Growth and reproductive potential of the invasive exotic vine *Vincetoxicum rossicum* in northern New York State

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Abstract: The alien invasive vine *Vincetoxicum rossicum* (Kleopow) Barbar. is problematic in the Lower Great Lakes Basin of North America. The lack of effective control strategies exacerbates the need for a better understanding of the growth and reproductive potential of *V. rossicum*. Thus, a 2-year field experiment was performed in a field site in 2003 and 2004 that was densely colonized by *V. rossicum*. Mean height of *V. rossicum* stems was 20% and 45% greater in naturally shaded plots compared with plots receiving full sun in 2003 and 2004, respectively. During the 2-year study, the density of stems 10 cm or taller averaged 134 stems·m^{-2}, substantially greater than reported in previous field studies for this species. The high densities of stems and seedlings indicate that this field site may be near or at carrying capacity. Each stem produced, on average, 17 mature follicles with some stems producing as many as 100 follicles. Each follicle yielded an average of 15 seeds, each composed of an average of two viable embryos. A typical *V. rossicum* stand in this site produced as many as 54 000 seedlings·m^{-2} annually. More flowers (2400 flowers·m^{-2}), follicles (2250 follicles·m^{-2}), and total seeds (32 000 seeds·m^{-2}) were produced in plots receiving intermediate light compared with plants in full sun (1650 flowers·m^{-2}, 1600 follicles·m^{-2}, and 25 000 seeds·m^{-2}) or shaded (1600 flowers·m^{-2}, 2000 follicles·m^{-2}, and 28 000 seeds·m^{-2}) plots. Seeds harvested from follicles in the low light plots were 41% more likely to be dormant than seeds collected from follicles in full sun plots. Seeds collected from plants in full sun plots had the lowest frequency (~36%) of single embryo seeds and the highest frequency (~64%) of multiple embryo seeds. These findings suggest that *V. rossicum* growth and reproductive output is influenced by light environment. While competitive strategies differ between the light environments, the decrease in viability and germination in shaded sites may not be large enough to affect population growth over multiple generations. The substantially greater growth and reproduction of *V. rossicum* reported in this study relative to previous research may explain the increasing abundance and range expansion of this species in many Lower Great Lakes regions of Ontario and New York State.

Key words: Cynanchum rossicum, dog-strangling vine, invasive plants, light environment, polyembryony, reproduction.

Résumé : La vigne adventice *Vincetoxicum rossicum* (Kleopow) Barbar. est problématique dans la partie inférieure du bassin des Grands Lacs, en Amérique du Nord. L'absence de stratégies de lutte efficaces exacerbe le besoin de mieux comprendre la croissance et le potentiel reproducteur du *V. rossicum*. Ainsi les auteurs ont conduit une expérience de deux ans sur le terrain, en 2003 et 2004, sur un site densément colonisé par le *V. rossicum*. La hauteur moyenne des tiges du *V. rossicum* était supérieure de 20 % à 45 %, dans des parcelles naturellement ombragées, comparativement à des parcelles recevant le plein soleil, en 2003 et 2004, respectivement. Au cours de l'étude de deux ans, la densité des tiges de 10 cm ou plus, était en moyenne de 134 tiges·m^{-2}, ce qui est substantiellement plus élevé que ce qui a été rapporté dans les études antérieures sur cette espèce. La forte densité des tiges et des semis indique que ce site d'étude serait près ou au maximum de la capacité de support. Chaque tige produit, en moyenne, 17 follicules matures, certaines tiges produisant jusqu'à 100 follicules. Chaque follicule produit une moyenne de 15 graines, chacune composée de deux embryons viables. Un peuplement typique du *V. rossicum* produit sur ce site, 54 000 plantules par m^2, annuellement. On observe une plus forte production de fleurs (2400 fleurs·m^{-2}), de follicules (2250·follicules·m^{-2}) et de graines (32 000 graines·m^{-2}) dans les parcelles recevant une luminosité intermédiaire, comparativement aux plantes recevant le plein soleil (1650 fleurs·m^{-2}, 1600 follicules·m^{-2} , et 28 000 graines·m^{-2}). Les graines récoltées des follicules venus dans les parcelles faiblement éclairées ont 41 % plus de chance d'être dormantes que les graines récoltées dans des follicules venus dans des parcelles pleinement ensoleillées. Les graines récoltées sur des plants venus en plein soleil montrent la plus faible fréquence (~36%) de graines à d'embryons simples et la plus forte incidence (~64%) de graines à embryons multiples. Ces observations suggèrent que l'effort de croissance et de reproduction du *V. rossicum* est influencé par l'environnement lumineux. Alors que les stratégies compétitives diffèrent entre les environnements lumineux, les diminution de viabilité et de germination, observées sur les sites ombragés, pourraient ne pas être suffisantes pour affecter la croissance de la population au cours de multiples générations. La croissance et la reproduction substantiellement plus importantes rapportées ici, comparativement aux recher-

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ches précédentes, pourraient expliquer l'augmentation de l'abondance et l'expansion de l'habitat de cette espèce, dans plusieurs régions de la partie inférieure des Grands Lacs, de l'Ontario et de l'État de New-York.

Mots clés : *Cynanchum rossicum*, vigne étrangle chien, plantes envahissantes, environnement lumineux, polyembryonie, reproduction.

[Traduit par la Rédaction]

Introduction

Vincetoxicum rossicum (Kleopow) Barbar. [= *Cynanchum rossicum* (Kleopow) Borhidi] – (pale swallow-wort or dog-strangling vine) is an introduced herbaceous perennial vine in the Asclepiadaceae. The first reported collection in North America of this native of the Ukraine and Southwestern Russia was made in 1889 in Toronto Junction, Ontario, Canada, and in the United States in Monroe and Nassau Counties of New York State in 1897 (Sheeley and Raynal 1996). In Canada, this species is distributed throughout southwestern and eastern Ontario and southwestern Quebec (Sheeley 1992; Sheeley and Raynal 1996; Kartesz 1999; DiTommaso et al. 2005*b*). *Vincetoxicum rossicum* is also well established in the northeastern region of the United States with its current distribution extending as far south and west as Missouri. Although *V. rossicum* is less widely distributed in North America than the closely related invasive congener *Vincetoxicum nigrum* (L.) Moench. (black swallow-wort or black dog-strangling vine), *V. rossicum* is thought to be the more aggressive of the two species (Sheeley and Raynal 1996).

