American Journal of Botany 95(4): 447–453. 2008.

SURVIVAL AND PERFORMANCE OF THE INVASIVE VINE VINCETOXICUM ROSSICUM (APOCYNACEAE) FROM SEEDS OF DIFFERENT EMBRYO NUMBER UNDER TWO LIGHT ENVIRONMENTS[1]

EMILY E. HOTCHKISS,[2] ANTONIO DITOMMASO,[2,3] DANIEL C. BRAINARD,[4]
AND CHARLES L. MOHLER[2]

[2]Department of Crop and Soil Sciences, Cornell University, Ithaca, New York 14853 USA; and [4]Department of Horticulture, Michigan State University, East Lansing, Michigan 48824 USA

The nonnative vine *Vincetoxicum rossicum* threatens several ecosystems in the Lower Great Lakes Basin of North America. One feature that may contribute to its invasiveness is the production of some seeds with multiple embryos (polyembryony), which may be beneficial as a bet-hedging strategy in variable environments. However, lower seed reserves per embryo in polyembryonic seeds may entail costs in low-light environments. The effect of seed from three embryonic classes (1, 2, or 3 embryos/seed) on *V. rossicum* survival and growth was studied under two forest understory light environments: full canopy (shade) or canopy gaps (light) in New York state. Two seedling cohorts were planted, in May 2004 and in May 2005. The survival and growth of seedlings was monitored biweekly for two (2005 cohort) or three (2004 cohort) seasons. For both cohorts, plants grown in canopy shade had reduced survival and growth compared with those grown in gaps. Contrary to expectations, seed embryo number had no effect on the final height, survival, or dry mass of plants in either habitat. Our results suggest that any fitness advantage provided by polyembryony may be habitat (light) dependent and not a general trait that affords *V. rossicum* a benefit in all habitats colonized.

Key words: *Cynanchum rossicum*; dog-strangling vine; forest gaps; growth; invasive species; pale swallow-wort; population dynamics; shade.

Invasive nonnative plants are disrupting natural habitats and reducing species diversity in ecosystems throughout the world (D'Antonio and Vitousek, 1992: Pimm et al., 1995). Ecological research on invasives to date has focused largely on identifying attributes of these plants that make them successful invaders as well as on determining those characteristics of a habitat that make it more susceptible to invasion by nonnative species (Vitousek, 1990; Gordon, 1998; Hierro et al., 2005; Richardson and Pyšek, 2006). Two plant traits that have been repeatedly identified as particularly important in the invasion process are fecundity (Richardson and Cowling, 1992) and the ability to survive under variable environmental conditions (Groves, 1986; Holdgate, 1986; Roy, 1990; Goodwin et al., 1999; Richards et al., 2006).

During the last decade, the nonnative invasive vine pale swallow-wort or dog-strangling vine, *Vincetoxicum rossicum* (Kleopow) Barbar. [Apocynaceae; syn. *Cynanchum rossicum* (Kleopow) Borhidi], has become increasingly problematic in both natural and seminatural systems of the Great Lakes Basin (Sheeley and Raynal, 1996; DiTommaso et al., 2005b). Dense monospecific stands of *V. rossicum* in alvar (i.e., shallow limestone barrens) systems have disrupted nesting sites of native grassland birds and threatened endangered plant species (Bonanno, 1999; Lawlor, 2000; DiTommaso et al., 2005b). The presence of this species may also threaten native butterflies through competition with native hosts and disruption of ovipositioning and larval development (DiTommaso and Losey, 2003; Mattila and Otis, 2003; Casagrande and Dacey, 2007). Unfortunately, control efforts to date aimed at *V. rossicum* have been largely ineffective. The lack of effective control methods has resulted in substantial increases in population densities and distribution of this invasive vine in both full sun old-field habitats and shaded forest understories in its introduced North American range (DiTommaso et al., 2005b).

Differences in the light environment of plants can have significant effects on their survival and growth (Kaelke et al., 2001; Brainard et al., 2005; Cole and Weltzin, 2005; Moran and Showler, 2005; Leicht and Silander, 2006; Flory et al., 2007). Light availability also plays a major role in determining how plants allocate resources to different structures (Morgan and Smith, 1979). For example, under low light, *Impatiens parviflora* DC. can increase internode length as a shade avoidance response (Young, 1981). Although most plant species are adapted to habitats with a narrow range of light availabilities (e.g., open habitats or forest understories), some plants can establish and grow in habitats having a broad range of light availabilities because they possess a greater degree of phenotypic plasticity than more habitat-restricted species (Sultan, 1987, 2000; Richards et al., 2006).

Seeds of *V. rossicum* are polyembryonic, a characteristic that is prevalent in gymnosperms but is relatively uncommon in angiosperms (Maheshwari, 1950). Polyembryony is the occurrence of multiple embryos in a single seed (Lakshmanan and Ambegaokar, 1984). The location within the seed where the multiple embryos develop can be used to distinguish between several known types of polyembryony. The multiple embryos in *V. rossicum* are derived from either the nucellar cells in the micopylar region of the seed coat (von Hausner, 1976) or result

---

[1] Manuscript received 12 June 2007; revision accepted 15 January 2008.

