Does polyembryony confer a competitive advantage to the invasive perennial vine *Vincetoxicum rossicum* (Apocynaceae)\

Megan L. Blanchard, Jacob N. Barney, Kristine M. Averill, Charles L. Mohler, and Antonio DiTommaso

Determining which traits may allow some introduced plant species to become invasive in their new environment continues to be a key question in invasion biology. *Vincetoxicum rossicum* is an invasive, perennial vine colonizing natural and seminatural habitats primarily in the northeastern United States and southeastern Canada. More than half its seeds exhibit polyembryony, a relatively uncommon condition in which a single seed produces multiple seedlings. For evaluating the potential consequences of polyembryony on invasiveness, *V. rossicum* plants derived from seeds of three embryonic classes—singlets, doublets, and triplets (one, two, and three seedlings per seed, respectively)—were paired in all combinations intra- and interspecifically and with the co-occurring native herbs *Solidago canadensis* and *Asclepias syriaca* in a greenhouse study. *Vincetoxicum rossicum* biomass was 25–55% greater and follicle production 55–100% greater under intraspecific competition compared with interspecific competition. However, within a competitive environment, follicle production varied little. Regardless of competitive environment, *V. rossicum* originating from seeds with a greater number of embryos typically performed no better than plants arising from seed with fewer embryos (singlets = doublets = triplets)—except intraspecifically where doublets outperformed singlets, and with *S. canadensis* where triplets outperformed singlets. Our findings suggest that overall performance and fitness of *V. rossicum* is higher in monocultures than in mixed stands and that its ability to invade new habitats may not be attributable to the production of polyembryonic seeds.

Key words: Apocynaceae; *Asclepias syriaca*; common milkweed; competition; *Cynanchum rossicum*; dog-strangling vine; invasive plants; pale swallow-wort; *Solidago canadensis*.

An important focus of plant invasion biology research continues to be the determination of traits that allow some introduced species to become invasive in their new environment (Hierro et al., 2005; Richardson and Pyšek, 2006). Similarly, the role that plant competition from resident vegetation may play in enhancing the resistance of some plant communities to invasions has also been an active research area (Daehler, 2003; Levine et al., 2004; Going et al., 2009). A more in-depth understanding of the reproductive biology of invasive species may provide some insight into why some plant species become invasive while others do not and how these traits may affect competitive outcomes.

Polyembryony, multiple embryos produced within a single seed, is exhibited by a number of angiosperms, yet little is known about the origin or ecological consequences of this reproductive phenomenon. In plants, 78% of polyembryonic cases arise from maternal tissue (adventitious polyembryony), and 19% arise from cleavage of the fertilized embryo (cleavage polyembryony) (Ganeshiah et al., 1991). Embryo cleavage results in genetically identical embryos that are different from the mother’s genotype. Cleavage polyembryony is commonly found in gymnosperms, but it is not common among angiosperms (Maheshwari, 1950). In adventitious polyembryony, all embryos are genetically identical to each other and the maternal plant. For multiple embryos originating from maternal tissue such as the seed coat or endosperm, it has been proposed that polyembryony is a maternal strategy to counteract losses suffered due to sibling competition (Ganeshiah et al., 1991). Willson and Burley (1983), however, suggested the possibility of facilitation, or at least reduced competition, among genetically identical offspring.

If embryos from a polyembryonic seed are genetically similar, “seed individuals” serve as the larger proxy for individual fitness. However, each embryo is an individual in the competitive sense, and if at least one embryo survives, then the population continues. Genotype fitness for a plant originating from polyembryonic seeds is additive (i.e., each embryo’s reproductive output should be summed for each seed individual) compared with a plant arising from a single-embryo seed that has only this single source for reproductive output. From an invasive species perspective, it only matters that the population increases in size regardless of how it is achieved. For the plant invasion process, if polyembryonic seeds increase the probability of a given genotype surviving, as well as increasing the probability of adding individuals to the next generation, then this reproductive strategy should be favored over one resulting in single-embryo seeds. Surprisingly, despite these potential evolutionary advantages of the polyembryonic strategy, the response of polyembryonic individuals (genetically unique seeds) in intraspecific competition with individuals of different embryonic classes (i.e., doublets, triplets) or in competition with other plant species has seldom been studied. Most studies of polyembryonic plants have been limited to crops, particularly

