiTommaso et al. 2005b). Root allocation allows gradual resource accumulation and thereby supports competitiveness and fitness (see "Life-Form and Life History"). Root-to-shoot ratios are typically higher in *V. rossicum* than in *V. nigrum* (Milbrath et al. 2016). For *V. rossicum*, Averill et al. (2010) reported root-to-shoot ratios of 2.6 and 3.5 (two sites, two seasons after sowing). McKague and Cappuccino (2005) reported root-to-shoot ratios of nearly 1 in mature *V. rossicum* and greater than 3 in seedlings.

Root-to-shoot ratios are sensitive to abiotic and biotic environments. Milbrath (2008) reported high root-to-shoot ratios in *V. rossicum* (1.9 in mature plants and greater than 3 in seedlings), relative to consistently low ratios in *V. nigrum* (less than 1) under high light (488 to 916 $\mu\text{mol s}^{-1} \text{m}^{-2}$). Under low light (12 to 25 $\mu\text{mol s}^{-1} \text{m}^{-2}$), there was no interspecific difference. DiTommaso et al. (2021) reported a root-to-shoot ratio of 1.4 in *V. rossicum* and 0.5 for *V. nigrum* under sufficient soil moisture. Soil moisture deficit increased these root-to-shoot ratios to 3.0 in *V. rossicum* and 1.2 in *V. nigrum*. Cappuccino (2004) reported that root-to-shoot ratios were marginally greater in smaller patches of *V. rossicum* relative to larger patches (plants in larger patches produced more vegetative biomass). Root-to-shoot ratios in *V. rossicum* may be higher under interspecific competition than intraspecific competition (Blanchard et al. 2010). Sanderson and Antunes (2013) found that competition for nutrients against *S. canadensis* increased the root-to-shoot ratio of *V. rossicum* by 40% (1.72 to 2.41) relative to *V. rossicum* grown alone. Conversely, competition against *V. rossicum* did not significantly increase the root-to-shoot ratio of *S. canadensis*. Taken together, these data indicate that plasticity in resource allocation represents an important component of *V. rossicum*'s response to competition.

Stress Tolerance

Vincetoxicum rossicum and *V. nigrum* overwinter as seeds and by perennating buds on the root crown (DiTommaso et al. 2005b). Overwintering belowground allows *V. rossicum* to survive very cold temperatures, including minimum temperatures of -35 C in Ontario (Dickinson and Royer 2014, p. 40; Dickinson et al. 2021). Crown buds sprout at the beginning of the growing season

or after aboveground damage, such as from spring frosts or stem removal (DiTommaso et al. 2005b; McKague and Cappuccino 2005; LRM, personal observation). Regrowth from axillary buds also allows for tolerance to damage, especially under high light (see "Management Options: Cultural").

Vincetoxicum species can tolerate seasonal (not prolonged) flooding, but do not occupy wetlands (DiTommaso et al. 2005b; Lawlor 2002). *Vincetoxicum rossicum* establishment may be reduced in poorly drained soil (Averill et al. 2010). In a greenhouse experiment, *V. rossicum* height and *V. nigrum* biomass were reduced by recurring drought (Joline and DiTommaso 2016). Another greenhouse experiment showed that drought reduced growth (height, number of nodes, and biomass production) and reproduction, especially in *V. rossicum* (DiTommaso et al. 2021). *Vincetoxicum nigrum* maintained higher rates of shoot growth and reproduction under drought (DiTommaso et al. 2021). In a field study of *V. hirundinaria* in Sweden, supplemental watering (324 mm in addition to 130-mm rainfall) increased folicle (but not flower) production in the treatment year and the following year (Ågren et al. 2008). Like water availability, soil pH does not narrowly constrain *Vincetoxicum* distributions (see "Habitat") but can affect performance. For example, some authors have reported reduced biomass under low pH (Magidow et al. 2013; Sanderson et al. 2015). The presence of *Vincetoxicum* species in urban environments and along roadsides (Cadotte et al. 2017; DiTommaso et al. 2005b; Potgieter and Cadotte 2020) might be facilitated by a tolerance to salinity or chemical toxins, but this hypothesis requires experimental testing.

Ecophysiology

Although both *V. rossicum* and *V. nigrum* are physiologically capable of tolerating low-light conditions, *V. nigrum* mostly occupies high-light sites (Averill et al. 2011, 2016). *Vincetoxicum rossicum* is found in a variety of environments, but generally achieves higher survival, growth, and reproduction under high light (see "Habitat"; "Reproduction: Seed Production and Dispersal"; Hotchkiss et al. 2008; Milbrath 2008; Milbrath et al. 2017). Ambient light levels help determine specific leaf area in *V. rossicum* (Rochette 2019; Yasui 2016). Smith et al. (2006) reported that *V. rossicum* plants grown under low light exhibited a classic shade phenotype (taller, thicker stems and larger, thinner leaves) that resulted in an increased tendency to climb over nearby plants. More generally, tall stems and high specific leaf areas may help *V. rossicum* invade and dominate existing plant communities (Livingstone et al. 2020a).

Vincetoxicum rossicum adopts a "sit-and-wait" strategy in low-light sites under forest canopies (Averill et al. 2011, 2016; Hotchkiss et al. 2008). These plants can photosynthesize efficiently and store resources belowground until canopy disturbance increases light penetration, enabling substantial aboveground growth and seed production. This strategy can be understood as a special application of the long juvenile phase characteristic of *Vincetoxicum* species and especially *V. rossicum* (see "Life-Form and Life History"). The waiting strategy of *V. rossicum* has been observed at both plant and population scales: a forest population can persist at low density until disturbance releases additional resources (Averill et al. 2011; Sheeley 1992).

Phenology

In eastern Canada and the northeastern United States, seed germination and seedling emergence of *V. rossicum* and *V. nigrum*

usually occur in a spring flush (often beginning in May) with germination and emergence continuing at decreasing rates through summer and autumn (often ending in October) (Averill et al. 2010; DiTommaso et al. 2005b; Milbrath et al. 2017). Although not all newly dispersed seeds exhibit dormancy (DiTommaso et al. 2005a, 2005b), germination and emergence are rare in the autumn relative to the spring (Milbrath et al. 2017). Most autumn-germinating seeds germinate from the seedbank (i.e., they are more than 1 yr old; Milbrath et al. 2017). After the establishment year, new shoots often emerge in late April or early May (DiTommaso et al. 2005b). In northern New York, *V. rossicum* plants attained their maximum heights in late June or early July (Smith et al. 2006); Averill et al. (2011) indicated that maximum stem lengths for both species occurred by August across New York sites.