Reproduction in *V. rossicum* occurs primarily by wind- and animal-dispersed seeds. This species also reproduces vegetatively by tillering from root crowns (Sheeley 1992; Christensen 1998). Seeds of *V. rossicum* are polyembryonic, a condition in which multiple genetically identical embryos are produced within a single seed (Sheeley 1992; DiTommaso et al. 2005*b*). While *V. rossicum* growth is prolific in well-drained calcareous soils, it is tolerant of a wide range of soil and environmental conditions (Sheeley 1992). This species is increasingly problematic in Christmas tree plantations as well as forest understories, old fields, and pastures (Christensen 1998; DiTommaso et al. 2005*b*). Recent observations show it possibly becoming troublesome in no-tillage maize (*Zea mays* L.) and soybean (*Glycine max* L. Merr.) cropping systems (DiTommaso et al. 2005*b*). Control efforts to date have been met with limited success. Mechanical control has been ineffective, and few herbicides have been approved for use.

To maximize resources, many weed species express phenotypic plasticity via changes in height, architecture, and resource allocation (Sugiyama and Bazzaz 1997; Agrawal 2001). Many plants alter not only their height and biomass accumulation in response to light availability but also reproductive traits such as flowering and seed maturation timing, seed size, and seed dormancy (Willson and Price 1980; Sanchez et al. 1981; Cavers and Steel 1984; Brainard et al. 2005). Not surprisingly, *V. rossicum* plants have shown large height variability in response to different light availabilities. For instance, in a study by Sheeley (1992) near Syracuse, New York, *V. rossicum* plants growing in full sun (2048.1 ± 90.5 $\mu E \cdot m^{-2} \cdot s^{-1}$) had a mean height of 65.1 cm, while plants growing in a relatively shaded site (429.5 ± 139.7 $\mu E \cdot m^{-2} \cdot s^{-1}$) had a mean height of 136.3 cm. Sheeley (1992) also noted that *V. rossicum* total stem densities (including seedlings) reached 2019 $stems \cdot m^{-2}$ in the full sun site and only 780 $stems \cdot m^{-2}$ in the shaded site. Similarly, Lawlor (2000) reported higher *V. rossicum* stem (>25 cm tall) densities (185 $stems \cdot m^{-2}$) in an open site near Watertown, New York, compared with a nearby shaded site (61 $stems \cdot m^{-2}$). In a shaded site, Sheeley (1992) found that *V. rossicum* plants produced an average of two follicles per plant, with each follicle containing seven viable seeds. Thus, the mean annual seed output at this site was estimated to be 1330 $seeds \cdot m^{-2}$. In contrast, in the open full sun site, Sheeley (1992) found plants produced a mean of eight follicles, each with 10 seeds, for an annual seed output of 2090 $seeds \cdot m^{-2}$. Seeds of *V. rossicum* collected from an old field site near Aurora, New York, in late August were more likely to germinate than seeds collected from an adjacent shaded forest understory site (DiTommaso et al. 2005*a*). However, these site differences in seed germinability were not significant for seeds collected from the same sites in November. Germination levels of seeds collected by DiTommaso et al. (2005*a*) in their New York State sites ranged from 30% to 50%. Similarly, Sheeley (1992) reported a mean germination of 46% for *V. rossicum* seeds collected from a full sun site near Syracuse, New York, while Cappuccino et al. (2002) found on average that 44.5% of seeds collected from multiple sites near Ottawa, Ontario, germinated. While the occurrence of polyembryony in *V. rossicum* has not been directly linked to light availability in previous studies, the proportion of seeds producing more than one embryo or seedling has varied considerably between the studies. For example, 78% of seeds collected from a rights-of-way site receiving full sun near Syracuse, New York, were polyembryonic (Sheeley 1992), whereas only 55% of seeds collected in multiple old-field sites near Ottawa, Ontario, were polyembryonic (Cappuccino et al. 2002).

The growth and reproductive potential of *V. rossicum* in its introduced range has neither been determined for multiple growing seasons nor for large expanding populations. The main objective of this 2-year field study was to determine the growth and reproductive potential of *V. rossicum* plants in a densely infested location of northern New York State, where the growth of this species appears to be especially prolific. A second objective was to assess whether differences in light availability affected growth and reproduction in this species. We hypothesized that *V. rossicum* plants growing under the highest light levels exhibit greater growth and fecundity compared with plants growing under lower light levels.

Materials and methods

Field site characteristics

A 2-year fully replicated field study was established in May 2003 at Henderson Harbor, New York (43°51′N, 76°14′W) in a 5.7 ha old field dominated by *V. rossicum* for approximately 5 years prior to this study. The site was located on a Benson–Galoo complex occluding Galway silt loam. Soils at the site were characteristically shallow, ranging from 0 to 61 cm in depth with a mean pH of 6.7 and organic matter content of 14.5%. Associated herbaceous species at the site included *Galium aparine* L., *Alliaria petiolata* (Bieb.) Cavara and Grande, *Echium vulgare* L., *Potentilla recta* L., *Solidago* spp., and *Carduus acanthoides* L. Tree species within the old field and adjacent wooded areas included *Juniperus virginiana* L., *Robinia pseudoacacia* L., *Fraxinus* spp., and *Ulmus americana* L.

A total of 36 treatment plots (2.0 m × 1.5 m), with a 0.5 m border around each plot, were established within four blocks at the field site. The four blocks were a minimum of 10 m apart and encompassed areas of the site that were exposed to full sun as well as partial to full shade as a result of the overstory tree canopy from an adjacent forested area. Thus, the different plots within a block experienced light availabilities ranging from full sun to full shade. A total of 12 plots each were established at the site in full sun, intermediate shade, and full shade environments. Leaf area index (LAI) was used as a measure of light availability in each of the 36 plots. The LAI of the overstory canopy in each plot was determined by photographing the overhead vegetation (if any) 1.5 m above ground level at noon on 1 June 2004 on an overcast day using a tripod-mounted Nikon D70 digital SLR camera (Nikon Corporation, Tokyo, Japan) equipped with a Sigma 8-mm F4 EX 360° fisheye lens (Sigma Corporation of America, Ronkonkoma, New York). Digital images were analyzed for LAI using Gap Light Analyzer version 2.0 software (Simon Fraser University, British Columbia, Canada, and Institute of Ecosystem Studies, New York, USA). LAI values between the plots ranged from 0.001 to 0.560 $m^2 \cdot m^{-2}$. Plots were assigned to one of three light availability classes: high (<0.119 $m^2 \cdot m^{-2}$), intermediate (0.120–0.299 $m^2 \cdot m^{-2}$), and low (>0.300 $m^2 \cdot m^{-2}$) based on natural breaks in the data obtained from the gap analyzer software, for a total of 12 plots per light availability class.