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citrus species (Bowman et al., 1995; Martínez-Gómez and Gradziel, 2003), and have focused on how polyembryony arises, the genetics of the multiple embryos, or uses and obstacles associated with breeding these plants for agricultural purposes (Scheckel et al., 2001). The possible role that polyembryony plays in invasive species dynamics is entirely unknown, but could provide insight into mechanisms of competitor displacement and evolutionary trajectories within introduced plants.

*Vincetoxicum rossicum* (Kleopow) Barbar. [= *Cynanchum rossicum* (Kleopow) Borhidi; dog-strangling vine or pale swallow-wort] is an herbaceous, perennial vine in the Apocynaceae, subfamily Asclepiadoideae. *Vincetoxicum rossicum* is self-pollinated and may also be insect-pollinated (St. Denis and Cappuccino, 2004). This introduced species is rapidly invading natural and seminatural communities in the northeastern United States and southeastern Canada, occurring from the Atlantic Coast to southern Michigan and from southern Ontario to southern Pennsylvania (Sheeley and Raynal, 1996; Kricsfalussy and Miller, 2008). The species forms dense stands and may displace both native and introduced species in invaded regions (DiTommaso et al., 2005). Invaded sites have been reported to have reduced diversity of arthropods (Ernst and Cappuccino, 2005), and the presence of *V. rossicum* has altered arbuscular mycorrhizal fungal (AMF) communities (Greipsson and DiTommaso, 2006; Smith et al., 2008) as well as nesting sites of several grassland birds (Bonanno, 1999). There has also been concern for native butterflies, especially the monarch butterfly (*Danaus plexippus* L.), whose natural host plant, the native common milkweed (*Asclepias syriaca* L.), may be competitively displaced by *V. rossicum* in old field habitats where the two species co-occur (DiTommaso and Losey, 2003; Mattila and Otis, 2003). Moreover, *V. rossicum* plants may serve as a population sink for monarchs—attracting and stimulating female monarch oviposition despite their unsuitability for larval development (DiTommaso and Losey, 2003; Casagrande and Dacey, 2007).

Reproduction and spread in *V. rossicum* occurs primarily via wind-dispersed seeds, but also through vegetative production of stems from rootstocks (Sheeley, 1992; DiTommaso et al., 2005; K. M. Averill et al., Cornell University, unpublished manuscript). Growth and reproductive output is highest in intermediate light environments in the presence of AMF (Smith et al., 2006, 2008). Seedlings have been shown to establish in areas of dense existing vegetation (Cappuccino et al., 2002; K. M. Averill et al., Cornell University, unpublished manuscript), affording *V. rossicum* an opportunity to readily colonize intact habitats. Over 50% of seeds produced by this species are polyembryonic (Sheeley, 1992; Cappuccino et al., 2002; St. Denis and Cappuccino, 2004; Smith et al., 2006). The multiple embryos in *V. rossicum* are derived from either the nuellar cells in the micropylar region of the seed coat (i.e., adventitious polyembryony) (von Hausner, 1976), or they result from cleavage of the embryo (Seefeldner, 1912). 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.

To our knowledge, there have been two previous studies that investigated the possible fitness advantage of polyembryony for a plant species in a competitive environment. Cappuccino et al. (2002) found that polyembryonic seeds of *V. rossicum* accumulated more total biomass when grown alone than did single-embryo seeds, though this advantage disappeared when grown in competition with an established grass sward. In a study examining the effects of gaps and polyembryony in a forest understory, Hotchkiss et al. (2008) found that polyembryonic status did not affect the survival or growth of *V. rossicum* plants. However, survival and growth of plants was greater in the higher light environment.

