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Tolerance of Swallowworts (*Vincetoxicum* spp.) to Multiple Years of Artificial Defoliation and Clipping

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The European vines pale swallowwort and black swallowwort are invading various habitats in northeastern North America. It is unclear how these plants might respond to potential biological control agents, as they experience little herbivore damage in North America, or longer durations of mowing given the reported lack of efficacy of mechanical control. We evaluated the effect of six seasons of artificial defoliation (50 or 100% defoliation once or twice per season) and clipping (once, twice, or four times at 8 cm above the soil level) on the survival, growth, and reproduction of mature plants of the two species grown in a common garden field experiment. No plants died from damage after 6 yr. Black swallowwort produced more aboveground biomass, whereas pale swallowwort produced more root biomass and root crown buds, compared with its congener species. For most damage treatments, root biomass and the number of crown buds and stems increased over time, whereas aboveground biomass and viable seeds per plant generally did not change. Substantial overlap in plant size and seed production occurred among damage treatments and species. The most severe defoliation treatment did not substantially limit growth and reproduction compared with undamaged plants. While two clippings per season sometimes prevented seed production, four clippings per season was the only type of damage that consistently prevented plant growth and eliminated seed production. Pale and black swallowwort display a high tolerance to aboveground tissue loss in high-light environments without plant competition. The annual increase in plant size calls into question the potential efficacy of a defoliating insect against field populations of swallowworts, and it seems likely the only benefits of a long-term mowing regime will be to eliminate seed production.

Nomenclature: Black (or Louise's) swallowwort, *Vincetoxicum nigrum* (L.) Moench, syn. *Cynanchum louiseae* Kartesz & Gandhi; pale (or European) swallowwort; *Vincetoxicum rossicum* (Kleopow) Barbarich, syn. *Cynanchum rossicum* (Kleopow) Borhidi.

Key words: Biological control, dog-strangling vine, invasive plant, mechanical control, natural areas, old field, vine.

Black swallowwort [*Vincetoxicum nigrum* (L.) Moench] and pale swallowwort [*Vincetoxicum rossicum* (Kleopow) Barbar.] are European twining vines related to milkweeds (Apocynaceae subfamily Asclepiadoideae). Black swallowwort is native to southwestern Europe, whereas pale swallowwort is native to the Ukraine and southern European Russia. These herbaceous perennial plants were introduced into North America in the mid to late 1800s, but have only become invasive within the last 30 to 40 yr (DiTommaso et al. 2005; Monachino 1957; Moore 1959; Pringle 1973; Sheeley and Raynal 1996). The primary region infested is the northeastern United States and southeastern Canada, especially New York State, the New England states, and Ontario (DiTommaso et al. 2005; USDA-NRCS 2015a). Both species are capable of growing under a range of soil and light conditions, although pale swallowwort appears to be more shade tolerant (Averill et al. 2010, 2011; DiTommaso et al. 2005; Hotchkiss et al. 2008; Magidow et al. 2013; Smith et al. 2006). Pale swallowwort reportedly reduces bird and arthropod densities in grasslands and fields (DiTommaso et al. 2005; Ernst and Cappuccino 2005), and both species pose a risk to threatened and endangered species, as well as the rare alvar (limestone barrens) ecosystems in the Lower Great Lakes region (DiTommaso et al. 2005; Lawlor 2000; Tewksbury et al. 2002). Although both species can occupy a range of habitats, open field infestations

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Management Implications

Pale swallowwort and black swallowwort are European viney milkweeds that have become invasive in eastern North America since the 1980s. Mechanical control is considered ineffective, but previous studies have only been conducted for 1 or 2 yr. Biological control is also being developed, but it is unclear how these plants might respond to damage such as defoliation over a period of years. We evaluated different artificial defoliation and cutting treatments over 6 yr in a common garden field experiment in Ithaca, NY, for their effect on swallowwort survival, growth, and reproduction. Black swallowwort produced more aboveground biomass, whereas pale swallowwort produced more root biomass and root crown buds, compared with the other species. However, they appeared to respond similarly to damage. No plants died after 6 yr of the different damage treatments, and in general, they increased in size (root biomass, number of crown buds and stems) or did not change (aboveground biomass, seeds per plant) over time. The most severe defoliation treatment (100% twice each year) did not substantially limit growth and reproduction compared with undamaged plants. This result calls into question the potential efficacy of a defoliating insect against field populations of swallowworts. Two clippings per season sometimes prevented seed production and should be considered the minimum frequency of mowing for this purpose. Four clippings per season was the only type of damage that consistently prevented plant growth and eliminated seed production, although it is not clear what the long-term effects of high-frequency mowing will be apart from eliminating seeds. Pale and black swallowwort display a high tolerance to aboveground tissue loss in high-light environments without plant competition.

typically have the highest densities and seed production, potentially serving as the primary source of propagules for spread of the two species (Averill et al. 2008; Lawlor 2000; Sheeley 1992; Smith et al. 2006).

Chemical control is currently the most effective management tool, but concerns exist because of the expense and effects on nontarget species of broad-spectrum herbicides that are currently registered for such use (Averill et al. 2008; Cain and Irvine 2011; DiTommaso et al. 2013; Lawlor and Raynal 2002; Mervosh and Gumbart 2015). Mechanical swallowwort control methods have been considered useful only for minimizing seed production (mowing, stem pulling, seed pod removal) or for small patches (digging out the rootstock) (Averill et al. 2008; Christiansen 1998; DiTommaso et al. 2013; McKague and Cappuccino 2005). In all cases, mechanical control studies were conducted for only 1 or 2 yr, with one or two clippings per season. For example, Averill et al. (2008) reported that while clipping pale swallowwort up to twice per season over 2 yr resulted in shorter plants and reduced follicle (seed pod) production, stand densities did not change, and swallowwort cover increased compared with control plots. Short-term mowing studies for other perennial species have also generally shown a lack of or inconsistency in efficacy (Bicksler and Masiunas 2009; Schooler et al. 2010; Summerlin et al. 2000; Stanley et al. 2011). Several years and greater within-season frequencies of mowing may be necessary to see any effect on long-lived perennial species, especially in terms of depletion of root reserves (Hakansson 1969; Ringselle et al. 2015).

