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Consequences of Density Dependence for Management of a Stage-Structured Invasive Plant (Alliaria petiolata)

ELEANOR A. PARDINI,[1] BRITTANY J. TELLER AND TIFFANY M. KNIGHT
Department of Biology, Washington University in St. Louis, St. Louis, Missouri 63130

ABSTRACT.—Management of invasive species often targets a particular life stage in structured populations. Evaluating the success of management requires measuring the survivorship and reproductive success of the targeted stage class, as well as assessing the possibility for increased fitness in the non-targeted stage class due to a release from density dependence. Management of the invasive biennial, *Alliaria petiolata* (garlic mustard) focuses on removing adults by pulling or clipping and is applied early or late in the reproductive season. We evaluated the effectiveness of different management types (unmanaged, clipped, pulled) and timing (early or late) on survival and fitness of targeted adult plants and non-targeted co-occurring juveniles. Viable seeds were produced by adults that were unmanaged, pulled early in the season and clipped at midheight early in the season. Unmanaged and pulled adults produced significantly more seeds than clipped plants; unmanaged plants produced seeds that were significantly heavier than seeds from clipped or pulled plants. Germination was lower for seeds from pulled plants than for seeds from unmanaged or clipped plants. The clipping treatment was most successful at reducing fecundity, but also resulted in the highest survivorship of co-occurring juveniles. Our study highlights the necessity of examining fitness of plants in the non-targeted life stage in order to fully evaluate the effectiveness of different management techniques. These results should be applicable to management of other stage-structured invasive species.

INTRODUCTION

Invasive plants threaten native plant species and the ecosystem functioning of plant communities (Mack *et al.*, 2000). In addition to the ecological problems caused by invasive plants, significant economic costs are associated with management activities to prevent further spread, control, eradicate and restore natural communities (Pimentel *et al.*, 2000, 2005). For example, in the United States, *Lythrum salicaria* (purple loosestrife) costs $45 million annually in forage losses and control costs (Pimentel *et al.*, 2000). Ecologists and land managers strive to find efficient methods to reduce the abundance and distribution of invasive plant species.

Many invasive species have stage-structured populations (*e.g.*, seedling, sapling and adult trees), and often only a single stage class the focused of management efforts. Effective management of a stage-structured invasive species depends on: (1) how effective management is at causing mortality in the targeted stage class, and (2) the effect of that management on individuals in the non-targeted stage class. We expect that in many cases a management technique that causes the intended mortality on the target stage class may inadvertently facilitate the non-targeted stage class due to a release of these individuals from density dependence. In order to evaluate the effectiveness of management in stage structured populations, the effects of management on all stage classes must be considered.

Management of invasive biennial and perennial species often focuses on adult plants, since these are easier to locate, and because preventing adults from reproducing is expected

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[1] Corresponding author: Telephone: (314) 935-7868; FAX: (314) 935-4432; email: epardini@wustl.edu

to control the spread of the population (*e.g.*, Sheppard *et al.*, 2002). For example, management of the invasive Brazilian pepper (*Schinus terebinthifolius*) focuses on adult trees, and involves cut-stump (cutting trees down and treating the stumps with herbicide) or basal bark (herbicides that pass through tree bark) applications (Doren *et al.*, 1991). Some treated adult plants can re-sprout and reproduce, causing the management practice to be ineffective. In addition to the type of management, the timing of application can also affect the effectiveness of the application. For example, in Brazilian pepper, basal bark treatments are most effective at killing the adult trees when applied while the trees are flowering (Doren *et al.*, 1991).

Although management of adults may reduce their ability to reproduce, there is little known about its effects on individuals in other stage classes. If the fitness of individuals is density-dependent, then removal of adults in the population might result in an increase in the growth, survivorship and fertility of unmanaged adults and juveniles in the population (Ratikainen *et al.*, 2008; Weiner, 1990). Strong density dependence has been demonstrated in several invasive plant populations, such as the woody species *Cytisus scoparius* (Paynter *et al.*, 2003) and *Mahonia aquifolium* (Auge and Brandl, 1997), and the herbaceous species *Alliaria petiolata* (Winterer *et al.*, 2005), *Brassica tournefortii* (Trader *et al.*, 2006) and *Tripleurospermum perforatum* (Buckley *et al.*, 2001). These studies have typically focused on density-dependent fitness of plants within a single life stage. We know little about the effects of removing adults on plants in other stages (but *see* Myers *et al.*, 1989; Winterer *et al.*, 2005). In a notable study, Myers and colleagues demonstrated that experimental removal of rosette and flowering *Centaurea diffusa* resulted in increased seedling survival and growth, and no net decrease in total plant density by the end of one season (Myers *et al.*, 1989).