Polyembryony may contribute to the invasive success of *V. rossicum* in several ways: (1) by increasing the fitness of a new population via the Allee effect (Cappuccino, 2004), (2) by increasing the likelihood that at least one embryo individual will survive through a “bet-hedging” strategy (St. Denis and Cappuccino, 2004; Ladd and Cappuccino, 2005), or (3) by the direct competitive advantage of having multiple stems that result from multiple embryo individuals. An embryo individual is defined here as the plant(s) arising from a single embryo, while a seed individual includes all plants arising from all embryos contained within one seed. The effect of direct competition on growth, survival, reproduction, and plant fitness is well established (Mack and Harper, 1977), as is the importance of competitive ability for successful invasion by nonnative species (Melgoza et al., 1990). However, how these traits translate to a polyembryonic system is unknown, especially as they relate to nonnative species success.

In this study, we sought to determine if the success of the highly invasive *V. rossicum* is associated with the biological

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**Table 1.** Embryo and seed individual ANOVA F-statistic and P-values for biomass and fecundity of *Vincetoxicum rossicum* under intraspecific competition (1v1, 1v2, 1v3, 2v2, 2v3, 3v3) and under interspecific competition with *Solidago canadensis* (goldenrod = GR) and *Asclepias syriaca* (common milkweed = MW). Follicle data were only collected for seed individuals.

<table>
<thead>
<tr>
<th>Source</th>
<th>Aboveground biomass</th>
<th>Belowground biomass</th>
<th>Total biomass</th>
<th>Root : Shoot</th>
<th>Follicle number</th>
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<td><strong>Intraspecific competition</strong></td>
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<tr>
<td>Embryo individual</td>
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<tr>
<td>Treatment (T)</td>
<td>21.2***</td>
<td>11.7***</td>
<td>23.6***</td>
<td>0.2</td>
<td>—</td>
</tr>
<tr>
<td>Seed individual (S)[T]</td>
<td>9.6***</td>
<td>6.8***</td>
<td>11.1***</td>
<td>0.7</td>
<td>—</td>
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<tr>
<td>Embryo individual (E)[S,T]</td>
<td>15.3***</td>
<td>9.0***</td>
<td>17.1***</td>
<td>0.9</td>
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<tr>
<td>Seed individual</td>
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<tr>
<td>Treatment (T)</td>
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<td>29.5***</td>
<td>3.6**</td>
<td>4.0*</td>
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<td>Seed individual (S)[T]</td>
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<td>43.9***</td>
<td>16.7***</td>
<td>0.4</td>
<td>6.2***</td>
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<td>Treatment (T)</td>
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<tr>
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<td>10.1***</td>
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<tr>
<td>Treatment (T)</td>
<td>1.2</td>
<td>12.2***</td>
<td>2.5*</td>
<td>1.0</td>
<td>0.9</td>
</tr>
</tbody>
</table>

* P < 0.05, ** P < 0.01, *** P < 0.0001
Fig. 1. Embryo individual means (+SE) for (A) aboveground biomass, (B) belowground biomass, (C) total biomass, and (D) root to shoot ratio of six intraspecific competition treatments. 1v1 = PSW1 (1 embryo) in competition with PSW1 (1 embryo), 1v2 = PSW1 (1 embryo) in competition with PSW2 (2 embryos), etc. Numbers were assigned to embryo individuals based on the order in which they emerged.
The phenomenon of polyembryony by examining its effects on competition with native species. The objectives of this study were to (1) determine whether polyembryony confers a competitive advantage to *V. rossicum*, (2) assess whether this advantage, if present, is more pronounced in intraspecific competition, and (3) determine whether the competitive advantage, if present, is proportional to the number of embryos per seed. We hypothesized that *V. rossicum* seed individual biomass would be proportional to embryonic status (i.e., triplets > doublets > singlets) and that polyembryonic seed individuals would outperform singlets in interspecific competitive environments.

