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Reproductive biology of *Vincetoxicum rossicum* (Kleo.) Barb. (Asclepiadaceae), an invasive alien in Ontario¹

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ST. DENIS, M. AND N. CAPPUCINO (Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6 Canada). Reproductive biology of *Vincetoxicum rossicum* (Kleo.) Barb. (Asclepiadaceae), an invasive alien in Ontario. J. TORREY BOT. SOC. 131:8–15. 2004.—We investigated the reproductive biology of the alien invasive vine *Vincetoxicum rossicum* (Asclepiadaceae) and evaluated pollinator visitation rate in the field, evidenced by missing pollinaria, to flowers of isolated plants and those of plants in dense monocultures. Flowers in dense monocultures were visited less frequently than those on isolated plants surrounded by old-field grasses. Visited flowers were more likely to produce fruit and those fruits contained more polyembryonic seeds. However, a greenhouse experiment in which we cross- or self-pollinated flowers revealed no difference in fruit set, seed production, seed weight or embryony. This suggests that the higher fruit set and greater polyembryony of visited flowers in the field was not the consequence of visitation, but may have been the result of floral visitors having chosen the most vigorous flowers. Day-old flowers emasculated in the greenhouse experiment occasionally produced a fruit, indicating that the germination of self-pollen begins the day a flower opens. The ability to produce large numbers of selfed seeds is no doubt advantageous to this highly invasive asclepiad.

Key words: *Vincetoxicum*, Asclepiadaceae, pollination rates, self-compatibility.

Pale swallow-wort *Vincetoxicum rossicum* (Kleo.) Barb. (Asclepiadaceae; syn. *Cynanchum rossicum*) is a perennial herbaceous vine that was introduced to North America from Ukraine and Russia in the late 1800s (Sheeley and Raynal, 1996). It has become a pest of natural areas, forming dense monocultures in both old-field and understory habitats. Its spread in recent years throughout the Toronto and Ottawa metropolitan regions has caused it to be considered one of the important invasive plants of natural areas in Ontario (Ontario Invasive Plants Working Group, 2000). *Vincetoxicum rossicum* is also spreading throughout upstate New York and other northeastern states (Sheeley 1992), where it is threatening unique native habitats such as the alvar communities east of Lake Ontario (pers. comm. F. M. Lawlor, The Nature Conservancy).

Vincetoxicum rossicum spreads locally and colonizes new areas by wind-dispersed seeds. Most seeds do not travel far from the parent plant (Cappuccino et al. 2002); however, occasionally seeds are caught on rising air currents and could potentially travel long distances.

Since *V. rossicum* does not produce rhizomes (Sheeley 1992, Christensen 1998), if individual long-distance dispersers are to establish new focal populations far from the main infestation, they must be able to self-fertilize. Self-fertility is often observed in isolated or marginal plant populations (Baker 1955, Wyatt 1986, Barrett 1988, Daehler 1998a).

Many members of the Asclepiadaceae are self-incompatible and many have very low fruit-set (Wyatt and Broyles 1994), traits that would not be expected to contribute to invasiveness. Indeed, asclepiads are under-represented in global data sets of serious or widespread weeds (Daehler 1998b). A few weedy milkweeds, however, have been shown to be self-compatible (Wyatt and Broyles 1994). The black swallow-wort *Vincetoxicum nigrum* (L.) Moench. produces viable autogamous seeds (Lumer and Yost 1995), making this species a successful invader in southern New York state. In the present study, we examine the reproductive biology of *V. rossicum* in eastern Ontario. We assess rates of pollen removal in the field, compare fruit-set and germination of seeds from visited and nonvisited flowers, and compare the success of self- and cross-pollination in a greenhouse experiment.