A biological control program also has been in development for long-term suppression. Several candidate insect and pathogen agents have been assessed to varying degrees (Berner et al. 2011; Dolgovskaya et al. 2014; Gibson et al. 2014; Hazlehurst et al. 2012; Leroux 2014; Maguire et al. 2011; Weed and Casagrande 2010, 2011; Weed et al. 2011a,b). Given the frequency with which leaf-feeding insects have been used in other programs (Winston et al. 2014), it was reasonable to assume that a similar type of agent would be used against swallowworts. However, early in the program it was not clear how swallowworts might respond to such damage. Few organisms feed on swallowwort in its invaded range, and damage to swallowwort stands is minor to nonexistent (Milbrath 2010). A greenhouse impact study using artificial defoliation indicated that swallowwort was very tolerant to leaf loss under high-light conditions, and repeated defoliation was likely needed (Milbrath 2008). It was therefore of interest to evaluate the effect of defoliation over multiple years and under field conditions. Artificial herbivory studies can provide insights into the type or amount of damage that must occur on a target weed to significantly affect individual plant performance (Raghu and Dhileepan 2005).

The objective of this experiment was to determine the effect of multiple seasons of aboveground tissue removal, including different percentages or frequencies, or both, of tissue removal by stem clipping and artificial defoliation, on the growth, reproduction, and survival of mature pale and black swallowwort plants grown in the field under high-light conditions.

Materials and Methods

Field Site. The experiment was conducted in a 40 by 60-m field on the Cornell University campus, Ithaca, NY (42°26′36″N, 76°30′00″W). The soil is a deep, moderately well drained Williamson series (coarse-silty, mixed, active, mesic Typic Fragiudepts) very fine sandy loam with pH 6.9 (USDA-NRCS 2015b). The field had been planted to corn or fallow sections the previous 4 yr, and before that it had been in pasture. The field was plowed, disked, fitted, and seeded with a grass seed mixture (Ithaca blend, Agway, Ithaca, NY) comprising perennial ryegrass (*Lolium perenne* L.), red fescue (*Festuca rubra* L.), and Kentucky bluegrass (*Poa pratensis* L.) in late April 2008. The grass was used to suppress weeds and prevent soil erosion. Twenty-three rows of 40-m by 90-cm-wide landscape cloth were then installed every 2 m over the newly seeded grass to reduce weed and grass competition within rows of transplanted swallowwort.

Experimental Design and Treatments. The study period was from May 2008 to September 2014. Rootstocks of black swallowwort (Bear Mountain State Park, Rockland County, NY; 41°18′N, 73°58′W) and pale swallowwort (Elbridge, Onondaga County, NY; 43°0′N, 76°24′W) were collected in the fall of 2007, washed of soil, and stored in moist vermiculite at 4 C until May 2008. After cold storage, rootstocks were weighed for fresh biomass, which served as a covariate in statistical analyses. Rootstocks were then planted every 2 m (within and between rows); a 10 by 10-cm hole was cut into the landscape cloth around each swallowwort transplant. No damage treatments were imposed during the 2008 growing season to allow swallowwort plants to reestablish their root systems. However, any follicles (seed pods) produced were removed to prevent swallowwort seeds from dispersing into the field site. The area immediately surrounding target plants was weeded of unwanted vegetation by hand periodically, and the grass alleyways were mowed as needed using a rotary mulching mower.

Two experimental designs were used. For biomass data involving destructive harvest of plants, the design was a three-way factorial treatment structure in a completely randomized design with two swallowwort species (black and pale swallowwort), eight damage treatments (undamaged control; stems clipped once, twice, or four times per season; 50% defoliation once or twice; 100% defoliation once or twice), and four harvest dates (after 1, 2, 4, and 6 yr of damage). Each treatment combination was replicated five times for a total of 320 experimental units. The second design was for data measured repeatedly over the course of the study from the last harvest group of plants (henceforth referred to as year 6 plants). This design included three factors in a repeated measures design: two swallowwort species and eight damage treatments in a two-way factorial treatment structure in a completely randomized design with repeated measures on years. Each treatment combination was replicated five times for a total of 80 experimental units measured up to six times.

Plants were assessed for mortality each year before the first damage treatment of the season. Removal of aboveground biomass commenced during the 2009 growing season and continued annually for a total of 6 yr. Damage treatments that were repeated within the growing season occurred at monthly intervals toward the end of each calendar month. Plants that were clipped, which was a surrogate for mowing, had all stems cut 8 cm above the soil surface either once (June), twice (June, July), or four times (May, June, July, August). The clipped-once timing was based on the optimal time as determined by McKague and Cappuccino (2005) to minimize seed production from a single clipping, although they cut their plants at the soil surface. Plants that received 50% artificial defoliation had all the leaves cut in half, perpendicular to the leaf axis, so that 40 to 60% of the leaf was removed, and also had all stem tips cut just below the second node. With two rounds of 50% defoliation, only new leaves produced after the first defoliation were cut in half, and any new stems produced had their stem tips removed. Plants that received 100% artificial defoliation had all the leaves cut off and all stem tips removed. With two rounds of 100% defoliation, all new leaves and stem tips were removed. Removal of stem tips was to simulate feeding damage that often occurs to the apical meristem by herbivorous insects (Schat and Blossey 2005; Schooler et al. 2006). Artificial defoliation occurred either once (July) or twice (June, July). The timing of a single defoliation was based on field observations by Förare (1995) on a defoliating moth of swallowwort, *Abrostola asclepiadis* (Denis & Schiffermüller) (Lepidoptera: Noctuidae).