**MATERIALS AND METHODS**

**Plant material and germination**—Seeds of *V. rossicum* and *A. syriaca* were collected in fall 2005 from several old-field sites near Aurora, New York, USA (42.7°N, 76.6°W). The seeds were stored dry at 5°C. Seeds were wet-stratified for 6 wk at 5°C before the experiment. *Solidago canadensis* L. seeds were collected from the same old fields and were stratified in flats containing moistened Cornell soil mix (1:1:1 mixture of peat, perlite, and vermiculite without nutrients) for 6 wk at 5°C.

After stratification, seeds of *V. rossicum* were transferred to moistened germination paper in an air-tight plastic container and placed in a growth chamber with 25/17°C day/night temperatures and a 14-h photoperiod. Embryonic class was determined by recording the number of emerging radicles 3, 5, 7, and 8 d after sowing. Seeds of *A. syriaca* were germinated in petri dishes in the same growth chamber, beginning 2 d after sowing of *V. rossicum*, while *S. canadensis* seeds were placed directly in the greenhouse to stimulate germination 3 d prior to sowing of *V. rossicum*. We used these different seed sowing dates for the three test species because of differences in their germination timing. The pregerminated *V. rossicum* seeds were planted in 72-cell plug trays, 7–9 d after sowing. Only singlets (hereafter PSW1), doublets (PSW2), and triplets (PSW3) were used for the following experiments due to an insufficient number of higher embryo seed individuals.

Prior to transplanting, trays were placed in a greenhouse for 15 d at 24/21°C day/night temperatures. Natural light was supplemented with 400 Watt high pressure sodium lamps to achieve a 16-h photoperiod. Seedlings were watered as needed and fertilized with 21-5-20 (N-P-K) mixed at 200 ppm five times per week. Tray positions on benches were rerandomized every 7 d to minimize bench effects on growth. Germinated seeds of *A. syriaca* and *S. canadensis* were planted in separate trays having the same dimensions under the same growing conditions.

**Transplanting and treatment setup**—Seedlings were transplanted into 2.7 L pots containing premoistened Cornell soil mix 15 d after germination, with each pot receiving two individuals. To assess the effects of interspecific competition, we planted seed individuals of *V. rossicum* from each of the three embryonic classes (PSW1, PSW2, and PSW3) with a single *A. syriaca* or *S. canadensis* individual, with 13 replicates. To examine the effects of intraspecific competition, we grew *V. rossicum* seed individuals from the three embryonic classes in all possible combinations, with 8–24 replicates depending on availability (e.g., fewer PSW3 individuals were available and thus only 8 replicates were used). Control pots (8 replicates) were also established in which *V. rossicum* seed individuals from all three embryonic classes, and *A. syriaca* and *S. canadensis* were grown alone. Bamboo stakes were placed in all pots a few days after planting to provide a trellis for the vining *V. rossicum*.
Data collection—For each seed individual, embryo individuals were labeled to track each quantified metric. Plants were harvested 15 wk after transplanting by cutting stems at the soil surface to separate above- and belowground components. The number of mature follicles per seed individual was counted. Belowground structures were washed free of soil and intertwined roots of different plants were separated, including separation of embryo individuals from one another. Above- and belowground material were dried at 65°C until constant mass was achieved, and biomass was determined by weighing.

Statistical analyses—To test for differences in time to emergence for each embryo among PSW1–PSW3, we performed an ANOVA followed by mean separation using Tukey’s honestly significant difference (HSD) test. To determine the effect of neighbor identity and embryonic class on V. rossicum performance (i.e., biomass and number of follicles), we performed a separate nested ANOVA for embryonic individuals and seed individuals. In the embryonic individual analyses, we used three fixed effects, including treatment (i.e., competitive environment), seed individual nested within treatment, and embryo individual nested within seed individual (treatment). For the seed individual analyses, treatment and seed individual nested within treatment were fixed effects. Means were separated using Tukey’s HSD. Analyses were performed separately for inter- and intraspecific competitive environments using the program JMP v6.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Embryonic class and germination—No differences were found across embryonic classes for days to germination of the first radicle ($F_{3,15} = 0.04, P = 0.98$) or second radicle ($F_{2,44} = 2.8, P = 0.06$). Regardless of embryonic class, all radicles emerged within 2.5 d of emergence of the first radicle (data not shown).