The authors thank the Hunter R. Rawlings III Cornell Presidential Research Scholars Program for funding to E.E.H; S. Darbyshire, N. Cappuccino, and an anonymous reviewer for providing valuable comments on an earlier version of the manuscript; and K. Averill, S. Morris, L. Smith, V. Hotchkiss, and summer student research assistants for help with field work.

[3] Author for correspondence (e-mail: ad97@cornell.edu); phone 607-254-4702; fax: 607-255-3207

from cleavage of the embryo (Seefeldner, 1912). Embryo cleavage results in genetically identical embryos that are different from the mother's genotype. Cleavage, the simplest method to produce additional embryos, is commonly found in gymnosperms.

Adventitious polyembryony results when embryos, additional to the zygote embryo, arise from diploid cells derived from the maternal sporophyte. These embryos are also genetically identical to each other and the maternal plant, but not to a fertilized zygote. Species closely related to *V. rossicum* have been studied and different polyembryony have been found. Guignard (1922) reported embryo cleavage in *V. nigrum* (L.) Moench., whereas Kordyum (1961) reported adventitious embryos developing from the integument in *V. hirundinaria* Medik. Adventitious polyembryony appears to be the form present in *V. rossicum*, but the ontogeny of supplementary embryos in this species has not been definitively identified. Seeds of *V. rossicum* most often contain two embryos, although up to eight embryos have been observed in a single seed (Smith et al., 2006). The probability of producing more than one embryo in this species appears to increase with seed mass (DiTommaso et al., 2005a).

Polyembryonic seeds have been hypothesized to confer several potential advantages in plants. One hypothesis suggests that increasing population densities resulting from the germination and establishment of polyembryonic seeds increases individual plant fitness via the Allee effect (Cappuccino, 2004; Ladd and Cappuccino, 2005). The Allee effect can be described as increased reproductive fitness of individuals when grown in patches rather than independently. In contrast to most other examples of Allee effects in plants, Cappuccino (2004) reported that the effect in *V. rossicum* was not due to differences in pollinator visitation rates, but rather, to more effective suppression of competing vegetation when growing in larger patches. A second hypothesis, "bet hedging," proposes that polyembryonic seeds afford plants more than one opportunity to establish in a given location, especially under variable conditions (Ladd and Cappuccino, 2005). Bet hedging may occur in *V. rossicum* because emergence of seedlings from polyembryonic seeds can be separated by as much as 20 d (N. Cappuccino, unpublished data). Ganeshiah et al. (1991) postulated that polyembryony evolved in plants as a maternal strategy to prevent brood reduction. Ladd and Cappuccino (2005) found that polyembryony in *V. rossicum* was advantageous for seedling establishment in an open field habitat. That is, the greater number of seedlings arising from a seed with multiple embryos in a given environment, the greater the likelihood that at least one seedling would survive damage or death.

However, the costs and benefits of polyembrony may vary with habitat. In particular, under conditions of low light, polyembryony may entail important costs. For a given seed size, each embryo in a polyembryonic seed is likely to have fewer seed reserves available for early growth than an embryo from a singlet seed. Therefore, seedlings arising from polyembryonic seeds may have slower initial growth and may be at a competitive disadvantage relative to those arising from singlets, especially under low light. Moreover, increased seedling densities from the germination of polyembryonic seeds in a single site may increase the intensity of sister-seedling competition and result in greater mortality of plants. Under the stress of low light, larger seeds may be more advantageous to plants than smaller seeds (Gross and Werner, 1982; Rees, 1996; Moles and Westoby, 2004). In a classic experiment, Grime and Jeffrey (1965) grew tree seedlings in shade tubes that imposed vertical light gradients and showed that larger-seeded species had an advantage both in reaching the top of the tubes and in surviving longer at the bottom of the tubes. Similarly, smaller seed reserves available to each embryo in a polyembryonic seed may entail costs under low light, resulting in lower survival, growth, and reproduction compared with nonpolyembryonic seeds. To date, no research has examined the effects of different light availabilities on *V. rossicum* seedling survival and growth over multiple years and for seedlings from seeds that varied in the number of embryos. The main objective of this study was to compare seedling survival and performance in *V. rossicum* seedlings produced from seeds with different numbers of embryos when grown in a forest gap and a shaded forest understory, two habitats in which this species commonly occurs. We hypothesized that polyembryony has a positive effect on survival (defined here as the presence of at least one shoot) and growth in *V. rossicum*, especially under the greater light availabilities of forest gaps relative to forest understories.

MATERIALS AND METHODS

Seed collection and germination—Mature follicles of *V. rossicum* used for this study were collected from an ecotone population found between an old field and mixed deciduous forest in Henderson Shores, New York (43°51′ N, 76°14′ W) in September 2003 and 2004. Seeds were removed from follicles by hand and individually weighed once the comas had been removed. Approximately 2000 seeds (2004) and 5000 seeds (2005) weighing between 5.1–7.0 mg were placed in plastic containers lined with moistened paper towels and cold stratified in a refrigerator at 4°C for 10 d. We chose seeds within this relatively narrow range for mass to assess strategies for allocating limited resources in polyembryonic *V. rossicum*. To stimulate germination, we moved containers to a growth chamber having a 14-h photoperiod and 32/25°C day/night temperatures for 8 d. At the end of this period, seeds were classified into one of four embryonic classes (i.e., 1, 2, 3, and 4+) based on the number of visible, unbranched radicles (~0.5 cm length) that emerged. We did not base our seed classification on the presence of hypocotyls because most of these structures were not visible at this time. Only seeds in the first three classes were used for this study because of a limited number of seeds with more than four embryos.