Data collection

Each of the 36 treatment plots were subdivided into three subplots: a 0.5 m × 0.5 m area used for nondestructive plant data collection during both the 2003 and 2004 field seasons and two 0.25 m × 0.5 m subplots used for destructive harvest in each of the 2 years. The total density of stems (>10 cm tall) in each undisturbed 0.5 m × 0.5 m subplot was determined at 2-week intervals from 20 May to 2 September of each year. The height and number of flowers and of follicles of 10 randomly selected *V. rossicum* stems (>10 cm) in each subplot were also determined at 2-week intervals. Seedling densities of *V. rossicum* were determined monthly in two randomly placed 0.1 m × 0.1 m quadrats in each 0.5 m × 0.5 m subplot.

In August of each year, aboveground tissue of *V. rossicum* in one of the two 0.25 m × 0.5 m subplots was harvested by cutting plant material at soil level. Harvested tissue was then separated into stems, leaves, and reproductive structures and dried at 65 °C for 7 d, then weighed to determine biomass.

On 2 September 2003 and 2004, mature but unopened follicles were randomly collected from all (including non-tagged) plants in the 36 0.5 m × 0.5 m permanent subplots. From each plot collection, a subsample of 100 follicles was weighed, and seeds from each follicle were counted and weighed. Preliminary tests indicated that stratification of seeds increased germination in this species, thus harvested seeds were stored dry, in a refrigerator at 4 °C for 6 months before initiating germination or viability tests. Before the germination experiment, seeds that lacked embryos (~29%) were discarded, since these can be visually distinguished from seeds having embryos (Cappuccino et al. 2002). For germination testing, 25 randomly selected seeds from each of the 36 permanent subplots were placed in 9 cm diameter plastic Petri dishes having two layers of filter paper moistened with 5 mL of distilled water. Four replicates of seeds for each subplot were established and returned to the refrigerator at 4 °C. After 2 weeks, Petri dishes were placed in a growth chamber having a 14 h light : 10 h dark daily cycle and temperature cycle of 25 °C light : 17 °C dark. Seeds were monitored every 2 d for germination during a 3-week period. The number of radicles emerging per seed was also recorded during this period. Germination was determined to have occurred when at least 2 mm of the radicle had emerged. At the end of 3 weeks, germinated seeds were counted and discarded. The remaining seeds that did not germinate following the 3-week trial period were visually examined for the presence of an embryo. In 2003, preliminary screening for seed viability was carried out using 50 randomly selected seeds from each subplot. Seeds were stratified, and germination was monitored for 3 weeks following the methods described above. All seeds having embryos but not germinating during the 3-week trial period were then subjected to tetrazolium testing to determine their viability (Moore 1960).

Statistical analyses

A PROC MIXED procedure in SAS (SAS Institute Inc. 2001) was used to test the effects of soil nutrient levels and light availability on *V. rossicum* stem density, height, aboveground biomass, seed mass, germination percentage, total number of seeds and seedlings, and frequency of polyembryony. The number of flowers and follicles per plant were analyzed using a negative binomial distribution using the PROC GENMOD procedure in SAS because of difficulties in normalizing data having a high frequency of "zero" values due to differences in timing of flower and follicle production in the different light environments. Flower and follicle densities on a per square metre basis were square-root transformed and analyzed for effects of light availability and soil nutrient levels using PROC MIXED. Mean separations to determine the effect of different light availabilities on plant parameters measured was carried out using Tukey adjusted differences of least squared means at the 95% confidence level. All PROC MIXED procedures were also run by year to determine differences in *V. rossicum* parameters between the 2003 and 2004 field

Table 1. Average monthly temperatures and total precipitation for 2003 and 2004, with 30-year averages for Watertown, New York, 26 km from the field site (average growing season and annual temperatures and precipitation are also shown).

	Temperature (°C)			Precipitation (mm)		
Month	2003	2004	30-year average	2003	2004	30-year average
January	–11.1	–12.5	–7.4	69.1	35.1	87.6
February	–9.1	–6.6	–6.4	70.4	39.6	63.0
March	–0.5	1.6	–0.6	89.9	68.3	72.6
April	4.6	6.7	6.5	62.5	88.6	77.7
May	13.6	15.1	13.5	170.9	117.1	84.6
June	18.0	17.5	18.5	74.9	93.5	86.4
July	21.4	20.9	21.2	94.5	114.8	84.3
August	21.8	19.5	20.3	245.5	118.4	100.3
September	17.6	17.7	15.6	66.8	76.2	125.7
October	8.9	10.1	9.0	162.6	71.1	95.8
November	4.9	4.3	3.1	150.4	102.1	114.6
December	–2.3	–3.7	–3.7	91.2	136.9	95.5
Growing season (April–October)	15.1	15.4	14.9	877.7	679.7	654.8
Average	7.3	7.5	7.4	112.4	88.5	90.7

seasons. The PROC PRINCOMP procedure in SAS was used to create eigen values and eigen vectors for a principal components analysis. S-Plus (Insightful Corporation, Seattle, Washington) generated a 14 × 36 correlation matrix of variables and samples to detect structure and relationships between the measured *V. rossicum* parameters.

Results

Climate and soil effects

Temperatures in 2003 were below average early in the growing season, but in July and August during late flowering and follicle development, mean temperatures exceeded the 30 years average by ~0.5 °C (Table 1). In 2004, mean temperatures from March to May were warmer by as much as 2 °C than in 2003 and the 30 years average, but generally cooler (~1 °C) and wetter conditions prevailed during June, July, and August. Precipitation also exceeded the 30-year average for both years in July and August (Table 1). Soil nutrient concentrations were typical for this region (Ketterings et al. 2003). Neither pH nor soil nutrient concentrations within treatment plots had a significant effect ($P > 0.05$) on *V. rossicum* growth and reproductive parameters measured (data not shown). Similarly, no relationships were detected between *V. rossicum* tissue nutrient concentrations and growth and reproductive parameters measured (data not shown).