Intraspecific competition—Aboveground, belowground, and total V. rossicum biomass varied as a function of neighbor identity, seed individual, and embryo individual (Table 1; Figs. 1 and 2). However, few differences in root to shoot ratio were found among embryo or seed individuals (Table 1, Figs. 1D and 2D). Regardless of seed class or competitive environment, biomass (aboveground, belowground, or total) varied little within an embryo class (i.e., first embryo in all seed individuals: Fig. 1A–C). Note that numbers were assigned to embryo individuals based on the order in which they emerged. However, the first embryo was generally larger than the second and third embryos, though no differences existed between the second and third embryos (Fig. 1A–C). Within a seed individual class (e.g., PSW2), biomass varied little among competitive environments (Fig. 2A–C). Aboveground and total biomass varied little, with the only major difference being that PSW2 was 85% larger than PSW1 in competition with each other. The doublet (PSW2) and triplet (PSW3) seed individuals had 40–70% more belowground biomass than singlet (PSW1) seed individuals (Fig. 2B). Root to shoot ratios were quite variable across embryo individuals and seed individuals, but there were no differences ($P > 0.05$). Follicle number varied little among seed individuals (Table 1, Fig. 3A), though in the PSW1 vs. PSW2 treatment, PSW2 yielded 72% more follicles.

Interspecific competition—Embryo individuals produced between 0 and 50% less aboveground biomass in interspecific competition compared with intraspecific competition (Figs. 1 and 4). Singlets typically outperformed the third embryo of triplets (PSW3) for aboveground, belowground, and total biomass (Fig. 4A–C). However, triplet seed individuals (PSW3) produced more belowground biomass (≥70%) than did singlets (PSW1) in competition with both S. canadensis and A. syriaca (Fig. 5B). Root to shoot ratios were not different ($P > 0.05$) for embryo or seed individuals. Follicle production remained unchanged regardless of seed individual or competitor (Fig. 3B).

No competition—Without competition, aboveground ($F_{3,31} = 10.1, P < 0.0001$), belowground ($F_{3,31} = 2.3, P = 0.09$), and total ($F_{3,31} = 11.6, P < 0.0001$) biomass varied among embryo individuals (Fig. 6), though root to shoot ratio did not vary ($F_{3,31} = 2.4, P = 0.09$). Singlet V. rossicum outperformed all polylembryonic individuals in aboveground and total biomass, and the second and third embryo of PSW3 for belowground biomass (Fig. 6A). Without competition, aboveground ($F_{2,16} = 4.8, P = 0.02$), belowground ($F_{2,16} = 6.5, P = 0.008$), and total ($F_{2,16} = 8.5, P = 0.003$) biomass also varied among seed individuals. Triplet seed individuals (PSW3) outperformed PSW1 seed individuals in aboveground, belowground, and total biomass with PSW2 being intermediate (Fig. 6B), though root to shoot ratio did not vary ($F_{2,16} = 0.7, P = 0.53$).
DISCUSSION

Our results suggest that *V. rossicum* individuals have reduced performance when grown in competition, especially interspecific competition. Within polyembryonic seed individuals (PSW2 and PSW3), early-emerging embryos typically outperform later-emerging embryos for biomass production. In intraspecific competition, seed individuals with more embryos do not generally perform better than lower embryonic class seed individuals for biomass production or reproductive output (except PSW2 > PSW1, Fig. 3A). Similarly, no differences existed between any seed individuals for aboveground biomass or follicle production when grown with either *S. canadensis* or *A. syriaca*. However, triplet *V. rossicum* seed individuals produced more belowground biomass than singlets under interspecific competition. Based on our results, polyembryonic seed individuals appear to have little competitive or reproductive advantage. We did find increased belowground biomass in polyembryonic individuals compared with single embryo seeds under either intra- or interspecific competition. Similarly, in a recent field study in central New York State, Hotchkiss et al. (2008) reported that seed embryo number had no effect on the final height, survival, or aboveground biomass of *V. rossicum* plants grown in the understory of a shaded forest or forest gaps.