Mature follicles (i.e., those that had begun to turn yellow but before dehiscence) were collected annually from all plants. Follicle collection typically began in August and continued at least weekly until either harvest of the plants (mid-September) or a hard frost for nonharvested groups of plants (typically mid-October). Follicles were retained for biomass only from plants that were harvested that season. In the case of year 6 plants, all follicles were counted each season, and up to 10 follicles were randomly sampled from each plant for further processing, except for the first year of the experiment in which all follicles were processed. The number of filled (potentially viable) and unfilled (nonviable) seeds per follicle was counted. The viability of a subsample of filled seeds (up to 40 per plant) was determined for each plant every year by cold-wet stratifying the seeds at 5 C for up to 3 mo and then stimulating seeds to germinate under favorable growth chamber conditions (30/15 C light/dark temperatures and 15-h photoperiod). The number of viable seeds per plant was calculated by multiplying the number of follicles per plant, the number of filled seeds per follicle, and percent germination of filled seeds.

Biomass from plants designated for destructive harvest was collected in mid-September. Plants were cut at the soil surface and the aboveground biomass was divided into a follicle and a stem-leaf fraction. Roots were excavated using a tree transplanter (Tree Toad Model M-24, Dassel, MN). The truncated cone of soil that was removed measured 41,385 cm^3. The root crown and roots were separated from the soil and washed, and the number of crown buds was counted. The biomass fractions were dried at 65 C for at least 7 d and weighed for dry mass. In mid-September, the year 6 plants were assessed for mortality, and the maximum stem length was measured. The number of stems and axillary branches also were counted. Reproductive data were collected all 6 yr of the experiment, whereas vegetative data were collected for only 5 yr (data not collected in 2013).

Statistical Analyses. We were unable to use data from eight plants because they died after the 2008–2009 winter from frost heaving. Data were transformed as needed using the logarithmic or square root transformation to improve normality and homogeneity of variance. Stem dry mass, follicle dry mass, total aboveground dry mass, root dry mass, and the number of crown buds per plant were analyzed by analysis of covariance with the initial fresh weight of the rootstock serving as the covariate (PROC MIXED, SAS 9.4, SAS Institute Inc., Cary, NC). Stem length and the number of stems, axillary branches, follicles, and viable seeds per plant were analyzed by a repeated measures analysis of covariance using an unstructured covariance structure (PROC MIXED). Stepwise removal of nonsignificant interaction terms was used to determine the best model for each parameter. Results for stem dry mass were similar to aboveground dry mass, and results for follicle dry mass and number per plant were comparable to viable seeds per plant, so they are not shown. Preselected groups of means were compared using Fisher's protected LSD test with the SLICE option and a modified Bonferroni correction (based on the actual number of comparisons being made for each parameter rather than all possible comparisons). Standard errors for back-transformed data were approximated using the methods of Deming (1964).

Results and Discussion

Swallowwort Biomass. No plants died after 6 yr of the different artificial defoliation or clipping treatments. Aboveground biomass (stems, leaves, and follicles) significantly increased over time for the control plants and decreased for plants clipped four times (Damage by Year interaction, $F_{21,274} = 4.70$, $P < 0.001$; Figure 1A). Other damage treatments did not differ in biomass over the 6 yr, although trends for an increase (50% defoliation once or twice, 100% defoliation once), decrease (clipped twice), or possible stasis (100% defoliation twice, clipped once) in biomass were evident (Figure 1A). During the first year (2009), most treatments were similar to each other in aboveground biomass, and this generally remained true in later years (Figure 1B). Starting the second year (2010), plants clipped four times had less biomass than other plants, and by the fourth year (2012) plants that had been clipped twice also were smaller than some other damage treatment groups. By the sixth year (2014), control plants were only significantly larger than plants clipped two or four times or that had received two rounds of 100% defoliation (Figure 1B). The percentage of aboveground dry mass in year 6 for black swallowwort follicles was approximately 0% (clipped two or four times), 29% (clipped once), or 50% (all other treatments). For pale swallowwort, the percent contribution of follicles to the aboveground biomass was approximately one-half the values given above for black swallowwort, except that plants clipped two or four times also produced no or very few follicles. Pale swallowwort follicles were observed throughout the experiment to be about one-half or less the length of follicles typically seen in wild stands (normal follicle length 59 $\pm$ 7 mm, $n = 10$), whereas black swallowwort follicles appeared to be of normal size. This may indicate that site conditions were suboptimal for pale swallowwort follicle development, although the specific reason is unknown.

Root dry mass was generally greater for pale swallowwort plants in the sixth year of damage compared with the first, and sometimes second, year within most damage treatments. A similar, albeit weaker, pattern was observed for black swallowwort (Species by Damage by Year interaction, $F_{21,246} = 1.79$, $P = 0.020$; Figure 2). Although root mass in most damage treatments appeared to increase over the 6 yr of the experiment, it is unclear whether plants in the 100% defoliation twice (both species) and clipped twice (black swallowwort) treatments were beginning to decrease in root mass. However, root dry mass of plants that were clipped four times showed no increase in size during the experiment (Figure 2). Within a given year, there was substantial overlap among most damage treatments. Not until the fourth year did plants with smaller root masses (such as clipped four times) start to differ consistently from treatments with large root masses (comparison of means not shown, but see Figure 2). In a previous field study by McKague and Cappuccino (2005), clipping pale swallowwort once at the soil surface resulted in less stem biomass compared with nonclipped plants but had no effect on the root mass of mature plants. Previous short-term defoliation studies of swallowwort have given variable results. Milbrath (2008) reported reductions in both aboveground and root dry mass with artificial defoliation in a greenhouse study, particularly with two rounds of 100% defoliation. However, these plants had small root masses at the start of the experiment. Defoliation of swallowwort by different insects reduced aboveground biomass but did not affect root biomass (Maguire et al. 2011; Weed and Casagrande 2010; L.R.M. and J.B., unpublished data).