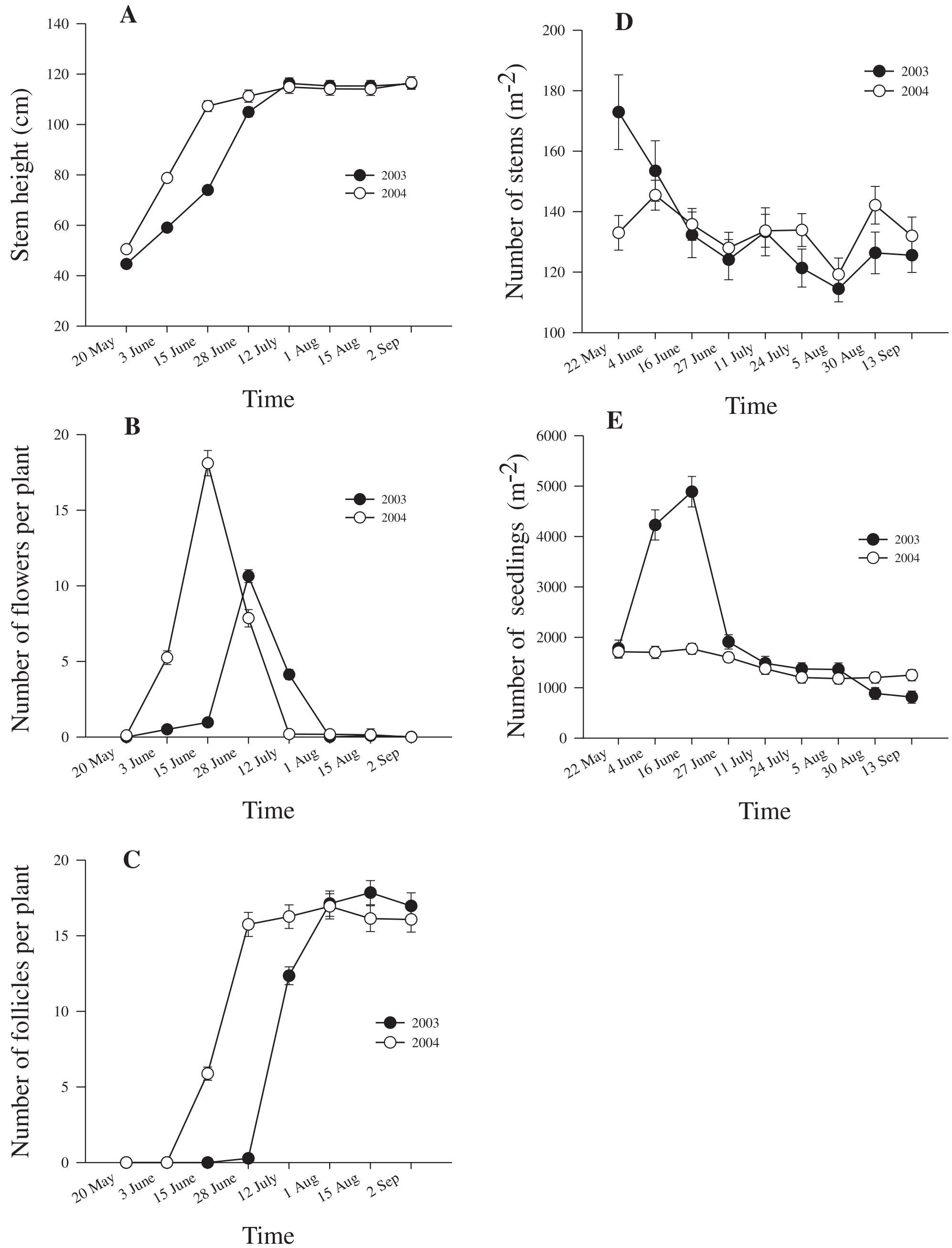
Stem densities and biomass accumulation

In both years, the maximum height of *V. rossicum* plants was achieved in late June or early July (Fig. 1A). However, there were no significant differences in the mean height (~116 cm) of plants at the end of the 2003 and 2004 growing seasons (Fig. 1A). Stem densities fluctuated significantly ($P < 0.0001$) from 126 stems·m^{-2} in late August 2003 to 142 stems·m^{-2} at the end of August 2004 (Fig. 1D). Although most notable in 2004, stem densities declined in both years at the end of the growing season following follicle maturation and seed dispersal. Linear regression showed that allocation of biomass to vegetative or reproductive structures was not related to stem density ($R^2 = 0.03$, $P = 0.1649$). Reproductive (flowers and follicle) biomass was significantly greater in 2004 relative to 2003 ($P = 0.0051$) (Table 2). Vegetative (leaves and stems) and total aboveground biomass did not differ between years (Table 2). Mean seedling densities were significantly greater in 2003 (2070 seedlings·m^{-2}) than in 2004 (1440 seedlings·m^{-2}) (Fig. 1E). In 2003, densities peaked at 4800 seedlings·m^{-2} by mid-June before quickly leveling off by late June. This drastic peak in seedling density was not observed in 2004. Seedling densities fluctuated in both years but appeared to level off at a density of ~1800 seedlings·m^{-2} in 2004. Seedling density was inversely related to stem densities in both years (2003; $r = –0.31$, 2004; $r = –0.45$).

Reproduction

Only 7.5% of the 360 tagged stems failed to produce mature follicles by the end of either growing season. The mean number of flowers produced per stem during the 15 June 2003 sample date (~2) was significantly lower ($P < 0.0001$) than the mean number of flowers (~18) produced 1 year later (Fig. 1B). Flower production peaked (~11 flowers per plant) 2 weeks later (28 June) in 2003 relative to 2004. The total number of immature and mature follicles produced per stem leveled off in late July and early August in 2003, remaining constant through early September. In 2004, follicle production leveled off in mid-June and remained high through early September (Fig. 1C). The mean number of seeds produced per follicle (~15) in 2003 was significantly higher than the number of seeds produced per follicle in 2004 (~14) ($n = 1800$, $P = 0.0206$) (Table2). The predicted number of seeds (~28 000 seeds·m^{-2}) was the same for 2003 and 2004, while the predicted number of seedlings was higher in 2003 (~50 000 seedlings·m^{-2}) than in 2004 (~47 000 seedlings·m^{-2}), although differences were not significantly different ($P = 0.3236$) (Table 2). The mass

Fig. 1. Mean (±SE) *Vincetoxicum rossicum* height (A), number of flowers per plant (B), number of follicles per plant (C), density of stems >10 cm (D), and density of seedlings <10 cm (E) for tagged plants at different sample dates in 2003 and 2004 at Henderson Harbor, New York.



of follicles was significantly greater in 2004 than in 2003 (P = 0.003). However, mean seed mass (~ 5.1 mg) was not significantly different between the two years.