Flowering and follicle development overlap (DiTommaso et al. 2005b). A generic phenology for *V. rossicum* and *V. nigrum* in the northeastern United States would predict most flowering and follicle development between June and early autumn, with seed dispersal beginning in August. The exact timing depends on species, climate, and habitat characteristics. In central and northern New York, flowering of *V. rossicum* can begin in mid- to late May and peak from late May to late June (Lawlor 2000; Sheeley 1992; Smith et al. 2006). Flowering may peak approximately 5 wk after the emergence of shoots (Sheeley 1992). Follicle production may level off between mid-June and early August, remaining high until early September (Smith et al. 2006). In New York, seed dispersal in open habitats often begins in late July or early August (Lawlor 2003). In Ontario, *V. rossicum* flowers from late May or June to August, although plants that resprout after being damaged may flower until the first frost (Christensen 1998; St. Denis and Cappuccino 2004). Christensen (1998) reported that follicle development in southern Ontario occurs between mid-June and mid-August, seed dispersal begins by late August, and stems are dead by the end of September (Christensen 1998). Farther north near Ottawa, Ontario, follicle dehiscence may not begin until September, with seed release continuing through November (Cappuccino et al. 2002). Seed maturation, follicle dehiscence, and senescence are sometimes delayed (2 wk up to 1 mo) in shaded populations of *V. rossicum* relative to populations under high light (Christensen 1998; Lawlor 2000; Livingstone et al. 2020b; Milbrath et al. 2017).

Within a growing season, the flowering period may be longer in *V. nigrum* than *V. rossicum*. Unlike *V. rossicum*, which may stop flowering as soon as early August in New York, *V. nigrum* can continue flowering until the first hard frost (Milbrath et al. 2016). Otherwise, phenology is generally similar between the two species. In southeastern New York, flowering of *V. nigrum* typically begins in mid- to late May, peaks in mid- to late June, and tapers off in July (Lumer and Yost 1995). Within this region, flowering tends to begin earlier at more southern sites and continue later (into August) at shadier sites (Lumer and Yost 1995). In the northeastern United States (New York and New England states), *V. nigrum* seed broadcast begins in late July or early to mid-August but may continue as late as October (Lumer and Yost 1995; URI CELS Outreach Center n.d.).

Mycorrhiza and Bacterial Symbionts

Vincetoxicum species associate with arbuscular mycorrhizal fungi (AMF), which may improve performance in their introduced range. For example, Smith et al. (2008) measured high rates of

AMF root colonization in *V. rossicum* field-collected in New York, relative to co-occurring species such as *S. canadensis* and *A. syriaca*. Greenhouse experiments showed that soil containing AMF from the field site facilitated *V. rossicum* survival (relative to sterilized soil) and growth (relative to sterilized soil, sterilized soil reamended with an AMF-free microbial wash, or soil inoculated with an AMF isolate from Alabama, USA). Greipsson and DiTommaso (2006) also observed high rates of root colonization in *V. rossicum*. Soil invaded by *V. rossicum* contained four times as many AMF spores as nearby non-invaded soil and had a higher mycorrhizal infectivity potential. *Vincetoxicum rossicum* has been described as a fungal generalist, associating with AMF (e.g., *Rhizophagus* spp. and *Funneliformis* spp.) with which nearby native plants may not associate (Bongard et al. 2013b). Although *V. rossicum* may be capable of associating with diverse AMF, observed AMF communities are not always diverse. Dickinson et al. (2021) observed a low diversity of AMF colonizing *V. rossicum* roots across 54 sites in southern Ontario: only three species appeared at more than 5% of sites, two of which appeared at all sites. The authors suggested that these AMF species might resist antagonism by other fungal partners and might also resist allelochemicals such as (–)-antofine. Bongard et al. (2013a) reported that native plants living in close association with *V. rossicum* were colonized at higher densities and by different AMF communities than native plants living without *V. rossicum*. Changes to soil AMF communities due to *V. rossicum* likely develop over multiple growing seasons (Day et al. 2015a). Although *V. rossicum* often exerts a powerful influence on AMF communities, this influence is not always dominant. Bongard and Fulthorpe (2013) found that garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande] could decrease the density of AMF on *V. rossicum*, but *V. rossicum* had less effect on *A. petiolata*.

Vincetoxicum–soil feedbacks are not exclusively mediated by AMF. Dickinson et al. (2021) identified 30 endophytes, including 12 known pathogens, whose abundances were positively correlated with aboveground biomass production in *V. rossicum*. In addition, aboveground biomass was positively correlated with the percentage of the fungal community represented by these 12 known pathogens. The authors suggested that fungal pathogens might promote *V. rossicum* invasion by negatively affecting competing plants. The authors also noted the presence of dark septate endophytes colonizing *V. rossicum*; like AMF, dark septate endophytes may provide their hosts with water and nutrients. The results of this field study (Dickinson et al. 2021) were consistent with an earlier report (Day et al. 2016) that *V. rossicum* can host fungi that increase its total biomass but do not facilitate native species and might even contribute to inhibitory effects on *S. canadensis*. In *S. canadensis*, unlike other native species, rhizosphere biota from *V. rossicum*–invaded soil appear to have a stronger negative effect on biomass than rhizosphere biota from uninvaded soils (Dukes et al. 2019). In its North American range, *V. rossicum* does not yet appear to be strongly inhibited by pathogenic fungi (see “Dispersal and Establishment”; “Management Options: Biological”). Despite the presence of pathogenic fungi, soil biota from invaded soils may have a net positive effect on *V. rossicum* with no evidence of pathogen accumulation over long time periods (100 yr; Day et al. 2015b).

Fewer research projects have focused on bacteria. Thompson et al. (2018) reported that invasion by *V. rossicum* did not explain much variation in bacterial community composition (unlike fungal community composition), soil respiration, or available soil nitrogen (N). In contrast, Bugiel et al. (2018) reported that invasion by

V. rossicum explained a significant portion of variation in bacterial community composition. Plant–soil feedbacks might also be mediated by the availability of nitrogen and other nutrients, but understanding these feedback mechanisms will require further research on nutrient dynamics in communities invaded by *Vincetoxicum* species (Liu 2020).

Reproduction

Floral Biology

Vincetoxicum rossicum, *V. nigrum*, and *V. hirundinaria* (in Finland) can produce seeds by insect-mediated cross-pollination or self-pollination (Leimu 2004; Lumer and Yost 1995; St. Denis and Cappuccino 2004). These species, like other members of the subfamily Asclepiadoideae, have complex floral structures that facilitate insect pollination. Pollen is dispersed in a structure called a pollinarium, which consists of pollinia (sac-shaped masses of pollen grains) from two adjacent anthers connected by sterile structures called the translator (Kunze 1991). A notch in the center of the translator enables pollinarium dispersal by catching onto the proboscis (or perhaps leg) of an insect as the proboscis is removed from a floral nectary (DiTommaso et al. 2005b; Kunze 1991).