Aboveground biomass, averaged over years and damage treatments, was greater for black swallowwort (23.6 $\pm$ 1.7 g) than for pale swallowwort (15.2 $\pm$ 1.1 g; $F_{1,274} = 18.70$, $P < 0.001$). In contrast, pale swallowwort generally had a larger root mass than black swallowwort in the latter years of the experiment (Figure 2). For example, the root dry mass of control plants was 284.66 $\pm$ 67.89 g and 87.34 $\pm$ 20.81 g for pale and black swallowwort, respectively. As noted above, a sizeable percentage of aboveground biomass for black swallowwort is from seeds. Black swallowwort seeds are approximately three times greater in mass than pale swallowwort seeds (Milbrath 2008). Milbrath (2008) also reported greater aboveground and follicle dry mass for black swallowwort, and greater root dry mass for pale swallowwort, than for its congener. Reported root : shoot ratios

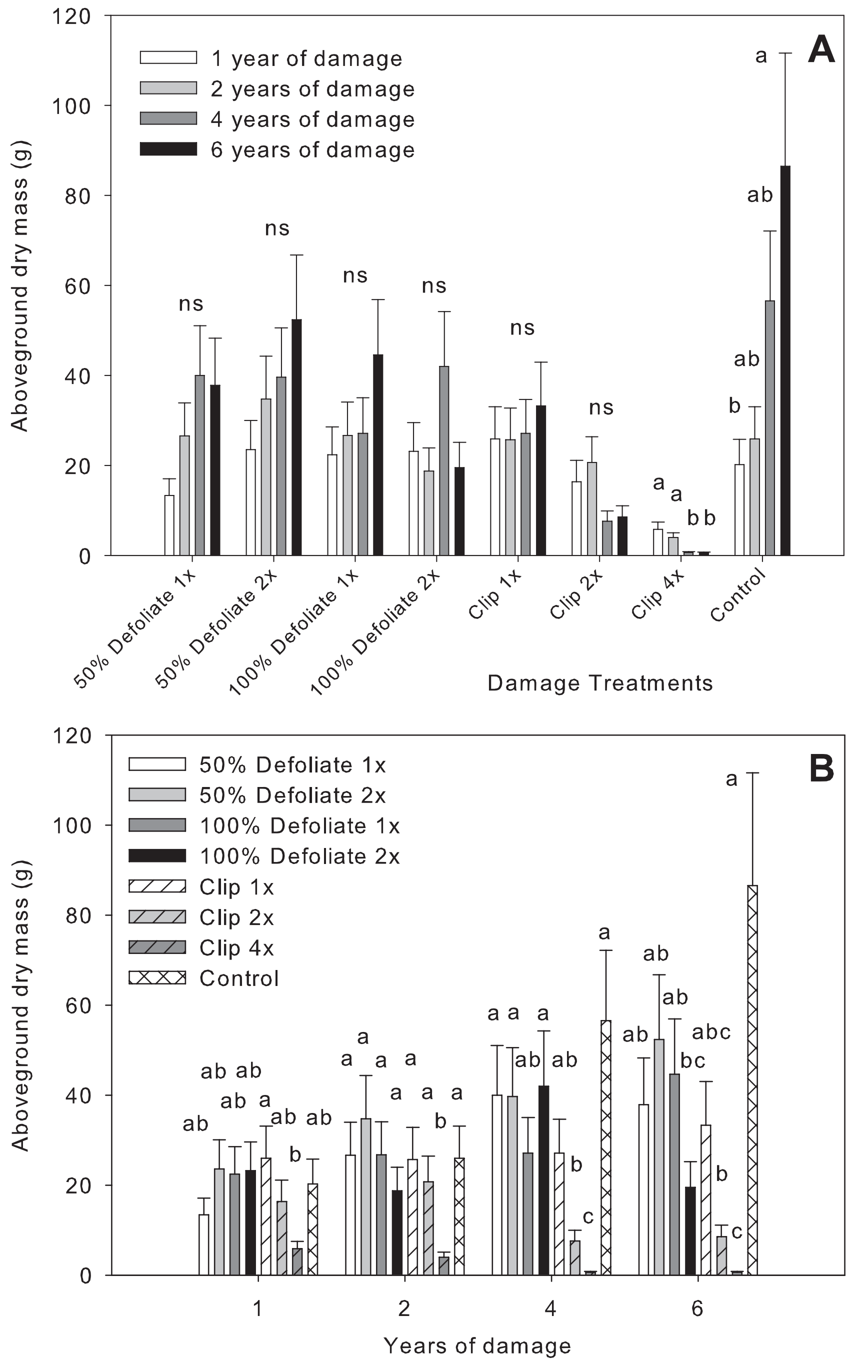

Figure 1. Mean (+ SE, back-transformed) aboveground dry mass for black and pale swallowwort plants receiving eight types of damage each year for up to 6 yr (see text for full damage descriptions). Bars denoted by the same letter are not significantly different (A) within each damage treatment or (B) within each year of damage (Fisher's protected LSD test, $P > 0.05$). ns indicates no significant differences.

for pale swallowwort have been near or > 1, whereas for black swallowwort, they have been < 1 (McKague and Cappuccino 2005; Milbrath 2008). Nevertheless, these differences in resource allocation do not appear to have affected the resulting plant performance of individual plants under the damage regimes imposed, even after several years.