Effect of light availability on growth and reproduction

Light availability had a significant effect on many *V. rossicum* growth and reproductive parameters and mostly varied by year. For instance, plants experiencing the lowest light levels due to tree canopy shading were significantly taller (20% and 45% in 2003 and 2004, respectively) than plants experiencing the highest light levels (P = 0.009) (Table 2). The light environment had no effect on the total number of seedlings·m^{-2} recorded in both years. The number of seedlings present was always highest in high light plots and lowest in shaded plots (Table 3). Differences in light availability did not have a significant effect on *V. rossicum* stem densities (P = 0.2264), but a significant light availability by year interaction was observed. Plants in full sun plots had the greatest stem densities in 2004 for the earliest sampling dates (22 May and 4 June); however, no differences were observed in these plots in 2003. Light availability did not affect total (P = 0.2169) or vegetative biomass (P = 0.3589), but in 2004, reproductive biomass was 78% and 21% greater for plants growing in intermediate light avail-

Table 2. Mean (±SE) vegetative and reproductive output of *Vincetoxicum rossicum* in 2003 and 2004 under three light availabilities.

Light availability[a]	Year	Height (cm)	Flowers·m^{-2}	Follicles·m^{-2}	Follicle mass (g)	Seed number·follicle^{-1}	Seed mass (mg)	Embryos·seed^{-1}	Potential seed number·m^{-2}
High	2003	101.7±3.0a[b]	1478±218a	1584±177a	0.19±0.0a	16.2±0.2a	4.8±0.2a	1.9±0.0a	25663±2864a
Intermediate	2003	125.8±3.6b	1619±196ab	2242±218a	0.14±0.0a	14.0±0.2a	5.1±0.2a	1.7±0.1a	31385±3050a
Low	2003	121.4±3.9b	1000±196b	1921±217a	0.16±0.0a	14.6±0.3a	5.4±0.2a	1.8±0.1a	28061±3166a
High	2004	90.1±3.4a	1758±186a	1629±229a	0.21±0.0a	14.8±0.3a	5.9±0.1a	1.8±0.0a	24118±3397a
Intermediate	2004	128.5±4.1b	3150±274a	2255±239b	0.15±0.0a	14.2±0.2a	5.4±0.2a	1.7±0.0ab	32022±3283a
Low	2004	131.0±4.3b	2203±218a	1998±267a	0.16±0.0a	14.2±0.2a	4.4±0.2a	1.5±0.1b	28379±3785a

Note: Values for height, flowers, and follicles were obtained from peak sampling dates.

[a]Light availability was calculated from the leaf area index (LAI) of the overstory canopy measured in June 2004 (high, <0.119; intermediate, 0.120–0.299; and low, >0.300 m^2·m^{-2}).

[b]Means for *V. rossicum* parameters with the same letter are not significantly different ($P > 0.05$) within a growing season. A PROC MIXED procedure in SAS was used for all of the analyses above, with the exception of PROC GENMOD used for flowers·m^{-2} and follicles·m^{-2}. Values are means of n = 120 for plant-related attributes and n = 1200 for follicle mass- and seed-related attributes.

ability plots compared with plants growing in the low and high light plots, respectively (Table 3).

The number of flowers produced both per plant and per square metre were significantly higher (62%) in the intermediate light availability plots compared with the low light plots in 2003 (P = 0.0324). Although the trend was similar in 2004, differences between the two light conditions were not significant (P = 0.3317). The total number of follicles produced per square metre in 2004 was also significantly greater in the intermediate light plots compared with plants growing in full sun (+38%) and shade (+13%) plots (Table 2). Light availability did not significantly affect the potential number of seeds or seedlings produced per square metre (P = 0.9704 and P = 0.6163, respectively) (Table 2); however, the total number of seeds per square metre was ~27% greater in intermediate light plots than in full sun plots, where plants produced even fewer (~13%) seeds per square metre than plants grown in shaded plots. In both years, light availability had no effect on the mean number of seeds produced per follicle or the mean mass of follicles and seeds (Table 2).

Germinability, viability, and polyembryony of seeds

Of all *V. rossicum* seeds collected in 2003 and 2004, 63% were viable and 37% were nonviable. There was no significant difference between the proportion of viable seeds between years. Most seeds were nonviable because they lacked an embryo (Table 4). There were no significant differences in the percentage of viable seeds that germinated (75% in 2003; 70% in 2004) between the two years.

Light availability had a significant effect on the proportion of seeds that were dormant (P = 0.0385) or lacked an embryo (P = 0.0146). Seeds produced under relatively lower light availabilities were 41% more likely to be dormant and 31% more likely to have nonviable seeds lacking embryos than seeds collected from plants growing under the highest light availabilities (Table 4). Seeds collected in the low light plots in 2004 had significantly lower (28%) germination relative to seeds collected from the high and intermediate light environments (Fig. 2).

Seeds having one or two radicles per seed were most common (Fig. 3), although as many as eight radicles emerging from a single seed were observed (data not shown). While there was no significant effect of light availability on the mean number of embryos produced per seed in 2003 (P = 0.7901), there was a difference in 2004 (P = 0.0009) (Table 3). In 2004, seeds collected from parent plants under the highest light availability produced more embryos than seeds collected from the two lower light environments. There was also a significant effect of light availability on the number of seeds producing one embryo (P = 0.0279) and two embryos (P = 0.0396). Seeds from the highest light environment plots produced the lowest proportion of single embryo seeds but the highest proportion of two embryo seeds, although these differences were greater in 2004 than in 2003 (Fig. 2).

Discussion

Growth responses to light availability

In our study, the morphological response of *V. rossicum*

Table 3. Mean (±SE) *Vincetoxicum rossicum* stem (>10 cm height) and seedling densities and aboveground dry biomass at three light availabilities for 2003 and 2004 in Henderson Harbor, New York.

				Aboveground biomass ($g \cdot m^{-2}$)		
Light availability[a]	Year	Stem density (>10 cm tall)	Seedling density (seedlings·m^{-2})	Stem + leaves	Flowers + follicles	Total
High	2003	137.3±9.5a	1136±225a	472.8±27.2a	237.6±23.2a	695.2±44.0a
Intermediate	2003	121.0±10.1a	900±201a	452.0±51.2a	208.8±22.4a	660.8±72.0a
Low	2003	118.3±9.5a	566±178a	374.4±52.0a	150.4±52.0a	524.0±78.4a
High	2004	150.9±12.0a	1654±194a	460.0±28.8a	220.0±20.8a	661.6±45.6a
Intermediate	2004	137.8±8.4a	1450±175a	546.4±54.4a	266.4±42.4b	812.8±93.6a
Low	2004	138.7±12.3a	654±156a	460.0±51.2a	149.6±51.2a	612.0±73.6a

Note: Means represent end of season values for stem and seedling densities under three light availabilities ($m^2 \cdot m^{-2}$). Means for *V. rossicum* parameters with the same letter are not significantly different ($P > 0.05$) for all sampling dates of the growing season. A PROC MIXED procedure in SAS was used for all of the analyses. Values are means of $n = 12$ for parameters under each light availability level.