Seedling production—In 2004, individual germinated seeds were planted at a depth of 1 cm in 125-cm^3 peat pots containing moistened Cornell soil mix (1 : 1 : 1 peat, perlite, and vermiculite without nutrients). Because of a shortage of seeds producing three radicles (i.e., triplets), only 161 triplet seeds were planted, whereas a total of 200 seeds each producing two (doublets) and one (singlets) radicle were planted. In 2005, 336 seeds of each embryonic class were planted. Trays containing 36 peat pots planted to a single embryonic class were watered and placed in a greenhouse having a 15-h natural photoperiod and 24/21°C day/night temperatures for the 2004 cohort. The 2005 cohort was planted in plastic trays with 120 individual compartments (80 cm^3) containing moistened Cornell soil mix. Tray positions in the greenhouse were rerandomized weekly to reduce variability in growing conditions. Seedlings were watered daily but were not fertilized. In early June 2004 (after 10 d of growth) and early May 2005 (after 10 d of growth), trays were moved outdoors for 4 d to acclimate seedlings before transplanting in the field. Mortality of seedlings was not recorded at this stage.

Field site preparation and seedling transplanting—The field site used for this 3-yr study was located at the Robert Musgrave Research Facility of Cornell University in Aurora, New York (42°73′N, 76°65′W). The site was located within a 1.5-ha deciduous woodlot comprised largely of small sized (<30 cm diameter) trees, including sugar maple (*Acer saccharum* Marsh.), red oak (*Quercus rubra* L.), ash (*Fraxinus* spp.), American hornbeam (*Carpinus caroliniana* Walt.), and American sycamore (*Plantus occidentalis* L.). Understory species included bracken fern [*Pteridium aquilinum* (L.) Kuhn], sedges (*Carex* spp.), trillium (*Trillium* spp.), trout lily (*Erythronium americanum* Ker.), poison ivy (*Toxicodendron radicans* L.), Virginia creeper (*Parthenocissus quinquefolia* L.), and grape (*Vitis riperia* L.). The site was located primarily on a

Kendaia and Lyons silt loam soil with an organic matter content of 10.5% and pH 7.0. Soils were somewhat poorly to moderately well drained.

A total of seven plots were randomly established at this site, with each plot consisting of two paired subplots measuring 3.05 × 4.58 m. One subplot was shaded by the overstory tree canopy throughout the day, and the other subplot was exposed to morning sunlight through natural gaps in the tree canopy. Sun subplots were oriented along a north–south axis and located in the northernmost section of the canopy gap to allow maximum penetration of sunlight. These natural gaps in the tree canopy were enhanced by the removal of small shrubs and trees <10 cm in diameter. Although some *V. rossicum* plants were present in the woodlot (<0.1 plants·m^{-2}), we selected plot areas having no or few established *V. rossicum* plants to reduce difficulty in identifying study plants reemerging in the following years. Within plots, all understory vegetation was removed by hand and by mechanical clipping before transplanting *V. rossicum* seedlings. To control established *T. radicans* and *V. rossicum* plants in several plots, however, we applied the broad spectrum herbicide glyphosate at 0.56 kg·ha^{-1} using a CO_2 backpack sprayer.

Seedlings of *V. rossicum* were transplanted on 11 June 2004 and 2 May 2005. In 2004, mean height of all sister seedlings was approximately 30, 22, and 18 mm for singlets, doublets, and triplets, respectively. In 2005, mean seedling height was 25, 21, and 18 mm for the three embryonic classes. In 2004, a total of 18 transplants (each containing sister seedlings originating from the same seed) were placed in each subplot along three rows spaced 1 m apart. The six transplants within a row were planted 0.6 m apart, and wooden stakes were used to mark the location of plants. In 2005, a total of 36 transplants were spaced 0.45 m apart in each subplot along three newly established rows between the 2004 rows. The 12 transplants within each row were spaced 0.3 m apart. Transplants were placed in each subplot such that every row contained two and four transplants from each of the three embryonic classes in 2004 and 2005, respectively, and every column contained one transplant from each embryonic class. Within a few days of field transplanting in 2004, some *V. rossicum* target seedlings were dug up and destroyed by small rodents. To protect transplants, we placed 20-cm squares made of 0.64-cm mesh size hardware cloth over all transplants and secured them to the ground with metal staples. Transplants destroyed or damaged by the rodents were immediately replaced with extra transplants from the same embryonic class. In 2004, 30 of the damaged triplet transplants (18 from shade subplots and 12 from sun subplots) were not replaced because of a lack of additional triplet transplants. For the 2005 transplants, the protective hardware cloth was not necessary because no seedling damage was observed.

Data collection—Soil samples from each of the 14 plots were collected on 11 August 2004, 10 August 2005, and 16 August 2006 using a standard 2.5-cm diameter soil corer to a depth of 15–20 cm and were submitted to the Cornell Nutrient Analysis Laboratory for chemical analysis. Light availability in each of the 14 subplots was determined on 11 August 2004, an overcast day, by photographing the overhead vegetation 1.5 m above ground at 1000 hours Eastern Daylight Time using a CI-110 Digital Plant Canopy Imager (CID, Vancouver, Washington, USA) to obtain solar beam transmission coefficient.