Materials and Methods. SPECIES DESCRIPTION. *Vincetoxicum rossicum* is a perennial herbaceous vine that climbs to a height of 1–2 m each growing season. The flat, star-shaped flowers are 1-cm across, range in color from maroon in the sun to pale beige in the shade, and are displayed in

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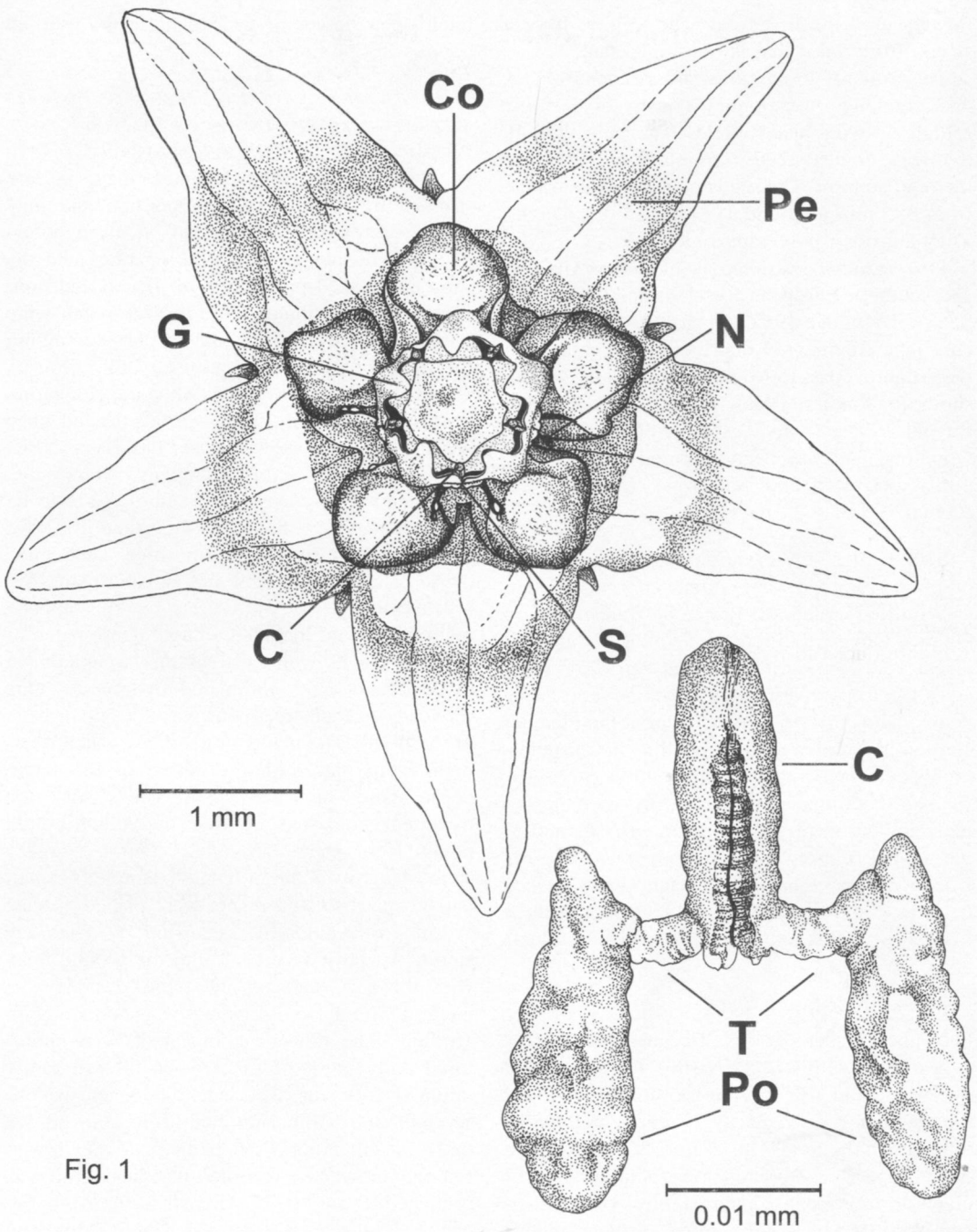


Fig. 1

Fig. 1. Flower morphology of *Vincetoxicum rossicum* (Kleo.) Barb. a. Whole flower showing the gynostegium (G), corona (Co), petals (Pe), stigmatic slit (S), corpusculum (C), and nectar area (N). b. A pollinarium, which consists of two pollinia (Po) attached to a corpusculum (C) by translator arms (T).

loose cymes in the leaf axils. The black corpuscula of five pollinaria are easy to see against the pale green background of the central gynostegium (Figure 1a). Each corpusculum is attached by translator arms to two pollinia (Figure 1b).