[a]Light availability was calculated from the leaf area index (LAI) of the overstory canopy measured in June 2004: (high, <0.119; intermediate, 0.120–0.299; and low, >0.300 $m^2 \cdot m^{-2}$).

plants to varying light availabilities was consistent with responses reported for most plants (Morgan and Smith 1976; Stoller and Myers 1989). For instance, plants growing in plots with high light availability had short, thin stems and small, thick leaves located along short internodes; while plants growing in both the intermediate and low light plots had considerably taller, thicker stems and larger, thinner leaves located along longer internodes. As a result of their tall stature, plants found in the intermediate and low light environments were also more likely to climb over and smother adjacent vegetation (L. Smith, personal observation). Although stem densities were generally greater in high light plots, densities were not significantly different from those found in the intermediate or low light plots. These findings indicate that native vegetation in low light habitats such as forest understories are especially at risk of being competitively displaced by *V. rossicum*, not only because of reductions in available space and nutrients but, more importantly, as a result of considerably lower light availabilities reaching understory plants that are overtopped by this vine.

A significantly greater number of *V. rossicum* stems (105.7 stems·m^{-2}) produced mature follicles at the Henderson Harbor, New York, site than in a full sun (21.8 stems·m^{-2}) and shaded (80.7 stems·m^{-2}) site near Syracuse, New York, reported by Sheeley (1992). At the Henderson Harbor site, approximately 90% of all plants taller than 25 cm produced at least one follicle in 2003, regardless of which light availability plot they grew in. In 2004, 90% of all plants receiving low or intermediate light produced follicles, and 95% of all plants in plots receiving full sun produced follicles. Moreover, *V. rossicum* plants at the Henderson Harbor site produced 7.5 times more follicles per stem and 3 times more seeds per follicle than plants sampled by Sheeley (1992). In the full sun Syracuse, New York site, *V. rossicum* plants produced, on average, 8 follicles per stem and 2 follicles per stem in the shaded site (Sheeley 1992). In our study, stems in the intermediate light plots produced the most follicles per stem (∼20) compared with high light (∼15) and shade (∼17) plots. Follicles sampled by Sheeley (1992) collected from plants in full sun (10 vs. 15) and under shade (7 vs. 15) contained substantially fewer seeds than follicles collected under similar light environments at Henderson Harbor, New York. Therefore, seed output at our site could be as high as 32 022 seeds·m^{-2}, but when the frequencies of polyembryonic seeds are considered, total embryo production may reach 54 000 embryos·m^{-2} in a single growing season. These embryo quantities are substantially greater than the 4680 and 2090 embryos·m^{-2} reported by Sheeley (1992) for a *V. rossicum* population in a full sun and a shaded site, respectively, near Syracuse, New York. These data as well as high stem and seedling densities observed during our 2-year study suggest that growth, reproductive output, and invasive potential of *V. rossicum* in New York State may have been seriously underestimated in previous research performed during only a single growing season and in possibly less favorable sites than those used in our study. The high stem and seedling densities recorded at Henderson Harbor, New York, indicate that this site may be at or near carrying capacity, at least in the densely infested areas sampled within the field. Fluctuations in stem densities may also, in part, be explained by experimenter disturbance of sample plots during data collection, since *V. rossicum* stems are fairly brittle and very susceptible to breakage.

The reason for the large decrease in seedling densities recorded between June and early July 2003 is not clear, since we did not follow the fate of individual seedlings, but one likely cause may have been density-dependent mortality, especially at such high initial densities (4800 seedlings·m^{-2}) (Harper 1977). Although coma-bearing seeds of this species can be dispersed by wind at great distances from the parent plant, most seeds fall within a few metres of the parent plant, resulting in intense intraspecific competitive interactions between emerging seedlings (Cappuccino et al. 2002; Ladd and Cappuccino 2005).

Reproductive potential and light availability

Plants in full sun plots produced more seeds per follicle and a significantly greater number of embryos per seed (polyembryony) than seeds from shaded plots. Also, seeds collected from plants in full sun plots were more likely to be viable, and to germinate than seeds harvested from plants grown in the lower light plots. While there may not have been significant differences in stem density or aboveground biomass between plants grown in the different light environ-

Fig. 2. Mean (±SE) germination percentage of *Vincetoxicum rossicum* viable seeds collected in 2003 and 2004 from plants at Henderson Harbor, New York, growing under three light availabilities.

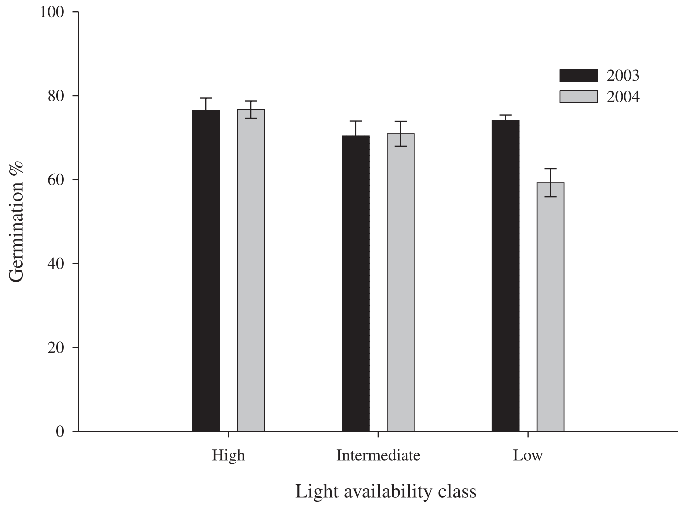
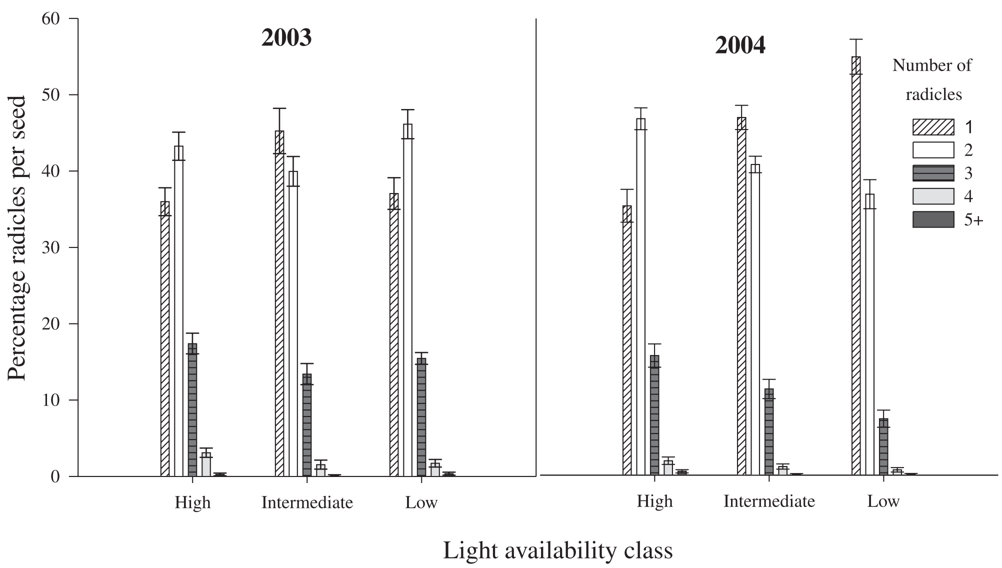