Survival of *V. rossicum* seedlings from both the 2004 and 2005 cohorts was monitored at 2-wk intervals throughout the growing season (May to October in 2004 and 2005, and May to early August in 2006). A transplant was considered to have survived if at least one sister seedling was present at the time of sampling. For each live sister seedling of a target transplant, the height was recorded every 4 wk. The mean height of sister seedlings for a given transplant was then calculated as the sum of all sister seedling heights divided by the number of sister seedlings. Mean height of plants for each subplot were calculated by summing the mean heights of all transplants and dividing by the number of transplants.

All live plants from both the 2004 and 2005 cohorts were harvested on 9 August 2006 by clipping plant tissue at the soil line. Aboveground biomass of each target plant (all tillers included) was weighed after oven-drying material at 65°C for 5 d. The mean aboveground biomass of plants for each subplot was calculated by summing the mean biomass of all transplants and dividing by the number of transplants.

Data analysis—For each sampling date and each plot, the percentage of initial plants surviving was calculated, along with the average height and aboveground dry biomass (last sampling date only) of all surviving plants. The effects of habitat and embryo number on survival, height, and aboveground biomass were analyzed using PROC MIXED in SAS (SAS Institute, 2001) for each cycle of the study. Habitat and embryo number were treated as fixed effects and block as a random effect. Survival data were either arcsine (2004 cohort) or arcsine square-root transformed (2005 cohort), height data were either not transformed (1-yr-old plants from both cohorts) or log-transformed (final height for both cohorts), and aboveground dry biomass data were log-transformed to improve assumptions of normality and equal variance of population distributions.

RESULTS

Site characteristics—Mean light penetration within the closed canopy plots (0.11 ± 0.02 mean light transmission coefficients) was approximately 60% lower than that in forest gap plots (0.28 ± 0.02 mean light transmission coefficients). Closed and gap habitats did not vary significantly in their soil characteristics (data not shown). Temperature and precipitation during the three years of the study were higher than 30-yr means.

Embryony class and light availability—Contrary to expectations, there were no significant interactions detected between embryonic class of *V. rossicum* plants and light availability for any of the parameters measured for either cohort [light × embryonic class interactions for 2004 and 2005 cohorts respectively: % survival ($F_{2,36} = 0.48$, $P = 0.62$; $F_{2,36} = 0.88$, $P = 0.42$); final height ($F_{2,36} = 0.15$, $P = 0.86$; $F_{2,36} = 0.34$, $P = 0.71$); final aboveground biomass ($F_{2,36} = 0.19$, $P = 0.82$; $F_{2,36} = 0.29$, $P = 0.75$)] (Fig. 1). In other words, the effect of embryo number on survival, height, and aboveground biomass did not vary with habitat.

Plant survival—After 3 yr, survival of plants (at least one sister seedling present) from the 2004 cohort was approximately 50% lower in the closed habitat (26%) compared with the gap habitat (52%) ($F_{1,36} = 5.57$, $P = 0.024$) (Fig. 1A). Similarly, after 2 yr, survival of plants from the 2005 cohort was approximately 40% lower in the closed habitat (25%) relative to the gap habitat (42%) ($F_{1,36} = 6.83$, $P = 0.013$) (Fig. 1B). Embryo number did not affect *V. rossicum* survival for either cohort (2004: $F_{2,36} = 0.08$, $P = 0.92$; 2005: $F_{2,36} = 0.27$, $P = 0.76$). For the 2004 and 2005 cohorts, survival was approximately 39% and 33%, respectively, for all three embryonic classes (Fig. 1A, B). At the end of the experiment, the mean number of sister seedlings for surviving plants did not differ between the three embryonic classes for either cohort year (2004: $F_{2,36} = 0.37$, $P = 0.70$; 2005: $F_{2,36} = 0.34$, $P = 0.72$) (Fig. 2).

Plant height and aboveground biomass—Habitat significantly influenced final height (2004: $F_{1,25} = 26.5$, $P < 0.001$; 2005: $F_{1,30} = 18.8$, $P < 0.001$) and final aboveground biomass (2004: $F_{1,25} = 30.4$, $P < 0.001$; 2005: $F_{1,30} = 16.6$, $P < 0.001$) of *V. rossicum* plants in both cohort years (Fig. 1). For the 2004 cohort and across all embryonic classes, the height and aboveground biomass of plants in the closed habitat were reduced 69% and 88%, respectively, relative to plants grown in gaps (Fig. 1C, E). Reductions in height and aboveground biomass for the 2005 cohort of plants across all embryonic classes and grown under forest canopy were 45% and 69%, respectively, relative to growth of plants in forest gaps (Fig. 1D, F). In both cohort years, the height of seedlings was significantly affected by embryo number only in the first year of growth (2004: $F_{2,34} = 6.22$, $P = 0.005$; 2005: $F_{2,35} = 7.40$, $P = 0.002$) (Fig. 3), with singlets taller than doublets or triplets. However, there was no significant interaction between light environment and embryonic class on height, indicating that having fewer embryos per seed was not more advantageous in the low light environment compared