Nectar is often visible at the base of the petals between the lobes of the corona (Figure 1a). Flowers are present on the plants from late May through August in Ontario, and damaged plants that resprout later in the season can produce

flowers until the first frost. The flowers have a sweet, fruity odor that is not unpleasant.

The fruits of *V. rossicum* are slender follicles 4–7 cm long. A fruit may consist of a single follicle or two joined follicles. The fruits dehisce to release comose seeds throughout the late summer and autumn. The seeds of *V. rossicum* range from 3–5 mm long and 1–12 mg in dry weight. They are often polyembryonic.

Vincetoxicum rossicum is native to Ukraine and southern European Russia around the Black Sea (Pobedimova 1952). In North America it occurs in a fragmented distribution ranging from the Atlantic coast to Michigan and from Ontario south to southern Pennsylvania (Sheeley and Raynal 1996). It invades old fields as well as woodlots, and has been reported along roads, utility corridors and fencerows (Sheeley and Raynal 1996).

STUDY SITE. Observations and experiments on pollen removal were conducted at the Fletcher Wildlife Garden, off Prince of Wales Drive in Ottawa, Ontario (45° 25' N, 75° 43' W) and adjacent fields on Agriculture and Agri-food Canada's Central Experimental Farm. Several large, dense stands of *V. rossicum* occur at the Fletcher Garden in wooded areas as well as in old fields. Fields adjacent to these monocultures of *V. rossicum* are dominated by grasses and interspersed with goldenrod (*Solidago canadensis* L. and *S. altissima* L.), aster (mostly *Aster novae-angliae* L.), raspberry (*Rubus* sp.), vetch (*Vicia cracca* L.) and common milkweed (*Asclepias syriaca* L.). These fields contained isolated individuals of *V. rossicum*.

EFFECT OF PLANT ISOLATION ON VISITS TO FLOWERS—OBSERVATIONS. Because the corpuscula of the pollinaria are visible to the unaided eye, we could use missing pollinaria to assess the frequency of visits by potential pollinators to plants in the field. On 15 June 2001 and again on 5 July, we compared the visitation rate of plants in large, dense monocultures of *V. rossicum* with that of isolated plants. Isolated plants were growing in three separate fields dominated by grasses and were at least 50 m from the closest conspecific. Plants in dense monocultures were chosen haphazardly from monospecific stands of *V. rossicum* adjacent to each of the three fields. The number of plants chosen depended on the size of the stand and the availability of isolated stems and ranged from eight to 27 on 15 June and from 14 to 27 on 5 July.

Each open flower of each plant was observed for missing pollinaria.

EFFECT OF ISOLATION ON VISITS TO FLOWERS AND EFFECT OF VISITATION ON SEED SET, SEED WEIGHT AND GERMINATION—EXPERIMENT WITH POTTED PLANTS. Isolated plants may be less stressed by intraspecific competition and may have better floral displays, so we used potted plants to further assess visitation rates and the subsequent seed production of visited and non-visited flowers. Plants from a large patch were transplanted into 6-litre plastic pots containing ProMix (Premier Horticulture, Ltd., Dorval, Quebec) in early May 2003, when the elongating stem was < 10 cm. They were fertilized once with OsmoCote slow-release fertilizer (NPK: 14–14–14; The Scotts Company, Marysville, Ohio) and watered as needed until ready to be transported to the field. On 4–5 June 2001 we set the potted plants out in three treatments: dense patch, small patch and isolated plant. Six neighboring fields were used for this experiment; each field included a large, dense patch of *V. rossicum* as well as areas that were not yet invaded and were dominated by grasses. One replicate of each treatment was set out in each of the fields. The plants in the dense-patch treatment were placed in the centre of the large, dense stands of *V. rossicum*. The small-patch treatment consisted of five individual potted plants (four stems around a central “target” stem, which was the only stem sampled). Small patches and isolated plants were placed at least 50 m from naturally occurring *V. rossicum* stems. All pots were sunk into the ground flush with the soil surface. The topmost node was marked with a 1-cm segment of a soda straw on 18 June. The flowers at this node were monitored daily until 30 June, when all had either initiated fruits or abscised. Whenever we observed that a pollinarium had been removed, we tied a string around the pedicel of the flower. For each flower we recorded whether a fruit was produced. From 10–17 August, as the fruits began to dehisce, we harvested the fruits and counted the number of filled and unfilled seeds. Two plants were lost when curious mammals dug into the pots and broke the stems.