In Ontario, up to 25% of naturally growing *V. rossicum* flowers had been visited by insects, as evidenced by the removal of pollinaria (St. Denis and Cappuccino 2004). In New York, Lumer and Yost (1995) reported that *V. nigrum* plants were cross-pollinated exclusively by flies. The flies—mostly small, unspecialized species with short tongues—were apparently attracted by the dark color and strong odor of *V. nigrum* flowers. At least 14 species visited the flowers, six of which carried pollinia. Although observations of floral visitors in Ontario and New York are typically rare, other researchers have reported visits by flies, ants, bees, wasps, and beetles (Christensen 1998; Maclvor et al. 2017; Milbrath 2010; St. Denis and Cappuccino 2004). Nocturnal visitors are possible but have not been documented if present. In Europe, *V. hirundinaria* is mainly pollinated by large flies, moths, and bees (Leimu 2004). Further research is needed to clarify which (if any) insects are important pollinators of invasive *Vincetoxicum* species and how pollinator availability affects population dynamics.

Self-pollination (autogamy) is a rare trait in *Vincetoxicum* sensu lato and elsewhere in the Asclepiadoideae (Liede-Schumann et al. 2016). This trait has been reported in only 5 of 68 *Vincetoxicum* representatives surveyed by Liede-Schumann et al. (2016), including *V. rossicum*, *V. nigrum*, and *V. hirundinaria*. Self-compatibility tends to facilitate establishment in uncolonized areas after long-distance dispersal events (“Baker’s law”; Baker 1955, 1967). Consequently, self-compatibility could promote invasiveness in diverse taxa (Pannell et al. 2015), including groups within the Asclepiadoideae (Ward et al. 2012). Disadvantages of self-pollination are often—but not always—insignificant in the short term. In a glasshouse study of *V. hirundinaria* in Finland, cross-pollination increased fruit set (both initiated and mature, despite increased abortion) relative to self-pollination (Leimu 2004). These differences were not observed in an analysis including only self-fertile individuals. A field study in Finland found that *V. hirundinaria* reproduces primarily by outcrossing, perhaps due to inbreeding depression among the offspring of self-pollinated plants (Muola et al. 2021). Evidence for inbreeding depression in *V. hirundinaria* is mixed, partially due to substantial methodological differences between studies (Leimu 2004; Leimu and Mutikainen 2005;

Muola et al. 2011). In a greenhouse study of *V. rossicum* in Ontario, pollination method (self-pollination or cross-pollination) did not affect fruit set, seed production, seed weight, or embryony (St. Denis and Cappuccino 2004). Similarly, pollination method did not affect the germination rate of *V. nigrum* seeds in New York, which was measured at 40% for seeds produced by self-pollination and 49% for seeds produced by open pollination (Lumer and Yost 1995).

Seed Production and Dispersal

Vincetoxicum seeds are primarily wind-dispersed, with some animal dispersal and anthropogenic transport over long distances (see “Dispersal and Establishment”). Adaptations for wind dispersal include a membranous marginal wing and a large coma (DiTommaso et al. 2005b). Viable seed production per follicle is reported to be 5 to 13 (mean of 8) in *V. rossicum* and 7 to 12 (mean of 10) in *V. nigrum* (Averill et al. 2011). Follicle size parameters, especially weight, are correlated with the number of seeds per follicle in *V. rossicum* (Sheeley 1992). In a high-light greenhouse environment, mature *V. nigrum* produced more follicle dry mass, seeds per follicle, and seeds per plant than mature *V. rossicum* (Milbrath 2008). Because *V. nigrum* seeds are heavier than *V. rossicum* seeds (20.3 vs. 7.2 mg; Milbrath 2008), total seed mass would be larger in *V. nigrum* even if seed numbers were similar. In agreement with the fact that *V. nigrum* begins reproducing earlier than *V. rossicum* (see “Life-Form and Life History”), nondefoliated *V. nigrum* seedlings produced follicles (4 plant⁻¹) and seeds (27 plant⁻¹) under high light, whereas *V. rossicum* seedlings typically did not reproduce (Milbrath 2008). Under low light, seedlings did not flower and mature plants of both species flowered but did not produce follicles or seed (Milbrath 2008). Similarly, in a common garden experiment in central New York, more than 12% of *V. nigrum* seedlings but less than 1% of *V. rossicum* seedlings produced follicles in their first growing season (Magidow et al. 2013). Follicle production does not typically occur in the first year under natural levels of stress and competition.

Among *Vincetoxicum* plants, maturity and site may explain more variation in fecundity than species. In a study of six New York populations of *V. rossicum* (forest and field) and *V. nigrum* (field only), Milbrath et al. (2017) measured fecundity (viable seeds per plant) in small (one to two stems) and large (three or more stems) flowering plants. For small flowering *V. rossicum*, fecundities were 4 and 67 seeds plant⁻¹ at forest sites, compared with 95 and 177 seeds plant⁻¹ at field sites. Large flowering *V. rossicum* had fecundities of 221 to 1,051 seeds plant⁻¹. *Vincetoxicum nigrum* fecundities were 17 and 98 seeds plant⁻¹ at the small flowering stage, then 48 and 963 seeds plant⁻¹ at the large flowering stage. Although the effect of species on field population fecundity was significant for small flowering plants, these data are a stronger illustration of between-site variation. In central and southeastern New York, *V. rossicum* and *V. nigrum* produced similar numbers of viable seeds (130 and 100 seeds stem⁻¹ yr⁻¹, respectively) in old-field habitats (Averill et al. 2011). *Vincetoxicum rossicum* usually produced very few viable seeds in forests (fewer than 25 seeds stem⁻¹ yr⁻¹) but produced up to 170 seeds stem⁻¹ yr⁻¹ at a higher-light forest site (Averill et al. 2011). The authors suggested that the establishment and maintenance of low-light (forest) populations sometimes depends on propagule pressure from nearby high-light (field) populations. If so, management of high-light populations should limit the expansion of low-light populations as well.



Figure 8. *Vincetoxicum rossicum* seedlings emerging from a polyembryonic seed. (Photo credit: Scott Morris.)