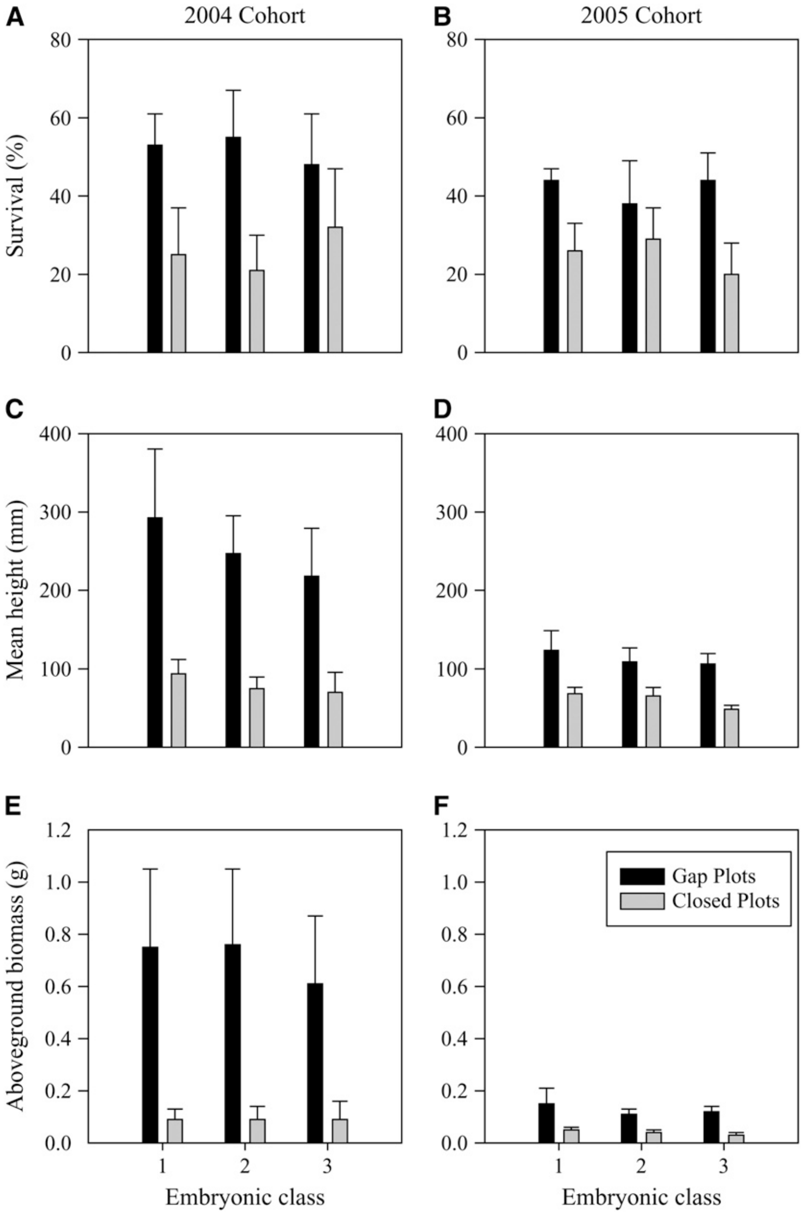

Fig. 1. The effect of light environment (forest gap or closed forest canopy) and embryonic class (singlet, doublet or triplet), on *Vincetoxicum rossicum* percentage plant survival (A, B), height (C, D), and aboveground biomass (E, F) at the end of two (2005 cohort) or three (2004 cohort) growing seasons. Note that plant survival refers to survival of at least one sister seedling arising from a given seed. For both cohorts, light environment had a significant effect on final survival ($P = 0.024$, $P = 0.013$), height ($P < 0.001$) and dry mass ($P < 0.001$). However, effects of embryonic class and interactions between embryonic class and light environment were not significant for either cohort ($P > 0.05$).

with the high light environment as hypothesized. Initial differences in height between embryonic classes were no longer detectable after the first growing season, and embryo number had no effect on final aboveground biomass (Fig. 1).

DISCUSSION

Light availability—The observed increases in survival, height, and aboveground biomass of seedlings grown in gap plots relative to shaded canopy plots support the hypothesis that *V. rossicum* fitness improves with greater availability of light in a forest environment. Light availability appears to be a major factor influencing *V. rossicum* seedling survival and fitness, although its effect may be partly indirect through modification of other abiotic factors such as soil temperature and moisture.