Seeds were then weighed and planted individually in compartmentalized seedling starter trays on 2 November 2001. Each compartment of the trays held approximately 50 cm³ of ProMix. Seeds were planted approximately 1 cm deep. Seed position was randomized, so that seeds

from a given fruit were interspersed throughout the trays. Seedling trays were kept in a greenhouse in which natural light was supplemented with artificial light (14:10 light:dark). Temperature varied from 20–35 C. The trays were watered and observed for germination daily.

Seeds that had not germinated by 21 December 2001 were placed in a cold room at 4 C for six weeks. After this stratification, they were returned to the greenhouse, where daily watering and recording of germination was resumed. At the end of the experiment, seedlings were gently removed from the soil to be sure that polyembryonic individuals were indeed separate and not simply multiple stems of a single individual.

HAND POLLINATION. Potted *V. rossicum* were grown in the greenhouse for six months from seed collected at several local sites. When these plants had begun to bloom, four flowers at a single node on each of seventeen plants were randomly assigned to the following treatments: 1) emasculation—removal of all five pollinaria, 2) self-pollen—emasculation and insertion of five pollinaria from another flower of the same plant, 3) cross-pollen—emasculation and insertion of five pollinaria from another plant, and 4) unmanipulated control. Pollinaria were removed by inserting an entomological pin (no. 000) beneath the corpusculum and pulling upward and outward. In the self- and cross-pollination treatments, a pollinarium was placed in each of the five nectar-filled cavities that lie directly beneath the corpuscula. Fruits forming from each of the flowers were noted. All other flower buds were removed from the plants as they were formed so that resources would be allocated to the four experimental flowers/fruits. When the fruits were ready to dehisce, the seeds were counted, weighed and planted to test for germinability as described in the previous experiment.

STATISTICAL ANALYSES. All analyses were performed using JMP version 3.2.5 (SAS Institute Inc. 1995). To assess the effect of isolation on visits by pollinators in the two censuses of naturally growing plants, as well as in the observations on potted plants, two response variables were calculated for each plant: the proportion of flowers that were visited (missing at least one pollinarium) and the mean number of pollinaria removed per flower. Because these variables were not normally distributed, separate Wilcoxon/Kruskal-Wallis rank-sums tests were used to test the effects of field and treatment.

Likelihood ratio χ^2 tests (JMP's logistic re-

gression platform) were performed to test the effects of parent plant and visitation (visited/not visited) on whether or not the flowers in the potted-plant experiment produced fruits. For the nine plants that produced two or more fruits, we used 2-way ANOVA to examine the effect of parent plant and flower visitation (yes/no) on the following response variables: number of seeds produced per fruit, mean seed weight per fruit, proportion of seeds germinating per fruit and mean number of seedlings produced by the seeds of a fruit. The proportion of seeds germinating was arcsin transformed prior to analysis.

Likelihood-ratio tests were used to determine whether fruit production (yes/no) differed for the four treatments in the hand-pollination experiment. ANOVAs were then used test for an effect of pollination treatment on seed weight, arcsin-transformed proportion germinating and mean embryony.

Results. EFFECT OF ISOLATION ON VISITS BY POTENTIAL POLLINATORS. On 15 June, the censused plants had from 2–13 open flowers (7.3 ± 0.25 , mean \pm SE). Isolated plants tended to have more open flowers (7.6 ± 0.3) than plants in dense patches (6.7 ± 0.44); however, this difference was not statistically significant (ANOVA: $F_{[1,88]} = 3.45$; $P = 0.06$). Of 661 flowers, 158 (23.9%) were missing at least one pollinarium. The proportion of flowers that were visited, as well as the mean number of pollinaria removed was higher for isolated plants than for plants in dense stands (Table 1a, b). Field was not a significant predictor of either proportion of flowers visited (Kruskal-Wallis $\chi^2 = 1.46$; d.f. = 2; $P = 0.480$) or mean number of pollinaria missing (Kruskal-Wallis $\chi^2 = 1.03$; d.f. = 2; $P = 0.597$).