Evaluating the success of management requires measuring the survival and reproductive success of the targeted stage class, as well as, assessing the possibility for increased fitness in the non-targeted stage class due to a release from density dependence. However, to date, few studies have considered all of these relevant response variables simultaneously. Here, we evaluate all of these responses in the invasive biennial plant, garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande). *Alliaria petiolata* was introduced to North America from Europe and was first recorded in New York in 1868 (Nuzzo, 1993a). It has since spread across Canada and has become well established in northeastern and midwestern United States (Refer to Nuzzo, 2000). This species experiences little tissue loss due to herbivory in North America (Blossey *et al.*, 2001), is capable of self-pollination (Anderson *et al.*, 1996; Cruden *et al.*, 1996) and possesses seed dormancy (Baskin and Baskin, 1992), so that once it establishes in a site, it is difficult to eradicate. It readily invades and dominates forest understories and has been associated with low plant diversity, decreased habitat suitability and interfering with native butterfly oviposition (reviewed in Blossey *et al.*, 2001; Nuzzo, 2000).

Management strategies have included manual removal of adult plants by clipping the above-ground portion of the plant or by pulling the entire plant out of the ground (Nuzzo, 1991). Clipped adult plants may be able to resprout because the entire taproot remains intact. Uprooted adults left at the site (*i.e.*, not removed in garbage bags) may be able to set seed before they die by using stored resources, particularly if the management occurs late in the season when fruits are nearly ripe (Solis, 1998). In addition, density dependence occurs in *Alliaria petiolata* (Winterer *et al.*, 2005), and thus removal of adults may facilitate juveniles. In this study, we quantified how the type of management and its timing affect reproductive success (quantity and quality of offspring produced) of adult *A. petiolata*, and how the management of adults affects the survival of the non-targeted stage class (juveniles).

METHODS

STUDY SPECIES AND SITE

Alliaria petiolata (Brassicaceae) is an obligate, biennial herb. Seeds germinate in early spring and juveniles form small basal rosettes during the first year. During the second year, individuals reach reproductive maturity and bolt, producing one to several flowering stems (up to 16, EAP and TMK, pers. obs.). Seeds require cold stratification for germination. Germination rates of 12–100% have been reported for garlic mustard seeds (Anderson *et al.*, 1996; Baskin and Baskin, 1992; Byers and Quinn, 1998; Cavers *et al.*, 1979; Davis *et al.*, 2006; Roberts and Boddrell, 1983). Survival of seeds in the seedbank is 0.95; estimates of germination from the seedbank range from 0.02 to 0.45 (Davis *et al.*, 2006). At our study site, adults flower in Apr. and May, set seed Jun. and Jul. and die in late summer. Single-stemmed plants produce an average of 22 fruits and multi-stemmed plants produce an average of 164 fruits; mature fruits (siliques) produce an average of 17 seeds that are shed around the maternal plant in mid to late summer (EAP, BJT and TMK, unpubl.).

Our study was conducted at Washington University's Tyson Research Center, located 40 km southwest of St. Louis, Missouri, USA. Tyson Research Center is a ~800 hectare field station, ~85% of which is second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) deciduous forest. *Alliaria petiolata* first invaded the site in 2000 and has continued to spread throughout the site despite annual management efforts (D. Larson and D. Schilling, pers. comm.). In the locations in which our experiments were conducted, *A. petiolata* was the most abundant plant in the understory.

EFFECTS OF MANAGEMENT AND ITS TIMING ON ADULT PLANTS AND THEIR PROGENY

To determine how management affects survival and reproductive success of adult plants we applied six management treatments randomly to 300 total plants (50 in each treatment). Treatments were (1) unmanaged, (2) pull entire plant and leave it on the ground, (3) clip main stems at ground level early in the growing season, (4) clip main stems at midheight (approximately 15 cm from ground level) early in the growing season, (5) clip main stems at ground level late in the growing season and (6) clip main stems at midheight late in growing season. Treatments 1 to 4 were applied on 26 Apr. 2006 when plants were flowering and in early fruit maturation stages. The late clipping treatments (5 and 6) were applied on 13 May 2006 when plants were finished flowering and fruits were maturing. To minimize microhabitat differences between haphazardly selected plants within the dense invasion, we applied treatments to sets of plants that contained plants of similar height and size (measured as the number of main stems) that were located close to one another (within 0.5 m^2). We were careful to choose plants that were close enough to each other so that they shared the same microhabitat, but not so close that the treatments of neighboring plants would disturb the target individual. To evaluate the effect of size on survival and reproduction, we chose 25 sets of single-stemmed plants and 25 sets of multi-stemmed (5 to 16 stems) plants. Preliminary analysis showed stem number was correlated with total plant fecundity, thus to account for initial plant size we used the number of stems as a covariate of plant size. Clipped stem portions were removed from the site to simulate bagging of managed plants, thus only fruits produced on resprouted stems contributed to fecundity of these plants.