Our results are consistent with those of previous studies demonstrating improved growth and fecundity of *V. rossicum* in more open habitats (Sheeley, 1992; Lawlor, 2000). However, as in previous studies, *V. rossicum* seedlings had a strong capacity to tolerate the deep shade of the closed habitat. In part, the tolerance of seedlings to low light is attributable to strong phenotypic plasticity in *V. rossicum*. For example, Sheeley (1992) noted greater internode length and greater specific leaf area for *V. rossicum* grown in the shade compared with the open. Our findings suggest that *V. rossicum* utilizes a “sit-and-wait”

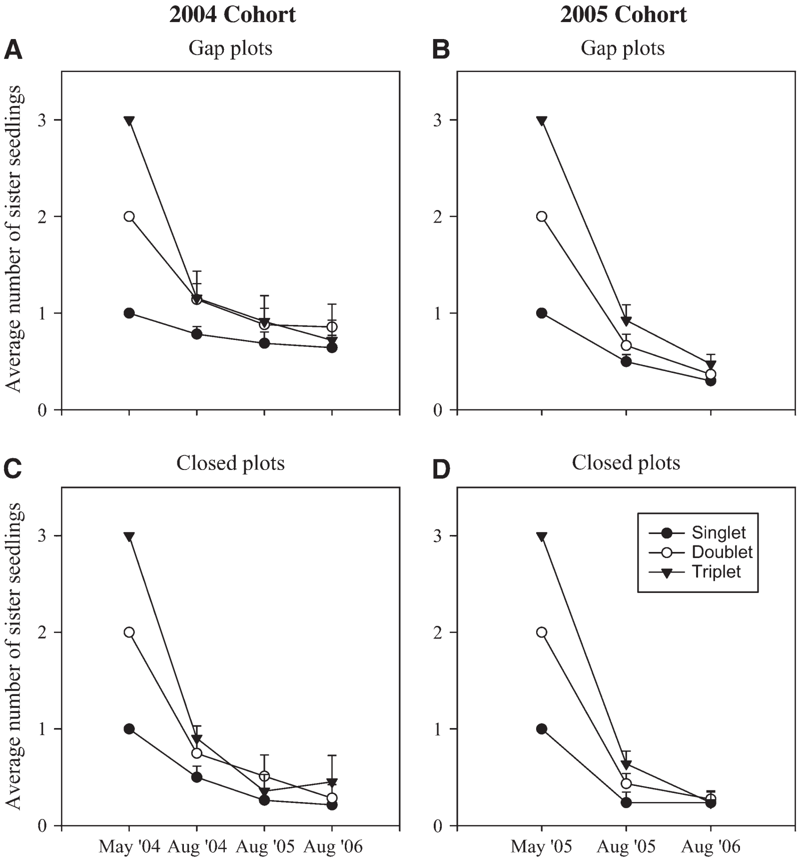

Fig. 2. Average number of surviving *Vincetoxicum rossicum* sister seedlings (±SE) originating from seed of three embryonic classes at planting and at the end of each growing season for the 2004 (A, C) and 2005 (B, D) cohorts under two light environments. For both cohorts, final sister seedling number was not significantly different ($P > 0.05$).

strategy typical of many forest understory plants that are able to survive under full canopy but rapidly respond when a disturbance such as treefall generates a gap. This shade tolerance and phenotypic plasticity may contribute to the invasive success of *V. rossicum* in forest communities.

Embryonic status—The number of embryos of individual seedlings had only transient effects on plant growth and did not influence height, aboveground biomass, or survival after two (2005 cohort) or three (2004 cohort) years of growth (Fig. 1). These results do not support the hypothesis that more embryos increase seedling growth and survival. Our findings are also not consistent with those of Ladd and Cappuccino (2005) showing that seeds bearing triplet or doublet seedlings had greater establishment success (having at least one surviving sister seedling) than singlets in an open, old field. By the end of the experiment, the number of seedlings surviving per seed was similar regardless of the initial embryo number of the seed (Fig. 2).

The absence of a polyembryony advantage in our study may be due to several factors. First, the effect of embryo number on survival is likely to depend on the characteristics of the habitat. For example, one of the principal hypothesized advantages of polyembryony is "bet hedging." If one seedling from a polyembryonic seed is lost to hazards such as herbivory or drought, seedlings arising from the other embryos could potentially replace it. However, the effects of polyembryony on fitness may vary with habitat characteristics with the costs being greater in the forested habitat of our study compared with the open field investigated by Ladd and Cappuccino (2005). In our study, light levels in both the gap and closed habitats were considerably lower than those in the open, old field used by Ladd and Cappuccino (2005). Under these lower light conditions, the seedlings arising from polyembryonic seeds might have been at a competitive disadvantage relative to singlet seeds with greater seed reserves, negating any potential benefit associated with bet hedging. Higher light levels in their study may have minimized this potential cost, resulting in the overall advantage conferred by polyembryony reported in their study.

A second reason for the observed lack of an advantage to polyembryony in our study may relate to the fact that seedlings were transplanted. By transplanting seedlings, hazards associated with field establishment were avoided, which may have reduced the potential benefits of polyembryony. On the other hand, the direct-seeding approach used by Ladd and Cappuccino (2005) may have biased their results because seedlings that did not emerge after germination would not have been recorded; if seedlings produced from polyembryonic seeds had greater preemergence mortality than seedlings produced from singlet seeds (as might be expected if polyembryonic seeds have lower seed reserves), then this approach would have overestimated the advantage of polyembryony. For example, if a *V. rossicum* polyembryonic seed having two embryos was sown by Ladd and Cappuccino (2005) and one of the germinated embryos failed to emerged, this case would be tallied as a "singlet" seed