Plants censused on 5 July had from 1–8 open flowers (3.68 ± 1.86). There was no difference in the number of open flowers between isolated plants and those in dense patches (ANOVA: $F_{[1,116]} = 2.29$; $P = 0.133$). Of 435 flowers, 89 (20.5%) had been visited at least once. Field had no effect on the proportion of flowers visited (Kruskal-Wallis $\chi^2 = 4.18$; d.f. = 2; $P = 0.120$) and a slight but nonsignificant effect on the number of pollinaria removed (Kruskal-Wallis $\chi^2 = 5.25$; d.f. = 2; $P = 0.075$). As in the first census, flowers of isolated plants were significantly more likely to have been visited and had more missing pollinaria than plants from dense monocultures (Table 1a,b).

Table 1. Two measures of pollinator visitation to *Vincetoxicum rossicum* flowers on plants growing in dense monocultures, plants in small patches and isolated plants. a) Proportion of flowers on a plant that were visited by potential pollinators, as evidenced by missing pollinaria. b) Mean number of pollinaria missing, averaged over all open flowers on a plant. For each treatment on each census date, the median, the number of sampled plants (in parentheses), the Wilcoxon/Kruskal-Wallis χ^2 for the between- or among-treatment comparison, the degrees of freedom and the associated P values are shown.

Census and date	Treatment			χ^2	d.f.	P
	Dense monoculture	Small patch	Isolated plants			
a) Proportion of flowers visited						
Naturally growing plants (15 June 2001)	0 ($N = 29$)	—	0.25 ($N = 61$)	15.30	1	<0.0001
Naturally growing plants (5 July 2001)	0 ($N = 59$)	—	0.25 ($N = 60$)	4.62	1	0.032
Potted plants (18–30 June 2001)	0.215 ($N = 6$)	0.571 ($N = 5$)	0.472 ($N = 5$)	4.38	2	0.110
b) Mean number of pollinaria missing						
Naturally growing plants (15 June 2001)	0 ($N = 29$)	—	0.33 ($N = 61$)	15.32	1	<0.0001
Naturally growing plants (5 July 2001)	0 ($N = 59$)	—	0.29 ($N = 60$)	5.58	1	0.018
Potted plants (18–30 June 2001)	0.29 ($N = 6$)	1.20 ($N = 5$)	1.05 ($N = 5$)	6.29	2	0.043

Like the naturally growing plants, flowers on potted plants placed in dense stands had more missing pollinaria than those placed among four neighbors in a small patch or those isolated from other plants (Table 1b). The proportion of flowers visited did not differ significantly among the three treatments (Table 1a). The field into which we placed the potted plants did not have a significant effect on either of these response variables (Kruskal-Wallis tests, $P > 0.6$ for both variables).

EFFECT OF FLOWER VISITATION ON FRUIT SET. Of the 156 marked flowers on the 16 potted plants, 39 (25.0%) produced a mature fruit. For the 15 plants that had more than one flower, there was no significant parental effect on the probability that a flower would produce a mature fruit (Logistic model: Likelihood ratio χ^2 for effect of parent = 21.87; df = 14; $P = 0.080$). Visitation, on the other hand, had a significant effect on fruit production; of the flowers that had been visited, 38.2% produced mature fruits, whereas only 17.8% of flowers that were not visited produced fruits (Logistic model: Likelihood ratio χ^2 for effect of visitation = 4.87; df = 1; $P = 0.027$).

EFFECT OF VISITATION ON SEED PRODUCTION, WEIGHT, GERMINATION AND EMBRYONY. For the nine potted plants that produced more than one fruit, parent plant had a significant or marginally significant effect on seed production, mean seed

weight, proportion of seeds germinated, and mean number of embryos emerging from each seed (Table 2). Whether or not a fruit was the product of a visited flower was a significant predictor of only the average embryony of seeds in that fruit (Table 2). Fruits from visited flowers contained seeds that produced 1.72 ± 0.054 (SE) seedlings; those from nonvisited flowers produced 1.54 ± 0.068 seedlings.