Polyembryony may confer an advantage upon *V. rossicum* through staggered emergence times of the multiple embryos (Ladd and Cappuccino, 2005). This bet-hedging strategy would increase the chances of some seedling survival in a temporally variable environment, similar to dormancy strategies, but over a shorter period of time (Venable and Brown, 1988; Rees, 1996). Our results contrast with observations made by other researchers who have demonstrated a greater staggering of germination within polyembryonic seed individuals (St. Denis and Cappuccino, 2004; Ladd and Cappuccino, 2005). We found that the difference between the germination of the first and third embryo was less than 2.5 d, which is likely too short to be meaningful on an ecological scale, and does not provide evidence for the supposed advantages. It is possible that the relatively ideal growing conditions in our greenhouse setting may have limited the staggering of germination timing in polyembryonic seeds. The staggering of germination could be a plastic trait that occurs when abiotic conditions are variable and not as uniformly favorable as under our controlled greenhouse environment. However, a bet-hedging strategy may still exist simply through increased numbers of seedlings. Hazards such as herbivory and wind damage may make it beneficial to have higher numbers of offspring with smaller embryos (as opposed to fewer with larger embryos), by increasing the chance that at least one seedling will survive. Ladd and
Cappuccino (2005) found that although mortality of embryo individuals from polyembryonic seeds was higher than for single embryos, the chances of at least one embryo individual from a polyembryonic seed surviving were greater than for single embryos.

Interestingly, we found little variation in follicle production among seed individuals when grown in intra- or interspecific competition. However, interspecific competition with *S. canadensis* and *A. syriaca* reduced follicle production up to 60% compared with *V. rossicum* grown intraspecifically. These results suggest that *V. rossicum* plants in monoculture are more fecund than *V. rossicum* plants growing in mixed stands when colonizing new habitats either along an invasion front or via long-distance seed dispersal. This evidence supports the notion of an Allee effect in *V. rossicum* (Cappuccino, 2004), where dense stands (or monocultures) have higher fitness than low-density populations or single individuals. Similarly, Cappuccino (2004) found that dense *V. rossicum* populations yielded higher per plant biomass and seed set than low-density populations or individuals.

Unlike in our greenhouse trials, during which *V. rossicum* achieved fruit set by the time of harvest, *V. rossicum* is slow to mature in the field, which McKague and Cappuccino (2005) attributed to a priority for allocating resources into belowground storage organs for use in subsequent growing seasons. However, in a recent greenhouse trial by Milbrath (2008), *V. rossicum* plants grown from seedlings did not flower during the 16-wk study. McKague and Cappuccino (2005) found that *V. rossicum* seedlings invested over 3-fold more resources in roots than shoots. Although we found that *V. rossicum* root to shoot ratio did not vary within a competitive environment, the root to shoot ratio under interspecific competition was 0.65, and under intraspecific competition, it was reduced to 0.47. Under competition with the common competitors *S. canadensis* and *A. syriaca*, *V. rossicum* performance is reduced, and a greater proportion of those resources are invested in belowground tissue. This strategy of increased belowground allocation when competition with other species is high may increase survival and competitive ability in future years. In contrast, when grown with other *V. rossicum* plants, more resources are invested in aboveground biomass, a strategy that perhaps allows this species to take advantage of resources while they are available and while competition with other species is low (Davis and Pelsor, 2001).