Fig. 3. Mean (±SE) percentage of *Vincetoxicum rossicum* seeds having one or more radicles for seeds collected from plants growing under three light environments during 2003 and 2004 in Henderson Harbor, New York (n = 3600).



ments, plants grown in higher light environments typically invest fewer resources into light-capturing structures (e.g., stems, leaves) and often reallocate a greater proportion of resources into reproductive structures such as flowers and seeds (Agrawal 2001). Total seed numbers may be higher in the intermediate and low light plots; however, plants from plots receiving the highest light produced ~1700 more viable seed than plants in low light plots. The higher number of *V. rossicum* seedlings found in the high and intermediate light availability plots compared with the low light plots was likely the result of several reproductive-related parameters enhanced by increased light availability including greater seed viability, increased frequency of polyembryonic seeds, and higher seed germination levels. Polyembryony may be an adaptive response to shortages in pollen despite the fact that this species can produce seeds by selfing (St. Denis and Cappuccino 2004). Another possibility is that polyembryony may be a mechanism by which *V. rossicum* increases the likelihood of high-density patches, which can increase fitness in this species by an Allee effect (Cappuccino 2004). Ladd and Cappuccino (2005) showed that while a higher proportion of polyembryonic seedlings died over a 3-year period in an old field site near Ottawa, Ontario, the probability of at least one seedling remaining from a polyembryonic seed was significantly greater than the probability of survival for single embryo seeds. The increased dormancy of seeds produced in the low light plots relative to high light plots in this study may be a form of adaptive shade avoidance, because germination under these competitive conditions may reduce the probability of seedling survival (Brainard et al. 2005).

Seed characteristics and light availability

In this study, we did not find a relationship between light availability and size of *V. rossicum* seeds. These results contrast with those of Willson and Price (1980) showing that

Table 4. Mean percentage (±SE) of total seeds collected in 2003 from plants growing under three light environments in Henderson Harbor, New York.

	Viable seed		Nonviable seed	
Light availability [a]	Germinated (%)	Dormant (%)	No embryo (%)	Dead (%)
High	64.4±3.7a	6.0±0.9a	23.0±2.5a	6.3±2.0a
Intermediate	56.2±3.6a	6.9±2.0ab	27.3±2.2ab	10.3±2.4a
Low	46.5±2.6a	10.0±2.8b	32.8±1.7b	11.5±1.6a

Note: The percentages of viable seeds that germinated or were dormant and of nonviable seeds that lacked an embryo or were dead are shown. Mean percentages of viable and nonviable seeds with the same letter in a column are not significantly different ($P > 0.05$). A PROC MIXED procedure in SAS was used for all of the analyses.

[a] Light availability was calculated from the leaf area index (LAI) of the overstory canopy measured in June 2004 (high, <0.119; intermediate, 0.120–0.299; and low, >0.300 $m^2 \cdot m^{-2}$). Values are means of n = 1200 for each light availability class.

shade in the closely related species *Asclepias syriaca* L. reduced seed size by 44% relative to seeds produced by nonshaded plants. It was expected that larger seed size would have been particularly advantageous in low light habitats such as forest understories, because it increases the ability of seedlings to capture light and nutrients (Kidson and Westoby 2000). Alternatively, the production of larger seeds by *V. rossicum* in high shade environments may be maladaptive, since heavier seeds cannot disperse as far (Cappuccino et al. 2002) thus limiting their ability to reach and colonize more open environments such as forest edges and old fields, where growth and reproduction of this species is generally enhanced.

The ability of *V. rossicum* plants in this study to produce a significant number of polyembryonic seeds, especially in high light environments, and the high proportion of seedlings in this species to survive to reproductive stage, particularly when compared with other herbaceous plants (Turnbull et al. 2000; Ladd and Cappuccino 2005), are likely critical attributes contributing to the rapid population expansion and invasiveness of this introduced vine in North America. This species is likely seed limited in its introduced range, since the production of more seeds is likely to result in a greater number of seeds reaching (largely via wind dispersal) new sites to colonize, thus increasing population size and expanding its range.

Although *V. rossicum* growth and reproduction was generally favoured under high and intermediate light conditions, plants growing in shaded conditions were nonetheless capable of producing large quantities of seeds (28 000 seeds·m^{-2}) and embryos (∼46 000 embryos·m^{-2}). While plants in full sun produced the lowest number of seeds, the higher occurrence of polyembryony in full sun plants resulted in the production of a greater number of potential seedlings than for more shaded plots. Therefore, this species has the ability to behave much like a shade-tolerant forest understory herbaceous species, maximizing resource capture and taking advantage of gap openings in the canopy to increase growth, but favoring habitats exposed to partial or full sun (Bierzychudek 1982). Leicht and Silander (2006) recently demonstrated that the exotic invasive liana *Celastrus orbiculatus* Thunb. (oriental bittersweet) has been a successful invader in the Northeastern United States, in part because of its ability not only to colonize and grow well in high light environments such as forest edges and open fields, but also in low light environments of forest understories.