Seed production per unit area depends largely on environmental conditions and plant density. Smith et al. (2006) measured follicle and seed densities in shade (2,000 follicles m^{-2} , 28,000 seeds m^{-2}), intermediate sun (2,250 follicles m^{-2} , 32,000 seeds m^{-2}), and full sun (1,600 follicles m^{-2} , 25,000 seeds m^{-2}) plots at a site densely infested with *V. rossicum*. Seeds produced in full sun had higher viability, less dormancy, and higher rates of polyembryony. End-of-season seedling densities under high light were 1,136 and 1,654 seedlings m^{-2} in the 2 study years. Seed production per unit area may be much lower in less dense patches. Sheeley (1992) reported that *V. rossicum* populations occupying shaded and open sites produced 1,330 seeds m^{-2} and 2,090 seeds m^{-2} , respectively. Mean seed production per flowering ramet was 15 in the shaded site and 85 in the open site (ramet density was higher at the shaded site).

Vincetoxicum seeds exhibit high rates of polyembryony (DiTommaso et al. 2005b; Figure 8). Polyembryony in *V. rossicum* appears to be adventitious (additional embryos arising from maternal tissue rather than cleavage of the fertilized embryo), but this ontogeny has not been definitively proven or studied in most other members of the *Vincetoxicum* genus (Blanchard et al. 2010; Hotchkiss et al. 2008). In *V. rossicum*, Sheeley (1992) reported that 22% of seeds contained one embryo, 35% contained two embryos, 40% contained three embryos, and 3% contained four embryos. These rates were comparable to an existing data set in which 13% of *V. rossicum* seeds contained one embryo, 39% contained two embryos, 35% contained three embryos, 8% contained four embryos, and 5% contained five embryos (von Hausner 1976 as cited by DiTommaso et al. 2005b). Smith et al. (2006) reported up to eight radicles emerging from a *V. rossicum* seed, although most seeds only had one or two radicles. Light availability had a positive effect on mean embryony in 1 of 2 yr (Smith et al. 2006). According to other estimates, nearly (Ladd and Cappuccino 2005) or more than (Cappuccino et al. 2002; St. Denis and Cappuccino 2004) half of *V. rossicum* seeds are polyembryonic and produce multiple seedlings. Seed weight sometimes increases with embryony in *V. rossicum*, but this effect is not consistent (Cappuccino et al. 2002; DiTommaso et al. 2005a). Other *Vincetoxicum* species have lower rates of polyembryony, with 62% to 78% (*V. nigrum*) and 95% (*V. hirundinaria*) of seeds

containing a single embryo (DiTommaso et al. 2017; von Hausner 1976 as cited by Sheeley 1992). Douglass et al. (2009) indicated that a *V. rossicum* seed was 10 times more likely to be polyembryonic than a *V. nigrum* seed.

Polyembryony may mitigate risks associated with environmental variability and increase the likelihood that a seed that undergoes long-distance dispersal will found a new population (DiTommaso et al. 2005b). Although an individual embryo in a polyembryonic seed may be less likely to survive than an embryo in a monoembryonic seed, a polyembryonic seed may be more likely to produce at least one surviving seedling (Ladd and Cappuccino 2005). Averill et al. (2010) reported that polyembryony increased emergence and survival in old fields. Staggered embryo emergence times (up to 20-d difference) may increase the likelihood that at least one seedling will avoid acute stresses (Ladd and Cappuccino 2005). When multiple seedlings survive, the clump of several seedlings may be more fit or more competitive than an isolated seedling (Ladd and Cappuccino 2005; Sheeley 1992). However, Cappuccino et al. (2002) found that polyembryonic *V. rossicum* seeds produced greater total seedling weights than monoembryonic seeds only in the absence of competition. Embryony did not affect total seedling weight under competition from grasses. Similarly, Blanchard et al. (2010) reported that polyembryonic individuals seldom outperformed monoembryonic individuals under intraspecific or interspecific competition. This finding suggests that polyembryony is not an adequate explanation for *V. rossicum* invasion of established plant communities, although it may provide some advantages. For example, seedlings from a single seed may share the costs of allelochemical production and rhizosphere priming (Blanchard et al. 2010). Hotchkiss et al. (2008) found that polyembryony did not increase survival or long-term growth in *V. rossicum* grown in forest gaps or full shade. The authors suggested that polyembryony might be more useful in high-light environments such as old fields. Taken together, these studies provide stronger evidence for polyembryony as a bet-hedging strategy in disturbed environments than polyembryony as an adaptation for increased competitiveness.

Seedbanks, Seed Viability, and Germination

Seed viability has been reported at 56% to 71% in *V. rossicum*, depending on light availability, and 68% in *V. nigrum* (Milbrath 2008; Smith et al. 2006). In *V. rossicum*, seeds produced under low light were more likely to be nonviable (unfilled; Smith et al. 2006). After discarding unfilled seeds, Magidow et al. (2013) reported viability rates of 88% and 86% for seeds of *V. rossicum* and *V. nigrum*, respectively, collected in August and viability rates of 100% and 93% for seeds of *V. rossicum* and *V. nigrum*, respectively, collected in October. Milbrath et al. (2017) measured initial viabilities of 93% to 99% among filled seeds of *V. rossicum* and *V. nigrum*.

The mechanistic basis of seed dormancy in *Vincetoxicum* is not well understood, but most seeds exhibit dormancy in addition to environmental requirements for germination. Most seeds germinate after overwintering, although some nondormant seeds are produced each autumn (DiTommaso et al. 2005a, 2005b; Lumer and Yost 1995; Milbrath et al. 2017). Milbrath et al. (2017) measured emergence rates of *V. rossicum* and *V. nigrum* in New York by sowing seeds in August or October and counting emerged seedlings over several seasons. Seed survival was highly variable (14% to 74%) and contributed to variation in estimated germination rates (emergence rates divided by seed survival rates).

Germination and emergence were typically concentrated in the spring after sowing, with lower rates in the second spring. At one site, emergence was higher in the second spring, perhaps because water was limiting in the first year. In field populations (*V. rossicum* and *V. nigrum*), autumn emergence was very rare in the sowing year (before the first winter) and moderately rare in the following year. Autumn emergence was not observed in forest populations (*V. rossicum*). Across species, habitat, and sowing time, emergence in the first year after sowing varied from 5% to 39%.