Competition for light is generally thought to result in size asymmetry between the competing individuals, with earlier-germinating or inherently taller plants (whether within or between species) preempting light and having a proportionally detrimental effect on smaller plants (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001). In this experiment, germination time varied little. However, the smaller individual embryo size of the polyembryonic seeds may have given them an initial size disadvantage (especially for the shorter individuals arising from a polyembryonic seed), which was enhanced by asymmetric competition. A threshold of initial light may
exist under which seedlings cannot compete effectively due to asymmetric competition. This possible size disadvantage would also explain the shift away from size asymmetry among embryo individuals arising from one seed when competing interspecifically as opposed to intraspecifically. If the resources are pre-empted by the competitor, none of the embryo individuals from polyembryonic seeds would be able to compete, regardless of differences in embryo size. Belowground competition is less well understood, and conflicting reports of symmetric and asymmetric competition exist (Prati et al., 1997).

However, it is generally agreed that belowground competition is size-symmetric, with roots acquiring resources proportional to their size (Schwinning and Weiner, 1998; Cahill and Casper, 2000; Schenk, 2006). The hypotheses that propose possible belowground asymmetric competition generally stress the importance of heterogeneous soil resources (Schwinning and Weiner, 1998). But our small, controlled experimental soil system containing a homogenized and evenly fertilized soil most likely did not provide enough of a directional resource to be pre-empted.
Our results confirm those of Cappuccino et al. (2002), who reported that higher embryonic class resulted in higher seed individual biomass when grown without competition. However, when grown in competition with grasses, polyembryony did not have an effect on seed individual biomass (Cappuccino et al., 2002). Study of invasive species suggests that different traits may be advantageous for establishment in a relatively intact community vs. a disturbed site (Horvitz et al., 1998). Therefore, while polyembryony may confer a competitive advantage to V. rossicum plants colonizing an established natural community, it may confer an advantage to V. rossicum plants colonizing disturbed sites with no or little resident vegetation. This is important because V. rossicum does seem to thrive in disturbed sites, where competitors such as A. syriaca and S. canadensis may be attempting to invade at the same time (K. M. Averill et al., Cornell University, unpublished data). It is notable, however, that V. rossicum also thrives in established communities (Sheeley and Raynal, 1996; K. M. Averill et al., Cornell University, unpublished data), which may result from guerilla-style invasion front movement into the intact community.

Several researchers have proposed that the competitive advantage of some invasive species may be due to allelopathy, the release of root exudates by one plant species to inhibit the growth of another (Ridenour and Callaway, 2001). This mechanism has proven to be important for the establishment of several invasive species, for which the native plants have not yet developed defenses (Ridenour and Callaway, 2001). Recent work has demonstrated that allelopathy may be an important mechanism facilitating the spread of V. rossicum into new regions (Douglass, 2008; Mogg et al., 2008; Douglass et al., 2009). In the case of V. rossicum, it is possible that the cost of producing these toxins is shared, and thus reduced, by very closely neighboring polyembryonic siblings. The genetic relatedness of the polyembryonic embryo individual from the same seed may also protect the seedlings from any variations in toxins that could arise from genetically unrelated or more distantly related members of the same species. However, Douglass (2008) found that the genetic variation within and among V. rossicum populations in New York State is relatively low.

We propose another possible reason why polyembryonic V. rossicum outperforms singlet seeds for belowground biomass but not aboveground biomass. Rhizosphere priming, the ability of roots to alter the soil surrounding them, can have positive or negative effects of rhizosphere priming of multiple embryo individuals. The priming should be beneficial for all embryo individuals from the same seed because they are genetically identical.

Despite the clear advantage of having polyembryonic seeds for colonizing highly disturbed sites with little or no competition from resident vegetation, V. rossicum seed individuals with multiple embryos performed no better than single embryo seeds under any of our competitive environments. Additionally, follicle production showed no plasticity within a competitive environment. Vincetoxicum rossicum displays evidence of the Allee effect, with seed individuals grown in an intraspecific competitive environment outperforming seed individuals grown in mixture with S. canadensis and A. syriaca. An appropriate next research step would be to study the extent of V. rossicum allelopathy and rhizosphere priming, as well as to determine the genetic basis for polyembryony in V. rossicum.

LITERATURE CITED