Vegetative Growth. The number of root crown buds per plant increased significantly in the fourth year of damage compared with the first and second years but only differed between the two swallowwort species in the sixth year (Species by Year interaction, $F_{3,295} = 3.18$, $P = 0.024$; Figure 3). Pale swallowwort plants had more than 100 crown buds in the sixth year compared with 68 crown buds for

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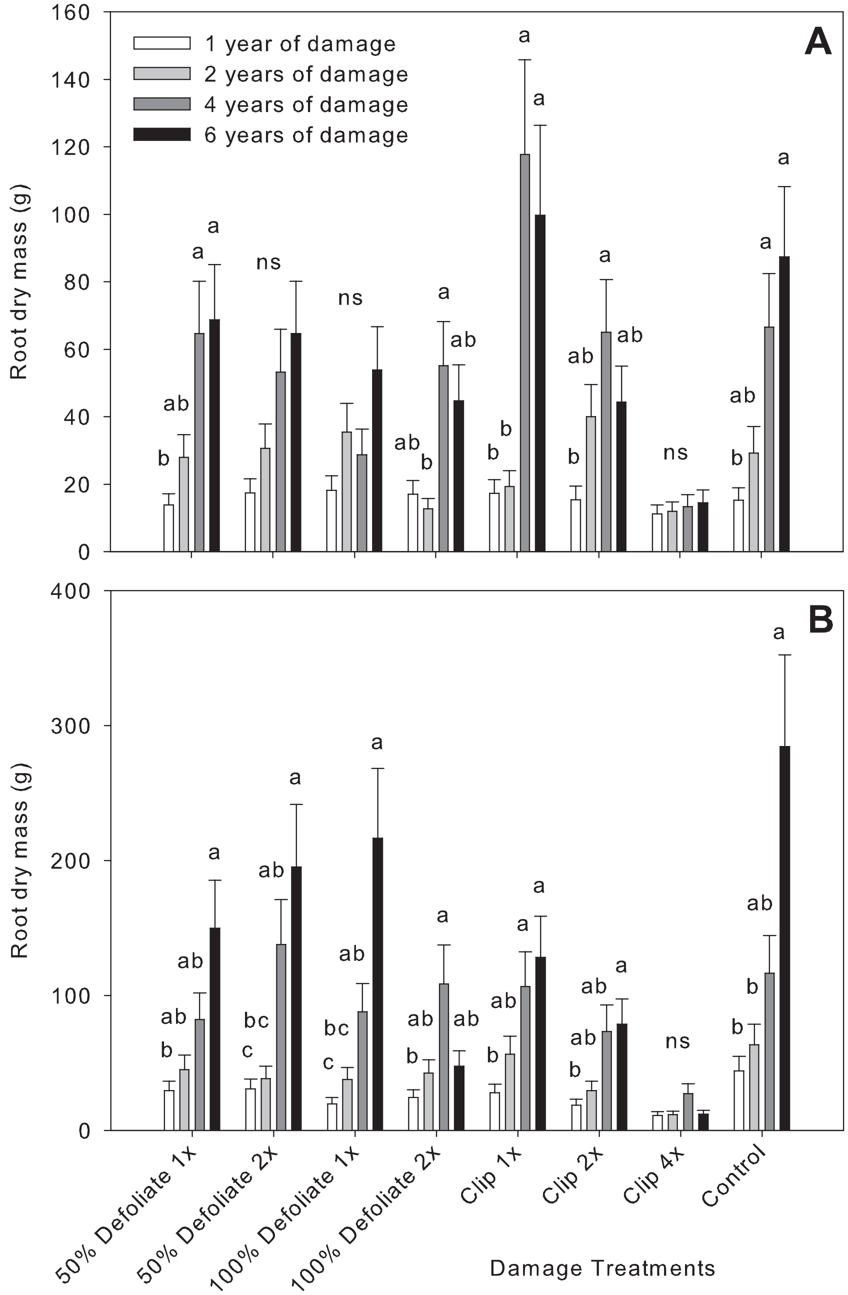

Figure 2. Mean (+ SE, back-transformed) root dry mass for (A) black swallowwort and (B) pale swallowwort plants receiving eight types of damage each year for up to 6 yr (see text for full damage descriptions). Bars denoted by the same letter are not significantly different within each swallowwort species and damage treatment combination (Fisher's protected LSD test, P > 0.05). ns indicates no significant differences.

black swallowwort. Averaged over years and species, plants clipped four times had fewer crown buds (26.7 ± 3.3) than plants from all other damage treatments (mean values 47 to 56; $F_{7,295} = 5.29$, $P < 0.001$). Crown buds are the source of the following year's stem number. Stem number per plant generally increased annually or every other year within most damage treatments (Damage by Year interaction, $F_{28,151} = 2.24$, $P = 0.001$; Figure 4). Plants clipped four times showed no significant increase in stem number. Also, plants completely defoliated twice appeared not to increase in stem number the last few years of the experiment (Figure 4). Stem number did not differ among damage treatments within years until the last year—control plants and plants clipped once had more stems than plants clipped four times (means separation not shown). Stem number did not differ between species until the last year (Species by