Seed characteristics and environmental conditions influence germination and emergence rates. In *V. rossicum*, germination rates have been reported to vary between 45% and 95% and increase under alternating temperature and light intensities (Dickinson and Royer 2014, p. 40). Sheeley (1992) tested the germination of *V. rossicum* seeds from New York under growth chamber and greenhouse conditions. Seeds were collected in October and stored under dark, cold conditions for approximately 1 mo (growth chamber) or 7 mo (greenhouse). The growth chamber experiment included a dark treatment and a light treatment (14-h photoperiod) with temperatures fluctuating in daily cycles (13 to 21 C early in the trial and 20 to 27 C subsequently). Germination rates were 36% in the dark treatment and 46% in the light treatment. Under greenhouse conditions (range: 25 to 31 C), the germination rate was only 23%. DiTommaso et al. (2005a) reported that the site of seed production, seed harvest date, and period of seed storage affected seed germinability in *V. rossicum* from New York. For example, fresh seeds (no storage period) collected from old-field sites in August had the highest germination rates (30% to 50%) of all groups tested. Fresh seeds collected from old-field sites in November had lower germination rates. Cold-dry storage had a large negative effect on germination in seeds collected in August relative to seeds collected in November. Among fresh seeds collected in August, seeds produced in a forest were more dormant (germinated at a lower rate) and heavier than seeds produced in an adjacent old field. The production of dormant *V. rossicum* seeds under low light has been reported elsewhere (Smith et al. 2006). Magidow et al. (2013) reported much higher germination rates for *V. rossicum* and *V. nigrum* in a growth chamber experiment (seeds from New York, cold-dry storage followed by germination at 0.6 cm soil depth, 25/17 C, 14-h photoperiod). Percentage germination (emergence) was higher on a Wascaic silt loam (75%) than a Hollis gravelly loam (66%) with no difference between species or soil pH levels. Species, soil type, and soil pH sometimes interacted to influence germination speed. Cold-wet stratification for at least 3 mo usually results in >95% germination (LRM, unpublished data).

There is mixed evidence for an effect of *V. rossicum* seed size on germination or emergence (Cappuccino et al. 2002; Douglass et al. 2009). Ladd and Cappuccino (2005) reported that larger *V. rossicum* seeds were slightly more likely to emerge under field conditions (seeds were sown in April in Ontario and emergence was tracked for 3 yr). Burial depth was a more important influence on emergence, with *V. rossicum* emerging at total (multiyear) rates of 51% for seeds sown on the surface and 72% for seeds buried at 1 cm (Ladd and Cappuccino 2005). Surface-sown seeds were more likely to remain dormant for at least 1 yr before emerging. In an outdoor experiment in central New York, seeds were surface-sown in November into outdoor pots (various soils), and seedlings began to emerge in May (Magidow et al. 2013). Seedling emergence rates were higher in *V. rossicum* than *V. nigrum* across soil types and pH levels. In the same geographic area, Averill et al. (2010) found that

emergence of *V. rossicum* (seeds sown at 2 mm) was typically lower and more dependent on disturbance treatment at a poorly drained site relative to a better-drained site.

Vincetoxicum rossicum and *V. nigrum* do not persist long in the seedbank. In a 4-yr pot experiment in an old field in central New York, most seedlings (92%) emerged in the first year after burial, and no seedlings of either species emerged in the third or fourth years (DiTommaso et al. 2017). No viable seeds were recovered after the second growing season, and seeds were badly deteriorated after the third growing season. Other reports have indicated that *V. rossicum* emergence is concentrated in the first year and very low by the third year (Averill et al. 2010; Ladd and Cappuccino 2005; Milbrath et al. 2017) and that *V. rossicum* seeds remain viable for 3 to 4 yr under field conditions (Dickinson and Royer 2014, p. 40). DiTommaso et al. (2017) also tested the effect of burial depth (0, 1, 5, or 10 cm) on emergence. *Vincetoxicum rossicum*, the smaller-seeded species, achieved its highest emergence rate (37%) at the 1-cm burial depth. Other burial depths resulted in lower emergence (11% at 0 cm, 6% at 5 cm, and 0.05% at 10 cm). *Vincetoxicum nigrum*, the larger-seeded species, had higher emergence rates (16% at 0 cm, 71% at 1 cm, 66% at 5 cm, and 26% at 10 cm). Burial at 5 cm (*V. rossicum*) or 10 cm (both species) often resulted in fatal germination, suggesting that *Vincetoxicum* recruitment could be limited by deep seed burial. However, it may be more practical to focus on preventing new additions to the seedbank.

Vegetative Reproduction

Invasive *Vincetoxicum* species do not appear to reproduce vegetatively. Plants can increase their stem number over time (see “Life-Form and Life History”), but all stems sprout from the same root crown. Early reports of *V. nigrum* reproduction by rhizomes (Lumer and Yost 1995) have not been confirmed (Averill et al. 2011). The rhizome-like structure observed connecting *V. nigrum* root crowns at one location in southeastern New York remains to be properly described (12% of sampled plants; LRM, unpublished data; Figure 1E).

Population Dynamics

The establishment and persistence of invasive *Vincetoxicum* populations depend on high survival rates, gradual resource accumulation, high seed production in mature individuals under good conditions, and long life spans. Milbrath et al. (2017, 2018) parameterized a demographic matrix model to identify the reductions in survival, maturation, and reproduction (vital rates) necessary to prevent population growth in lower-density patches of *V. rossicum* and *V. nigrum* in New York. Annual seed survival and seedling emergence were highly variable (see “Reproduction: Seedbanks, Seed Viability, and Germination”). Survival rates were typically high for seedlings and juveniles (72% to 100%, exceptions included a survival rate of 33% for *V. rossicum* seedlings at a heavily shaded forest site) and very high (98% to 100%) for flowering plants (Milbrath et al. 2017). Similarly, Ladd and Cappuccino (2005) reported 71% to 100% survival for first-year seedlings of *V. rossicum*, and Averill et al. (2011) reported 100% survival for established clumps of *V. rossicum* and *V. nigrum*. Seedling densities can decline up to approximately 80% within a season under very high densities (Smith et al. 2006). Some *V. nigrum* plants became reproductive as early as their third year of growth (Milbrath et al. 2017), whereas *V. rossicum* typically requires 6 or more years to begin flowering (LRM and AD, unpublished data). Few large

flowering plants (three or more stems) of *V. rossicum* were observed in forests (Milbrath et al. 2017), supporting observations that vegetative expansion occurs slowly, if at all, in established forest clumps of *V. rossicum* (Averill et al. 2011). Based on these data, Milbrath et al. (2018) projected that disruptions of some individual survival, growth, or fecundity rates could prevent population growth in slower-growing populations ($\lambda < 1.6$). However, control of rapidly growing populations ($\lambda = 1.6$ to 2.5) would require very large and simultaneous reductions in multiple vital rates (e.g., reductions in both seedling and adult survival).