Site characteristics

It is unclear what specific abiotic (e.g., site characteristics, climate) and (or) biotic (e.g., competition, genetic variability of population) factors present at the Henderson Harbor, New York, site may have resulted in a more vigorous and aggressive *V. rossicum* population than reported previously for populations in other New York State sites. It is possible that the very shallow soils at this site (0–30 cm) may be less favorable to the establishment and growth of many other plant species or that those plant species capable of establishing under such difficult growing conditions are not as competitive as *V. rossicum*. Ecophysiological differences in water potential and other soil physical properties between sites may also have contributed to the disparity in results between studies, but this warrants further study. The large differences in growth and reproduction of *V. rossicum* populations studied in New York State and in Ontario to date could also be due to genetic differences between the populations sampled. Although *V. rossicum* is capable of self-pollination, it is primarily an outcrossing species, a feature that may increase genetic variability between populations (St. Denis and Cappuccino 2004). Support for the view that genetically variable *V. rossicum* populations are likely present across its adventive range is provided by herbarium records, indicating that this species was likely introduced into different regions of Canada and the Northeastern United States separately (Sheeley 1992; DiTommaso et al. 2005*b*).

Findings from this 2-year study suggest that growth, reproduction, and potential of *V. rossicum* to spread are substantially greater than has been previously reported in New York State. While in the vicinity of our Henderson Harbor, New York site, this species already occurs in extensive and dense monospecific stands, this aggressive introduced vine may nonetheless not have attained its maximum growth potential and distribution range in this region of North America.

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References

Agrawal, A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science (Washington, D.C.), **294**: 321–326. doi:10.1126/science.1060701. PMID:11598291.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytol. **90**: 757–776. doi:10.1111/j.1469-8137.1982.tb03285.x.

Brainard, D.C., Bellinder, R.R., and DiTommaso, A. 2005. Effects of canopy shade on the morphology, phenology, and seed characteristics of Powell amaranth (*Amaranthus powellii*). Weed Sci. **53**: 175–186. doi:10.1614/WS-04-067R1.

Cappuccino, N. 2004. Allee effect in the invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae). Oikos, **106**: 3–8. doi:10.1111/j.0030-1299.2004.12863.x.

Cappuccino, N., MacKay, R., and Eisner, C. 2002. Spread of the invasive alien *Vincetoxicum rossicum*; tradeoffs between seed dispersability and seed quality. Am. Midl. Nat. **148**: 263–270. doi:10.1674/0003-0031(2002)148[0263:SOTIAV]2.0.CO;2.

Cavers, P.B., and Steel, M.G. 1984. Patterns of change in seed weight over time on individual plants. Am. Nat. **124**: 324–335. doi:10.1086/284276.

Christensen, T. 1998. Swallow-worts. Wildflower, Summer: 21–25.

DiTommaso, A., Brainard, D.C., and Webster, B.R. 2005*a*. Seed characteristics of the invasive alien vine *Vincetoxicum rossicum* are affected by site, harvest date, and storage duration. Can. J. Bot. **83**: 102–110. doi:10.1139/b04-154.

DiTommaso, A., Lawlor, F.M., and Darbyshire, S.J. 2005*b*. The biology of invasive alien plants in Canada. 2. *Cynanchum rossicum* (Kleopow) Borhidi (= *Vincetoxicum rossicum* (Kleopow) Barbar.) and *Cynanchum louiseae* (L.) Kartesz & Gandhi) (= *Vincetoxicum nigrum* (L.) Moench.). Can. J. Plant Sci. **85**: 243–263.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Kartesz, J.T. 1999. A synonymized checklist and atlas with biographical attributes for the vascular flora of the United States, Canada and the North American flora, version 1.0. North Carolina Botanical Garden, Chapel Hill, N.C. [CD-ROM].

Ketterings, Q.M., Krol, H., Reid, W.S., and Hunter, M. 2003. Jefferson County soil sample survey 1995–2001. CSS Extension Bulletin E03–4. Cornell University, Ithaca, N.Y.

Kidson, R., and Westoby, M. 2000. Seed mass and seedling dimensions in relation to seedling establishment. Oecologia, **125**: 11–17. doi:10.1007/PL00008882.

Ladd, D., and Cappuccino, N. 2005. A field study of seed dispersal and seedling performance in the invasive exotic vine *Vincetoxicum rossicum.* Can. J. Bot. **83**: 1181–1188. doi:10.1139/b05-093.

Lawlor, F. 2000. Herbicidal treatments of the invasive plant *Cynanchum rossicum* and experimental post control restoration of infested sites. M.S. thesis, State University of New York, College of Environmental Sciences and Forestry, Syracuse, N.Y.

Leicht, S.A., and Silander, J.A., Jr. 2006. Differential responses of invasive *Celastrus orbiculatus* (Celastraceae) and native *C. scandens* to changes in light quality. Am. J. Bot. **93**: 972–977.

Moore, P.R. 1960. Tetrazolium as a universally acceptable quality test of viable seed. Proc. Int. Seed Test. Assoc. **27**: 795–805.

Morgan, D.C., and Smith, H. 1976. Linear relationship between phytochrome photoequilibrium and growth in plants under simulated natural radiation. Nature (London), **262**: 210–212. doi:10.1038/262210a0.

Sanchez, R.A., Eyherabibe, G., and de Miguel, L. 1981. The influence of irradiance and water deficit during fruit development on seed dormancy in *Datura ferox* L. Weed Res. **21**: 127–132.

SAS Institute Inc. 2001. SAS/STAT® Users guide, Version 9.1. Statistical Analysis Systems Institute Inc., Cary, N.C.

Sheeley, S. 1992. The distribution and life history characteristics of Swallow-wort (*Vincetoxicum rossicum*). M.S. thesis, State University of New York, College of Environmental Sciences and Forestry, Syracuse, N.Y.

Sheeley, S.E., and Raynal, D.J. 1996. The distribution and status of species of *Vincetoxicum* in eastern North America. Bull. Torrey Bot. Club, **123**: 148–156. doi:10.2307/2996072.

St. Denis, M., and Cappuccino, N. 2004. Reproductive biology of *Vincetoxicum rossicum* (Kleo.) Barb. (Asclepiadaceae), an invasive alien in Ontario. J. Torrey Bot. Soc. **131**: 8–15.

Stoller, E.W., and Myers, R.A. 1989. Response of soybeans (*Glycine max*) and four broadleaf weeds to reduced irradiance. Weed Sci. **37**: 570–574.

Sugiyama, S., and Bazzaz, F.A. 1997. Plasticity of seed output in response to soil nutrients and density in *Abutilon theophrasti*: implications for maintenance of genetic variation. Oecologia, **112**: 35–41. doi:10.1007/s004420050280.

Turnbull, L.A., Crawley, M.J., and Rees, M. 2000. Are plant populations limited? A review of seed sowing experiments. Oikos, **88**: 225–238. doi:10.1034/j.1600-0706.2000.880201.x.

Willson, M.F., and Price, P.W. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. Can. J. Bot. **58**: 2229–2233.