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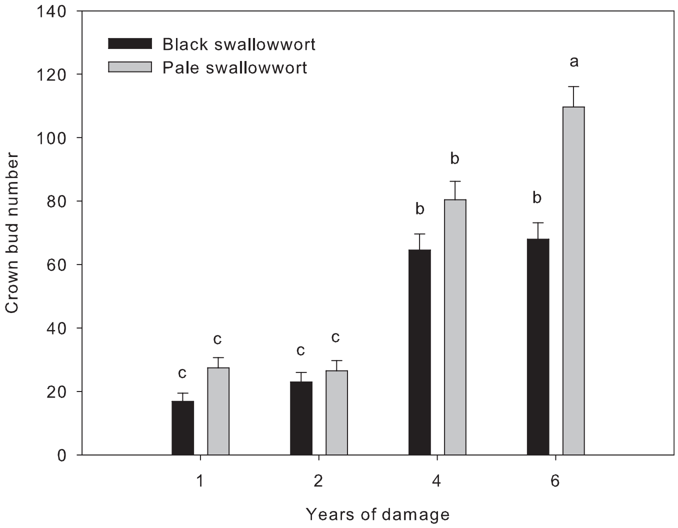

Figure 3. Mean (+ SE, back-transformed) number of crown buds for black and pale swallowwort averaged over eight types of damage that plants received each year for up to 6 yr. Bars denoted by the same letter are not significantly different (Fisher's protected LSD test, P > 0.05).

Year interaction, $F_{4,66.4} = 9.71$, $P < 0.001$). Both species had 5.1 ± 0.3 stems in year 1 (2009), which increased to 13.1 ± 1.3 (black swallowwort) or 23.7 ± 1.3 (pale swallowwort) stems by year 6 (2014). This represents a vegetative expansion of 1.6 and 3.7 stems plant^{-1} yr^{-1} for black and pale swallowwort, respectively, averaged across all damage treatments, which is similar to the range of values reported by Averill et al. (2011) for undamaged plants of either species in the field.

Within each species and damage treatment, maximum stem length at harvest was generally not different among years (Species by Damage by Year interaction, $F_{28,131} = 1.94$, $P = 0.007$; data not shown). Within years, most plants from the various species and damage treatment combinations also overlapped in stem length (averaging 60 to 135 cm), with the general exception that shorter plants occurred in the clipped treatments (e.g., < 20 cm when clipped four times). The number of axillary branches per plant fluctuated or did not differ over time for most damage types, except that it appeared branching increased to some extent for plants clipped once or twice (Damage by Year interaction, $F_{28,149} = 5.66$, $P < 0.001$; Figure 5). Within years, plants that were completely defoliated twice or clipped four times (early years) or clipped twice (later years) usually had more branches than control plants or those receiving 50% defoliation (means separation not shown). Minor differences existed in axillary branching among damage treatments within species (Species by Damage interaction, $F_{7,59} = 3.68$, $P = 0.002$; data not shown). Other studies have shown increased branching with increased frequency of damage

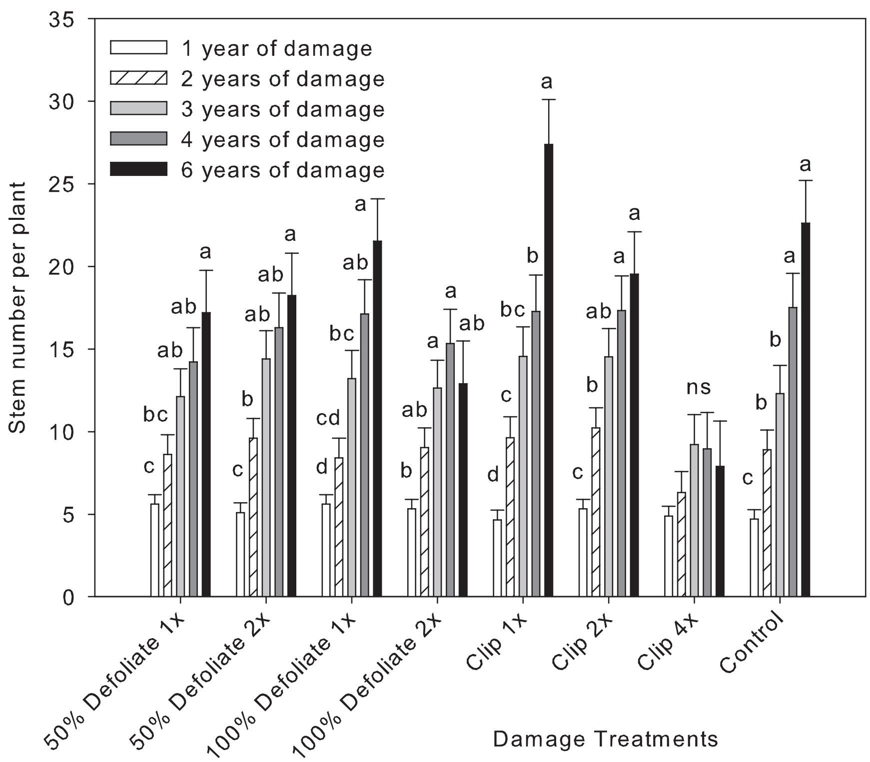

Figure 4. Mean (+ SE) number of stems for black and pale swallowwort plants receiving eight types of damage each year for up to 6 yr (see text for full damage descriptions). Bars denoted by the same letter are not significantly different within each damage treatment (Fisher's protected LSD test, P > 0.05). ns indicates no significant differences.