HAND POLLINATION. The emasculation treatment was not 100% effective; however it resulted in a significant reduction in the percentage of flowers forming fruits (Table 3; Likelihood ratio $\chi^2 = 20.8$, $P = 0.0001$). Percent fruit production in the other three treatments—self-pollen, cross-pollen and control—did not differ significantly (Table 3; Likelihood ratio $\chi^2 = 3.18$, $P = 0.20$). The three fruits that were formed by flowers in the emasculation treatment were single follicles. In the other three treatments 79.9% of the fruits had two follicles; there was no difference in the proportion of two-follicle fruits among these three treatments (Likelihood ratio $\chi^2 = 2.30$, $P = 0.316$).

The number of seeds per fruit did not differ significantly among treatments (ANOVA: $F_{[3, 36]} = 2.60$, $P = 0.070$); however, since only three fruits were produced in the emasculation treatment, the power to detect differences between this treatment and the other three is low. Comparison of the other three treatments—cross-pollen, self-pollen and

Table 2. Two-way ANOVA results for effect of parent plant and flower visitation on four dependent variables—seeds/fruit, mean seed weight, proportion of seeds germinating and mean embryony of seeds—in potted *Vincetoxicum rossicum* plants. Proportion germinating was arcsine transformed prior to analysis. Total d.f. = 32 for all analyses.

Dependent variable	Source	d.f.	F	P
Seeds/fruit	Model	9	2.56	0.030
	Parent-plant	8	2.61	0.034
	Visitation (yes/no)	1	0.01	0.906
Mean seed weight	Model	9	2.73	0.025
	Parent-plant	8	2.24	0.062
	Visitation (yes/no)	1	7.59	0.113
Proportion of seeds germinating	Model	9	2.23	0.058
	Parent-plant	8	2.31	0.055
	Visitation (yes/no)	1	0.68	0.417
Mean embryony	Model	9	2.66	0.023
	Parent-plant	8	2.40	0.047
	Visitation (yes/no)	1	7.72	0.010

control—revealed no significant difference among treatments (ANOVA: $F_{[2, 34]} = 0.615$, $P = 0.546$). No differences in seed weight were observed among the cross-pollen, self-pollen and control treatments (ANOVA: $F_{[2, 34]} = 0.354$, $P = 0.705$). Neither the arcsin-transformed germination rate nor the mean number of embryos emerging from seeds differed significantly among these three treatments (ANOVAs germination rate: $F_{[2, 34]} = 0.244$, $P = 0.785$; embryony: $F_{[2, 34]} = 1.82$, $P = 0.161$).

Discussion. *Vincetoxicum rossicum* has flat, regular dull-colored flowers and open nectar, characteristic of fly-pollinated plants (van der Pijl 1961). Of the flowers that we monitored daily in the field, 25–50% had at least one pollinarium removed. We rarely observed visits by insects other than ants. Flies large enough to carry pollinaria were not observed; smaller flies, such as gnats, that had been trapped by a pollinarium, were occasionally seen. It is unlikely that *V. rossicum* pollinaria are dislodged when brushed by neighboring plants swaying in the wind. The pollinaria are difficult to remove un-

less a thin object, such as an insect appendage, is drawn up the interstaminal slit. The lack of observation of floral visitors contrasts with Christensen's (1998) observations of flies and wasps visiting *V. rossicum*, although she notes that the diversity of floral visitors in some swallow-wort stands is impoverished. Lumer and Yost (1996) reported that *V. nigrum* flowers in southern New York State were visited by several dipteran species and that they had a fetid odor, consistent with pollination by flies. *Vincetoxicum rossicum* flowers, on the other hand, have a sweet, fruity odor. It is possible that some floral visitors to *V. rossicum* are nocturnal; however, the odor is quite pronounced during the daytime hours.

Flowers of isolated plants were more likely to have been visited than plants in dense monocultures. Natural plants in dense stands may be more stressed by competition than isolated plants, and produce a less attractive floral display, as was suggested by the slightly but non-significantly smaller number of flowers per plant in the monocultures. To avoid any bias caused by differences in plant quality, we supplemented our observations on natural plants with those on potted plants placed in large, dense patches, in small (5-plant) patches and in grass-dominated fields. As was the case for the observations on naturally growing plants, this experiment revealed a positive effect of isolation on the removal of pollinaria. This positive effect of isolation was unexpected, since isolated plants are often reported to receive fewer visits from pollinators (Jennersten 1988, Aizen and Feinsinger 1994, Kunin 1993, Steffan-Dewenter and Tschardt 1999). The lower visitation rate in

Table 3. Percent fruit formation of hand-pollinated *Vincetoxicum rossicum* flowers.