A severe *Vincetoxicum* infestation interferes with the growth of native plants by forming a dense mat of twining stems (DiTommaso et al. 2005b; Livingstone et al. 2020a). *Vincetoxicum rossicum* may establish stands that are larger and have higher *Vincetoxicum* cover than *V. nigrum* stands (Magidow et al. 2022). However, both species can establish near-monospecific stands (DiTommaso et al. 2005b; Figure 4). This ability reflects their growth habit and their potential for high stand densities, typically 100 to 200 stems m^{-2} under high light with up to 400 stems m^{-2} at some locations (Milbrath et al. 2018; Sheeley 1992; Smith et al. 2006). It is probably difficult for other species to survive in the dark understory under a mat of *V. rossicum* (Cappuccino 2004). Suppression of interspecific competitors is one reason that *V. rossicum* plants may perform better in large patches than in small patches or isolation (an Allee effect; Cappuccino 2004; Jackson and Amatangelo 2021). This hypothesis is consistent with greenhouse data showing increased *V. rossicum* performance under intraspecific competition relative to interspecific competition (Blanchard et al. 2010; Jackson and Amatangelo 2021). However, field studies using potted *V. nigrum* and *V. hirsutaria* plants in France have not fully supported an Allee effect (Maguire et al. 2011). The size and fecundity of *Vincetoxicum* patches depend not only on competitive dynamics but also on climate factors. For example, patches of *V. hirsutaria* in Sweden grew larger as the growing season lengthened in recent decades (Solbreck 2012; Solbreck and Knape 2017). Climate factors also influenced patterns of seed production and therefore seed predation (Solbreck and Knape 2017). These findings could provide insight into the potential effects of climate change on *Vincetoxicum* species in their introduced North American ranges.

Management Options

Phytosanitary Measures

Phytosanitary measures are not a major focus of *Vincetoxicum* management efforts. The propagation and transport of these weeds are prohibited across much of the North American range (Supplementary Table S1). However, no specific programs or recommendations have been developed to limit accidental transport.

Chemical

Herbicide applications generally provide good *Vincetoxicum* control. Lawlor and Raynal (2002) found that foliar spray applications of glyphosate (3.1 or 7.8 kg ae ha^{-1}) or triclopyr (1.9 kg ae ha^{-1}) provided better *V. rossicum* control than cut-stem applications of glyphosate (3.1 kg ae ha^{-1}) or triclopyr (1.4 kg ae ha^{-1}). In another experiment, they found that cut-stem glyphosate applications (3.1 or 6.2 kg ae ha^{-1}) outperformed cut-stem triclopyr applications (1.4, 2.8, or 5.6 kg ae ha^{-1}) at all application rates. No treatment prevented *V. rossicum* regrowth and new seedling emergence, so the authors concluded that long-term control would

require retreatment (Lawlor and Raynal 2002). Two- or three-application programs of glyphosate or triclopyr can achieve good *V. rossicum* control (Cain and Irvine 2011; Cain and Mervosh 2012; Christensen 1998; Mervosh and Boettner 2009). In some areas, single applications of triclopyr or imazapyr may suppress *V. rossicum* for up to two growing seasons (Averill et al. 2008; Cain and Irvine 2011; Cain and Mervosh 2012). Other herbicides that have been tested on *V. rossicum* include aminocyclopyrachlor, aminopyralid, imazapic, and metsulfuron (Gover and Rung 2015; Mervosh and Boettner 2009).

Vincetoxicum rossicum is more easily controlled with herbicides than with entirely nonchemical approaches. For example, Mervosh and Gumbart (2015) performed chemical or nonchemical control annually for 2 yr. In the third year, *V. rossicum* cover and vigor were lower in glyphosate treatments (foliar spray, 2.2 kg ai ha^{-1} , or cut-stem) than hand pulling or cutting treatments. A cut-stem triclopyr treatment provided an intermediate level of suppression, but a triclopyr foliar spray (1.7 kg ai ha^{-1}) was not superior to hand pulling or cutting. In a 2-yr study, Averill et al. (2008) compared the effects of triclopyr (1.9 kg ae ha^{-1} , first year only), clipping (once or twice per year), and triclopyr plus clipping (1.9 kg ae ha^{-1} plus one clipping in the first year, one clipping in the second year) on *V. rossicum* cover and density. The triclopyr and triclopyr plus clipping treatments were not significantly different. Both treatments were superior to the single-clipping and double-clipping treatments. At an old-field site, DiTommaso et al. (2013) found that *V. rossicum* was effectively suppressed by combination treatments (one cutting plus one herbicide application per year) but not by cutting alone (twice per year). Glyphosate (3.65 kg ae ha^{-1}) suppressed both *V. rossicum* and non-target species. For this reason, treatments with a high rate of triclopyr salt (4.87 vs. 0.93 kg ae ha^{-1}) or triclopyr ester (4.87 vs. 2.99 kg ae ha^{-1}) were considered most successful. DiTommaso et al. (2013) also tested the combination and cutting-only treatments in a forest understory (herbicides were applied at lower rates at this site because *V. rossicum* density was lower). At the forest site, most combination treatments reduced *V. rossicum* cover, but no treatment reduced *V. rossicum* stem density relative to the control. These findings underscore the influence of habitat on *Vincetoxicum* management outcomes. Only one chemical control study has been conducted with *V. nigrum*. Glyphosate greatly reduced *V. nigrum* biomass, but mowing several weeks before spraying did not always increase the effectiveness of herbicide treatments. Triclopyr was ineffective, but additional approaches including higher rates or greater frequency of application should be investigated (Milbrath et al. 2022).

Cultural

Vincetoxicum plants are difficult to kill by mowing or clipping because they recover from aboveground damage by drawing on root reserves. Annual or repeated mowing over 1 to 2 yr typically does not reduce *V. rossicum* density or cover and may even facilitate establishment by limiting interspecific competition for light (Averill et al. 2008, 2010; Christensen 1998; DiTommaso et al. 2013). In a 7-yr study in New York, Biazzo and Milbrath (2019) found that mowing *V. rossicum* three times per growing season reduced *V. rossicum* stem density, root crown density, and percent cover relative to an unmowed control, but these effects were only observed after 3 to 5 yr of treatment. Mowing six times per season provided no additional benefit. The authors concluded that mowing three times per growing season could suppress *V. rossicum* but would not eliminate existing patches. McKague and Cappuccino

(2005) determined that a properly timed, single clipping of *V. rossicum* at ground level could prevent seed production. However, if mowed at a standard 8-cm height, *V. nigrum* and *V. rossicum* can quickly regrow from axillary buds. Although two mowings or clippings per season greatly reduce that year's seed production, three mowings are needed to consistently eliminate it (Averill et al. 2008; Biazzo and Milbrath 2019; Milbrath et al. 2016).