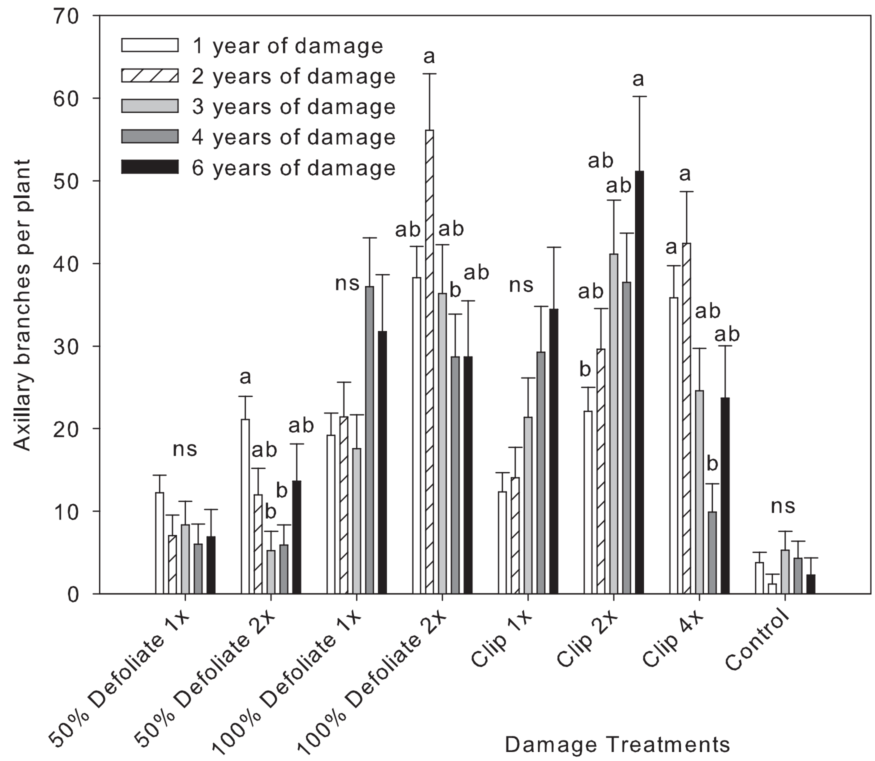

Figure 5. Mean (+ SE, back-transformed) axillary branches for black and pale swallowwort plants receiving eight types of damage each year for up to 6 yr (see text for full damage descriptions). Bars denoted by the same letter are not significantly different within each damage treatment (Fisher's protected LSD test, $P > 0.05$). ns indicates no significant differences.

to apical meristems (Milbrath 2008; L.R.M. and J.B., unpublished data). Branching is a common form of compensation to damage (Strauss and Agrawal 1999; Trumble et al. 1993).

Swallowwort Reproduction. Viable seed production by black swallowwort was generally not different over years within damage treatments (Figure 6A). Seed production was highest for a few treatments in the third year. For pale swallowwort, control plants and those receiving 50% defoliation (once or twice) produced more seeds by the sixth year relative to at least the first year, but this was not the case for other damage treatments (Species by Damage by Year interaction, $F_{35,146} = 3.22$, $P < 0.001$; Figure 6B). For both species, plants clipped twice produced few viable seeds (0 to 30 seeds per plant on average depending on the year), and those clipped four times produced no seeds. Within years, seed production was quite variable, resulting in large overlap among species and damage treatments (means separation not shown). For example, in the sixth year, undamaged pale swallowwort only produced significantly more seeds than pale swallowwort that had been clipped (all frequencies) or completely defoliated twice. Undamaged plants of pale swallowwort often cease flowering by early August, whereas black swallowwort can continue to flower even up to the first hard frost of the season (personal observations). Nevertheless, the reproductive output of swallowwort plants in natural stands is generally similar between the two species (Averill et al. 2011). Our results would additionally indicate that nonlethally damaging plants, apart from clipping (or mowing) two or four times at 8 cm, does not appreciably alter seed production. This contrasts with the study of McKague and Cappuccino (2005) in which a single clipping at ground level, properly timed, could prevent seed production. By clipping at 8 cm in our study, which is a common mowing height, the plants could more quickly regrow and flower from axillary buds. Doubleday and Cappuccino (2011) also showed that frequency of artificial defoliation (once or twice) did not affect seed output of pale swallowwort growing in full sun. Although they also reported that an increasing percentage of leaf removal could reduce seed production, this was only observed in one out of 2 yr.

Pale and black swallowwort display a high tolerance to aboveground tissue loss, whether by artificial defoliation or clipping, in high-light environments without plant competition. Whether this would be the case with increased intra- or interspecific plant competition is currently unknown. Four clippings per season was the only type of damage that consistently prevented an increase in vegetative growth and biomass and eliminated seed production over the 6 yr of our study. Nevertheless, root biomass did not decline from