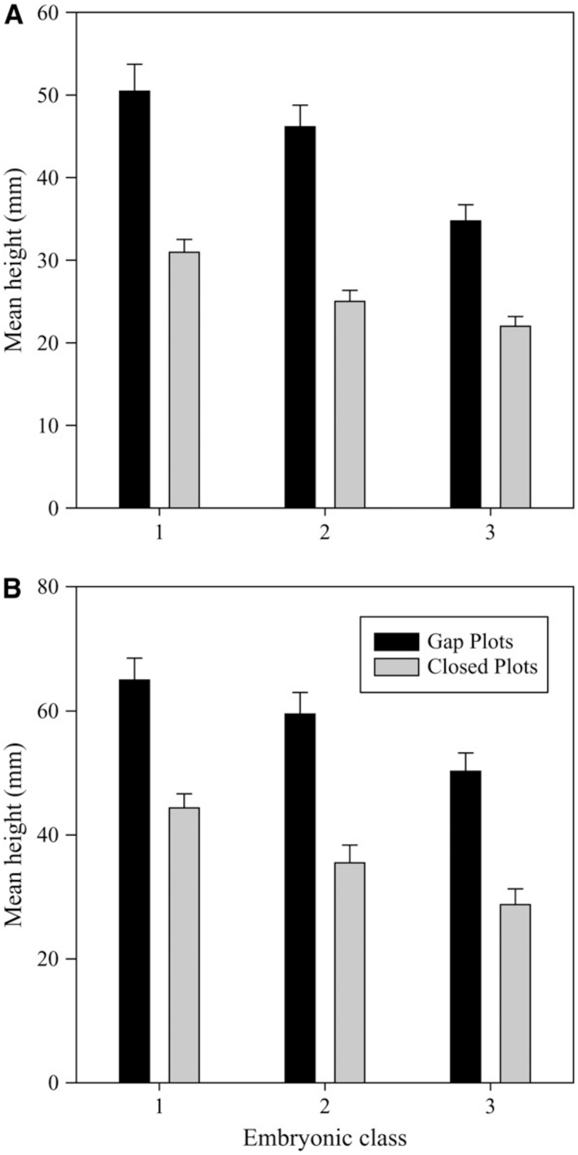

Fig. 3. Mean height (±SE) of surviving *Vincetoxicum rossicum* seedlings after one growing season for the 2004 (A) and 2005 (B) cohorts based on the initial embryonic class of seed. For both cohorts, light environment ($P < 0.001$) and embryonic class ($P = 0.004$; $P = 0.002$) had significant effects on height after one growing season. Interactions between light environment and embryonic class were not significant for either cohort ($P > 0.05$).

and not as a "polyembryonic" seed. This "singlet" seed would likely have a lower seed mass, and the resulting "singlet" seedling may not grow as well as a seedling emerging from a truly singlet seed with one embryo. This scenario would then dilute the growth advantage theoretically associated with larger, single-embryo seeds. To avoid these problems, development of an approach to determine the polyembryonic status of seeds before the experiment, followed by direct seeding would be ideal.

Embryo number and light availability—Contrary to expectations, the effect of embryo number did not vary with habitat for any of the responses measured (Fig. 2). We had hypothesized that the costs associated with reduced seed reserves per embryo for polyembryonic seeds would be greater in the closed habitat due to reduced light availability. The idea is that smaller seed reserves should result in smaller seedlings that are less able to capture light—a cost that should be more pronounced in low light. As expected, seedlings from polyembryonic seeds were shorter than those from singlets after one year of growth (Fig. 3). However, this initial height advantage of singlets did not translate into greater survival in either of the shaded habitats (Fig. 1). One explanation for this observation is that greater height does not necessarily translate into greater light capture under a forest canopy, where the canopy is far out of reach (Westoby et al., 1992). In both habitats, neighboring competing vegetation was removed, reducing the gradient of light availability with height. Another possibility is that the differences in light availability across habitats and the differences in heights across embryonic class were too small to lead to detectable differences in performance. The relatively small height differences recorded in our study are likely to be more important in an open field where the light gradient in the first 30–50 cm is much steeper.

Our study demonstrated that survival and growth of the invasive, herbaceous vine *V. rossicum* is favored in higher-light forest-gap understories relative to denser canopy understories. Contrary to expectations however, the levels of seed polyembryony in *V. rossicum* did not provide a survival or growth advantage in the higher light of forest gaps. It is possible that any advantage of polyembryonically derived *V. rossicum* plants will be apparent only in much higher light environments such as old fields. Therefore, our findings indicate that any fitness advantage afforded *V. rossicum* via the production of seeds having multiple embryos may be habitat (i.e., light availability) dependent and not a general trait that benefits this invasive plant in all habitats that it has colonized.

LITERATURE CITED

Brainard, D. C., R. R. Bellinder, and A. DiTommaso. 2005. Effects of canopy shade on the morphology, phenology, and seed characteristics of Powell amaranth (*Amaranthus powellii). Weed Science* 53: 175–186.

Bonanno, S. E. 1999. Jefferson County Alvar Megasite Conservation Plan. Nature Conservancy, Rochester, New York, USA.

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

Casagrande, R. A., and J. E. Dacey. 2007. Monarch butterfly oviposition on swallow-worts (*Vincetoxicum* spp.). *Environmental Entomology* 36: 631–636.

Cole, P. G., and J. F. Weltzin. 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. *Biological Invasions* 7: 477–488.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.