Among treatments other than mowing and clipping, the most effective solutions are often the most labor-intensive. Manual removal of *V. rossicum* follicles can limit seed rain, but maturing follicles must be removed throughout the late summer and early fall (DiTommaso et al. 2005b). Digging *V. rossicum* out of the soil is more effective than hand pulling, which usually fails to remove the root crown (DiTommaso et al. 2005b; Lawlor 2002). Once dug up, root crowns must be removed from the site because they can regrow if left on the ground. *Vincetoxicum rossicum* might even survive cultivation by regrowth from root crown fragments, although regularly tilled fields are not suitable habitats (DiTommaso et al. 2005b; Lawlor 2002). Trampling and burning may suppress *V. rossicum* but should not be expected to provide long-term control (DiTommaso et al. 2005b; Lawlor 2002). Light-excluding mulches (e.g., black plastic) can suppress *V. rossicum* if they are sufficiently durable (Christensen 1998; Miller and Kricsfalusy 2008). Many of these cultural methods are appropriate for controlling *Vincetoxicum* in small areas, but cannot be applied across larger, less intensively managed areas.

Biological

Vincetoxicum rossicum and *V. nigrum* harbor few arthropods, mainly with little to no damage, in their introduced North American range (see "Importance"; Carpenter and Cappuccino 2005; Ernst and Cappuccino 2005; Milbrath 2010; Milbrath and Biazzo 2012). In contrast, *V. hirsutaria* and other *Vincetoxicum* species host multiple herbivores in Europe and Asia, many of which were considered promising for biological control (Tewksbury et al. 2002; Weed et al. 2011b; LRM, unpublished data). As a guide to eventual biological control releases, artificial herbivory studies were initially conducted in North America. A study using natural infestations of *V. rossicum* in Ontario indicated that increasing damage intensity (0% to 90% of either leaf or root removal) reduced *V. rossicum* seed production in sunny sites up to 80% (Doubleday and Cappuccino 2011). Root damage was slightly more effective than leaf removal, but repeated leaf removal (twice vs. once) did not further reduce seed production (Doubleday and Cappuccino 2011). In contrast to this study, defoliation treatments (50% or 100% defoliation, once or twice per growing season for 6 yr) had little effect on growth or reproduction of *V. rossicum* and *V. nigrum* in a common garden experiment under full-sun conditions in New York (Milbrath et al. 2016). The results of Milbrath et al. (2016) also contradicted a greenhouse study in which repeated defoliation (100%, twice) was suggested to be valuable in reducing biomass and seed production in high-light environments (Milbrath 2008). Defoliation (100%) under low light, simulating a heavily shaded forest understory, caused high mortality of seedlings and mature plants of both *Vincetoxicum* species (Milbrath 2008). Thus, a combination of stressors might help manage forest infestations of these species, but tolerance to aboveground damage may hamper biological control efforts in open-field infestations.

The leaf-feeding moth *Hypena opulenta* Christoph (Lepidoptera: Erebididae) was collected in a forested area from *V. rossicum* and *Vincetoxicum scandens* Sommier & Levier in

Ukraine (Weed and Casagrande 2010). It was found to successfully develop only on *Vincetoxicum* species in no-choice tests, and it is expected to produce two generations per summer (Hazlehurst et al. 2012; Weed and Casagrande 2010). Laboratory and greenhouse impact assessments showed that *H. opulenta* significantly reduced aboveground biomass and seed production in mature *V. rossicum* and *V. nigrum* plants, with greater reductions occurring with greater frequency of defoliation and increased shading of the plants (Milbrath and Biazzo 2016; Weed and Casagrande 2010). Defoliation by *H. opulenta* also reduced seedling growth and killed *V. nigrum* seedlings that were completely defoliated twice under low light (Milbrath and Biazzo 2016).

Hypena opulenta was first released in Ottawa, Ontario beginning in 2013 and has successfully established at this site, producing two generations per summer (Bourchier et al. 2019). In the United States, *H. opulenta* has been annually released since 2017 (Connecticut, Massachusetts, Michigan, New York, Rhode Island), but establishment has yet to be reported for these release sites or additional Canadian sites (Alred 2021; Alred et al. 2022b; Livingstone et al. 2020b; LRM, personal observation). Although larvae will feed nocturnally on *V. rossicum* in high-light (meadow) environments in which they are released, they appear to prefer the shaded conditions of low-light (forest understory) habitats (Livingstone et al. 2020b; Rochette 2019). A field cage study showed that *H. opulenta* defoliation of *V. nigrum* was higher in a shaded environment, relative to a sunny environment, but the low levels of defoliation did not reduce *V. nigrum* fitness in either environment (Alred et al. 2022b). *Hypena opulenta* seems likely to be most useful in controlling slow-growing forest populations of *V. rossicum* and any similar populations of *V. nigrum* (forest populations of *V. nigrum* are not as common; Milbrath et al. 2018). Adult females lay single eggs, and the larvae do not aggregate, reducing the amount of feeding damage inflicted on individual plants unless *H. opulenta* populations reach high levels throughout an area (Bourchier et al. 2019). Pupal diapause is induced in *H. opulenta* at a threshold photoperiod of 15 h 35 min (Jones et al. 2020). Two generations per summer have been shown to occur at release sites >42°N latitude when *H. opulenta* was experimentally released by late June (daylength of 15 h 20 min or more; Alred et al. 2022b; Jones et al. 2020). However, the threshold photoperiod may result in only one generation per summer at more southern latitudes in North America, reducing the potential impact of *H. opulenta* on *Vincetoxicum* infestations. Other factors influencing establishment and population increase of the moth may include substantial pupal mortality, resulting from a combination of late-summer predation and overwintering mortality, and the availability of adult food sources (Jones et al. 2022; Seehausen et al. 2019).

Like *H. opulenta*, the European leaf-feeding moth *Abrostola asclepiadis* (Denis & Schiffermüller) (Lepidoptera: Noctuidae) can only successfully develop on *Vincetoxicum* species (Hazlehurst 2011). This moth is likely to be univoltine if released in North America, limiting its potential impact on *Vincetoxicum* species (Milbrath et al. 2019b). Under greenhouse conditions, defoliation by *A. asclepiadis* and other stressors (shading or competition with a grass) had additive effects on growth and reproduction of *V. rossicum* and *V. nigrum* (Milbrath et al. 2019a). However, a single defoliation by *A. asclepiadis* had no measurable impact on either species (plant growth measured 1 yr after defoliation) in an outdoor experiment and is not projected to control most populations of *V. rossicum* or *V. nigrum* (Milbrath et al. 2018, 2019a; Weed et al. 2011a). The potential for competition with *H. opulenta*

is also a concern because, while *A. asclepiadis* is found in sunny habitats, it prefers shaded patches of its typical host (*V. hirundinaria*) in Europe (Förare 1995; Förare and Engqvist 1996). No release petition has been submitted for this moth to date.