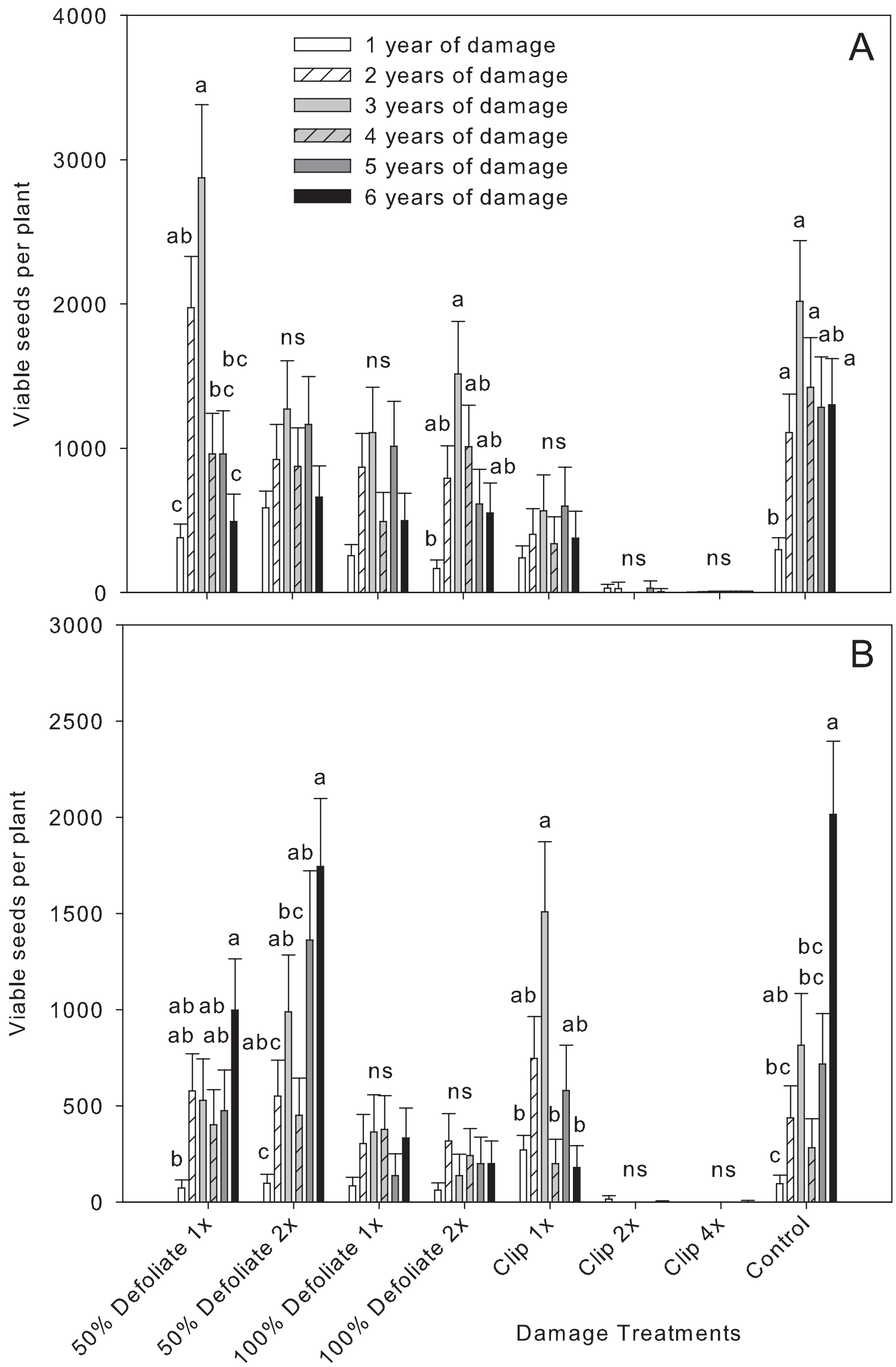

Figure 6. Mean (+ SE, back-transformed) viable seeds per plant for (A) black swallowwort and (B) pale swallowwort plants receiving eight types of damage each year for up to 6 yr (see text for full damage descriptions). Bars denoted by the same letter are not significantly different within each swallowwort species and damage treatment combination (Fisher's protected LSD test, $P > 0.05$). ns indicates no significant differences.

its size in the first harvest year, nor did any plants die from the treatment, suggesting that if this high-frequency clipping (mowing) were subsequently stopped or reduced in frequency, both swallowwort species could begin enlarging their root mass and reproducing. It is currently unknown how many years of this particular treatment would be needed to observe a significant reduction in root biomass and mortality. Other researchers have noted that less frequent clipping is not effective for preventing growth of mature pale swallowwort plants, although it may help reduce seed production (Averill et al. 2008; Christiansen 1998; DiTommaso et al. 2013; McKague and Cappuccino 2005). Our study confirms that this pattern holds over longer periods of management and for both swallowwort species. Clipping twice per season, but not once, greatly reduced seed output but did not prevent it, also noted by Averill et al. (2008), and should be considered a minimum frequency of mowing for this purpose. Further refinement of the timing of the two mowings should be investigated to prevent all seed production.

Given previous concerns over the effectiveness of mechanical control for swallowworts, it is fair to question the efficacy of a defoliating insect as a biological control agent, especially because defoliation might not be as destructive to a plant as mowing (e.g., McKague and Cappuccino 2005). Many defoliating insects have been used as biological control agents, including against perennial weeds, with varying degrees of suppression achieved (Winston et al. 2014). Currently, only one agent, the defoliating moth *Hypena opulenta* (Christoph) (Lepidoptera: Erebidae), has been released (in Canada) for swallowwort biological control (Young and Weed 2014). Previous simulated and real herbivory studies with swallowwort indicated minor to large effects on plant growth and reproduction (Doubleday and Cappuccino 2011; Maguire et al. 2011; Milbrath 2008; Weed and Casagrande 2010, Weed et al. 2011a). Artificial or simulated herbivory studies are generally considered representative of real herbivory when measuring plant performance (Hjältén 2004; Lehtilä and Boalt 2004; Raghu and Dhileepan 2005). However, any type of study of a short-term nature, or those not conducted in the field, have been criticized for how well their results apply to field populations of plants under longer time frames (Hunt-Joshi and Blossey 2005; Rayamajhi et al. 2010). The most severe artificial defoliation treatment that we used was to simulate a bivoltine insect that could completely defoliate swallowwort twice every season. Such damage may have limited biomass, stem number, and seed output in some cases by the sixth year relative to undamaged plants. However, a substantial decline in plant size or vigor was clearly not evident for either pale or black swallowwort. We would likely need at least another 2 to 4 yr to confirm whether such an outcome could occur. However, the annual increase in root dry mass and stem number for the remaining defoliation treatments, which involved less frequent or less amounts of leaf removal, calls into question the potential efficacy of a defoliating insect against open field populations of swallowworts. This result appears to be the same for both swallowwort species, despite known differences between the two species mentioned previously (resource allocation patterns, seed size, flowering phenology). Whether other stressors, such as plant competition or other forms of herbivory, would enhance defoliation damage is currently unknown. No other biological control agents currently are available for release against field infestations of swallowwort. At present, we expect land managers will be primarily reliant on traditional control tools for swallowwort control in high-light environments.

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