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

DiTommaso, A., F. M. Lawlor, and S. J. Darbyshire. 2005b. 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] *Canadian Journal of Plant Science* 85: 243–263.

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

Flory, S. L., J. A. Rudgers, and K. Clay. 2007. Experimental light treatments affect invasion success and the impact of *Microstegium vimineum* on the resident community. *Natural Areas Journal* 27: 124–132.

Ganeshiah, K. N., R. U. Shaanker, and N. V. Joshi. 1991. Evolution of polyembryony: Consequences to the fitness of mother and offspring. *Journal of Genetics* 70: 103–127.

Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plans species based on biological information. *Conservation Biology* 13: 422–426.

Gordon, D. R. 1998. Effect of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8: 975–989.

Grime, J. P., and D. W. Jeffrey. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53: 621–642.

Gross, K. L., and P. A. Werner. 1982. Colonizing abilities of 'biennial' plant species in relation to ground cover: Implications for their distributions in a successional sere. *Ecology* 63: 921–931.

Groves, R. H. 1986. Plant invasion of Australia: An overview. *In* R. H. Groves and J. J. Burdon [eds.], Ecology of biological invasions, 137–149. Cambridge University Press, Cambridge, UK.

Guignard, L. 1922. La fecundation et la polyembryonie chez les *Vincetoxicum. Mémoires de l'Académie Royale des Sciences de l'Institut de France II* 57: 1–25.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology* 93: 5–15.

Holdgate, M. W. 1986. Summary and conclusions: Characteristics and consequences of biological invasions. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 314: 733–742.

Kaelke, C. M., E. L. Kruger, and P. B. Reich. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light availability gradient. *Canadian Journal of Forest Research* 31: 1602–1616.

Kordyum, E. L. 1961. On polyembryony in *Vincetoxicum officinale* Moench. *Ukrayins'kyi Botanicnyi Zhurnal* 18: 48–54 [In Ukranian].

Ladd, D., and N. Cappuccino. 2005. A field study of seed dispersal and seedling performance in the invasive exotic vine *Vincetoxicum rossicum. Canadian Journal of Botany* 83: 1181–1188.

Lakshmanan, K. K., and K. B. Ambegaokar. 1984. Polyembryony *In* B. M. Johri [ed.], Embryology of angiosperms, 453–457. Springer-Verlag, New York, New York, USA.

Lawlor, F. 2000. Herbicidal treatment 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 Science and Forestry, Syracuse, New York, USA.

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

Maheshwari, P. 1950. An introduction to the embryology of angiosperms. McGraw-Hill, New York, New York, USA.

Mattila, H. R., and G. W. Otis. 2003. A comparison of the host preference of monarch butterflies (*Danaus plexippus*) for milkweed (*Asclepias syriaca*) over dog-strangler vine (*Vincetoxicum rossicum*). *Entomologia Experimentalis et Applicata* 107: 193–199.

Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology* 92: 372–383.

Moran, P. J., and A. T. Showler. 2005. Plant responses to water deficit and shade stresses in pigweed and their influence on feeding and oviposition by the beet armyworm (Lepidoptera: Noctuidae). *Environmental Entomology* 34: 929–937.

Morgan, D. C., and H. Smith. 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145: 253–258.

Pimm, S. L., G. J. Russel, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* 269: 347–350.

Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 351: 1299–1380.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981–993.

Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invasible, and which species invade? *In* B. van Wilger, D. M. Richardon, F. J. Kruger, and B. J. van Hensbergen [eds.], Swartboskloof-fire in South African Mountain fynbos, 161–179. University of Cape Town, Cape Town, South Africa.

Richardson, D. M., and P. Pyšek. 2006. Plant invasions: Merging the concepts of species invasiveness and community invisibility. *Progress in Physical Geography* 30: 409–431.

Roy, J. 1990. In search of the characteristics of plant invaders. *In* F. di Castri, A. J. Hansen, and M. Debussche [eds.], Biological invasions in Europe and the Mediterranean basin, 335–352. Cambridge University Press, Cambridge, UK.

SAS Institute. 2001. SAS/STAT User's guide, version 8.1. Cary, North Carolina, USA.

Seefeldner, C. 1912. Die Polyembryonie bei *Cynanchum vincetoxicum* (L.) Pers. *Akademie der Wissenschaftlichen Wien Sitzungsber, Mathematisch-Naturwissenschaftlichen Klasse I* 121: 273–296.

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, New York, USA.

Sheeley, S. E., and D. J. Raynal. 1996. The distribution and status of *Vincetoxicum* in eastern North America. *Bulletin of the Torrey Botanical Club* 123: 148–156.

Smith, L. L., A. Ditommaso, J. Lehmann, and S. Greipsson. 2006. Growth and reproductive potential of the exotic invasive vine *Vincetoxicum rossicum* in northern New York State. *Canadian Journal of Botany* 84: 1771–1780.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* 21: 127–178.

Sultan, S. E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* 12: 537–542.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57: 7–13.

von Hausner, G. 1976. Embryogenese und nucellar-polyembryonie bei *Cynanchum-Vincetoxicum*-Arten. *Beitrage zur Biologie der Pflanzen* 52: 101–126.

Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* 7: 368–372.

Young, J. E. 1981. Light quality and stem growth in *Impatiens parviflora* DC. *New Phytologist* 89: 47–59.