The European beetle *Chrysochus asclepiadeus* (Pallas) (syn.: *Eumolpus asclepiadeus* Pallas) (Coleoptera: Chrysomelidae) feeds on leaves as an adult and on roots as a larva. It was considered a promising *Vincetoxicum* biological control agent particularly due to its ability to significantly reduce root biomass and disrupt water and nutrient uptake (Maguire et al. 2011; Sforza et al. 2013b; Weed et al. 2011a, 2011b). Screening of *C. asclepiadeus* was halted for several years because larvae can develop on some non-target species, including North American *Asclepias* species (Bourchier et al. 2013). However, a recent study advocated reevaluating *C. asclepiadeus* as a potential agent (deJonge et al. 2020). European field tests have been underway since 2018 to better characterize whether it will attack non-target species under field conditions (LRM, personal observation).

The seed-feeding fly *Euphranta connexa* (Fabricius) (Diptera: Tephritidae), also from Europe, can successfully attack *V. rossicum* and *V. nigrum* in laboratory tests (Weed et al. 2011b) and should tolerate North American temperatures at most potential release sites (Leroux et al. 2016). Larval feeding usually destroys all seed within a follicle and potentially all seed within patches of *V. hirundinaria* (Leimu and Lehtilä 2006; Solbreck and Sillén-Tullberg 1986). It is projected to be an effective biological control agent if approved, potentially with greater impact than defoliating agents (Leimu and Lehtilä 2006; Milbrath et al. 2018). However, this species may occasionally oviposit on non-target species in laboratory tests (Bourchier et al. 2013). Additional screening has been halted in recent years in part due to logistical difficulties and to focus on *C. asclepiadeus* (LRM, personal observation).

Other insects from Europe and Asia that have been rejected as biological control agents due to a lack of host specificity or likely ineffectiveness include the leaf-feeding beetle *Chrysolina aurichalcea asclepiadis* (Villa) (Coleoptera: Chrysomelidae); the root-feeding beetles *Chrysochus chinensis* Baly, *Chrysochus goniostoma* Weise, and *Chrysochus globicollis* Lefèvre (Coleoptera: Chrysomelidae); and the gall-forming midges *Contarinia asclepiadis* (Giraud) and *Contarinia vincetoxici* Kieffer (Diptera: Cecidomyiidae) (Dolgovskaya et al. 2016; Weed and Casagrande 2011; Widenfalk et al. 2002; Widenfalk and Solbreck 2005). Recent studies with native North American *Chrysochus* species have not shown significant utilization of *V. rossicum* (deJonge et al. 2017, 2019).

Plant pathogens were not noted on *Vincetoxicum* species in North America during early research on these invasive species (DiTommaso et al. 2005b), although some pathogens have been reported from Europe (see “Importance”). More recently, a *Cercospora* leaf-spot fungus has been reported infecting *V. nigrum* in Michigan and Rhode Island, USA, resulting in significant defoliation, and a similar unidentified leaf-spot disease was reported on *V. nigrum* in eastern New York (Alred 2021; Alred et al. 2022b; LRM, personal observation). *Athelia rolfsii* (Curzi) C.C. Tu & Kimbr. (Southern blight, syn.: *Sclerotium rolfsii* Sacc., Atheliaceae) was observed causing *V. rossicum* mortality in a New York meadow (Gibson et al. 2012). In growth chamber experiments, *A. rolfsii* caused 60% to 100% mortality in 4- to 8-wk-old seedlings of both *V. rossicum* and *V. nigrum*; the pathogen was also virulent to adult plants of both species (Gibson et al. 2012, 2014; Pethybridge et al. 2021). This fungus was not affected by (-)-antofine (Gibson et al. 2014). Although several species of broadleaf

plants appear to be susceptible to this pathogen strain, it was suggested as a potential mycoherbicide for use in select habitats (Gibson et al. 2014). However, further development of *A. rolfsii* was abandoned, in part due to increased reports of its infection of New York table beet (*Beta vulgaris* L. subsp. *vulgaris*) fields (Pethybridge et al. 2021). The pathogen *Colletotrichum lineola* Corda (Glomerellaceae) was collected on the related species *V. scandens* in Russia (Berner et al. 2011). *Vincetoxicum rossicum* and *V. nigrum* exhibited disease symptoms when inoculated with *C. lineola*, but host range tests were not conducted, as the impact of *C. lineola* on the plants would likely be minimal (D Berner, personal communication).

General Outlook

Vincetoxicum rossicum and *V. nigrum* have invaded some regions of North America, particularly the northeastern United States and southeastern Canada, and some locations in Europe outside their native distributions (e.g., Norway). Continued spread within North America is very likely. Spread within Europe may be somewhat constrained by biotic factors. In North America, *V. rossicum* and *V. nigrum* can establish near-monocultures and produce large quantities of wind-dispersed seeds. Because both species tolerate a wide range of environmental conditions with potentially high survival of all life stages, they colonize diverse habitats, including cities. Our CLIMEX models suggest that many uninhabited regions of the world may be climatologically suitable for *Vincetoxicum* species. However, long-distance movement of these species appears minimal, with the greatest threat coming from deliberate introductions of *V. rossicum* or *V. nigrum* into new areas for horticultural purposes, as happened in North America and Europe. Regulatory measures to prevent importation will be crucial. Cultural management of existing infestations of *V. rossicum* and *V. nigrum* is impeded by substantial belowground reserves. Management programs that include herbicides may be more effective, although repeated herbicide applications are typically necessary. Biological control may be a useful approach for these weeds of primarily natural areas. However, the biological control agent *H. opulenta* has only recently been released in Canada and the United States, and few additional agents may be available. Future research should focus on the improvement of management programs, the identification of biotic and abiotic factors constraining *Vincetoxicum* distributions, and the development of potential distribution models at a resolution useful to land managers.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2023.7>

Acknowledgments. We thank Darren Kriticos (CSIRO) for his assistance with the CLIMEX model and DiTommaso Lab members Scott Morris and Ariadne Filothei Vazenis for their contributions to the text and figures. No conflicts of interest have been declared. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. USDA is an equal opportunity provider and employer.

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