Treatment	Fruit formation
Pollinaria removed	17.63 ($N = 17$)
Pollinaria removed, self-pollen added	82.35 ($N = 17$)
Pollinaria removed, cross-pollen added	82.35 ($N = 17$)
Control flowers	58.82 ($N = 17$)

dense monocultures of *V. rossicum* might be the result of a dilution effect. If relatively few potential visitors per unit area are presented with a large number of flowers, the probability that an individual flower will be visited is low. Single plants or small patches surrounded by grass, on the other hand, may be the only source of nectar in a large area, and the few flowers will not be passed up by foraging generalists seeking nectar.

In our field experiment using potted plants, 25% of the flowers produced fruits. This fruit-set was considerably higher than that of other asclepiads, even those given fertilizer as was done with our plants (Wyatt and Broyles 1994, Queller 1985, Willson and Price 1980). Our hand-pollinated greenhouse plants had even higher fruit-set (mean for all treatments except emasculation = 75%). In the field experiment, visits by potential pollinators were not necessary for fruit-set, but having been visited at least once increased the probability that a flower would produce a mature fruit. In addition, fruits produced by visited flowers contained seeds with more embryos. Results of the hand-pollination experiment, however, did not support this finding; flowers "pollinated" by the dissecting needle were no more likely to produce a fruit than the unmanipulated controls and their seeds were not more likely to be polyembryonic. It is possible that the positive association between visits and fruit set in the field was a spurious one, perhaps driven by pollinators being attracted to larger flowers, which may be more likely to produce fruits with a higher proportion of polyembryonic seeds. It is also possible that there may be inbreeding depression following selfing that is only expressed under field conditions.

Flowers that had all pollinaria removed by hand sometimes produced fruits as well. Although the pollinaria were removed when the flowers were only one or two days old, some pollen may have already started to germinate. Early germination of pollen could be an important trait assuring some seed-set in cases where floral visitors successfully remove all pollinaria without inserting any. The fruits produced by these partially emasculated flowers were single follicles and contained relatively few seeds.

We detected no obvious disadvantage to self-pollination. In the hand-pollination experiment, none of the response variables—fruit-set, number of filled seeds, seed weight or embryony—differed significantly between the self-pollination, cross-pollination and unmanipulated con-

trol treatments. Selfing may be disadvantageous if it produces inbreeding depression (Charlesworth and Charlesworth 1987), but evaluating this was beyond the scope of this study.

Over half of the seeds produced in both the field and greenhouse experiments were polyembryonic, producing two to four seedlings. Polyembryonic seeds can arise through several developmental pathways and in some cases may involve apomixis stimulated by fertilization of nearby ovules (Webber 1940). Polyembryony in plants has been discussed in terms of various strategies that increase maternal fitness (Willson and Burley 1983, Uma Shaanker and Ganeshiah 1996). To our knowledge, however, the comparative success of polyembryony in the field remains to be addressed. In a greenhouse experiment, Cappuccino et al. (2002) found that after correcting for the positive effect of overall seed mass, polyembryonic individuals had higher total seedling mass after 60 d growth than did individuals with a single embryo. Competition with grasses removed this advantage. Supplemental embryos in a polyembryonic seed often germinate several days later than the first seedling, suggesting a possible bet-hedging role for polyembryony, providing a propagule with a second chance at establishment when the first embryo is killed by frost, drought or herbivory.

Self-compatibility is likely to contribute to the invasive nature of *V. rossicum*, as Lumer and Yost (1995) have suggested for *V. nigrum*. We do not know the degree to which *V. rossicum* and *V. nigrum* are self-compatible in their native ranges; it is possible that their selfing ability has increased since their arrival in the New World. Within-population variation in selfing ability in alien plants is common and can dramatically influence invasion rates (Daehler 1998a).

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