For each plant that produced fruits, we estimated total fecundity (number of seeds) using a relationship between fruit number, fruit length and the average number of seeds per fruit. We recorded the length (mm) and number of seeds in 20 fruits from each of five representative plants in the population to yield the following linear regression: seed number per fruit = 0.4097(fruit length) − 1.7969 (adjusted $R^2 = 0.650$, $F_{1,98} = 184.62$, $P < 0.0001$). Based on this equation, total fecundity was estimated using the number of fruits and mean length of 12 haphazardly selected fruits for each plant. Twenty-seven of the 127 plants that reproduced had less than 12 fruits and we used the same relationship to estimate seed number. Fecundity (number of seeds) was natural log-transformed prior to analysis to meet assumptions of normality and heteroscedasticity. We used analysis of covariance (ANCOVA) to test for differences in total fecundity (SEEDS) among treatments, using initial number of stems (STEMS) as a covariate (PROC GLM; SAS Institute, 2002–2004) using Type III sums of squares because of unequal sample sizes among treatments. Because the LN(SEEDS) × STEMS interaction term was significant, we subsequently evaluated the differences among treatments in adjusted least squares mean fecundity at three different levels of initial plant size (1, 5 and 10 stems) (PROC GLM; SAS Institute, 2002–2004). Additionally, to evaluate the relationship between initial plant size and the number of seeds produced for each treatment, we performed a linear regression of (log-transformed) fecundity against the number of stems within each treatment (PROC REG; SAS Institute, 2002–2004).

To quantify the effects of management treatments on offspring traits, we collected all seeds from all adults that reproduced to examine seed weight, frequency of germination, germination timing and juvenile biomass. Fifty unmanaged, 50 pulled and 27 clipped (midheight, early season) plants produced about 76,500, 64,000 and 1950 seeds respectively. For each treatment, we bulked seeds across plants and haphazardly chose 100 seeds for analysis. Bulking seeds introduces the possibility that seeds could have been produced by the same maternal plant. However, given the high replication of maternal plants, only ~2 seeds out of the 100 are expected to share the same mother in the unmanaged and pulled treatments, and only ~3.7 seeds out of the 100 are expected to share the same mother in the clipped treatment. Thus, we believe this bias should not seriously compromise assumptions of independence for statistical tests. Seeds were individually weighed using a Mettler Toledo MX5 microbalance, and then randomly planted in individual cells (4 cm diam) in flats. Flats were placed in a dark cold room (4 C) on 10 Nov. 2006 for cold stratification.

Flats were removed from the cold room after 90 d on 2 Feb. 2007, placed on greenhouse benches and monitored daily for germination. Once germination appeared to be complete (after 26 d) we clipped, dried and weighed the above-ground portion of all juveniles. Flats with remaining ungerminated seeds were kept outside, and 11 individuals germinated after a late freeze in Mar. The distribution of days to germination for all individuals was, thus, bimodal and individuals from the two phases of germination would have to be treated as separate populations for analysis, with just a few individuals in the second phase. Accordingly, for statistical analysis of seed weight, we considered all seeds, for analysis of the frequency of germinants we considered all germinants, but for analyses of days to germination and juvenile biomass we considered only those individuals from the first phase of germination.

To test for differences among treatments in seed weight, we used analysis of variance (ANOVA) and Tukey's comparisons among least squares means (PROC GLM; SAS Institute, 2002–2004). To test the null hypothesis that the frequency of germinants versus non-germinants was independent of management treatment, we performed a chi-square analysis. We estimated odds ratios for two by two subset contingency tables to summarize any lack of independence among the variables following Agresti (2007) (PROC FREQ; SAS Institute, 2002–2004).

Considering only individuals in the first phase of germination, seed weight and above-ground juvenile biomass were approximately normally distributed with equally distributed variances among treatments. The distribution of number of days to germination was right skewed but transformations did not improve the distribution of the data or spread of variances, thus analyses were performed with untransformed data where necessary. To test for differences among treatments in the number of days to germination, we used ANOVA and Tukey's comparisons among least squares means (PROC GLM; SAS Institute, 2002–2004). To test for differences among the treatments in juvenile biomass, we used a full ANCOVA model, accounting for initial seed weight (WEIGHT) and the number of days to germination (DAYS) (PROC GLM; SAS Institute, 2002–2004). The WEIGHT term was highly insignificant in the full model ($F_{1,93} = 0.02$, $P = 0.8971$) and, along with interaction terms, was removed. The TREATMENT × DAYS interaction term was insignificant, so we proceeded to interpret the individual effects on juvenile biomass. In all cases, effects were treated as fixed and we evaluated significance against Type III sums of squares due to unequal sample sizes. We subsequently performed a linear regression of biomass against the number of days to germination within each treatment (PROC REG; SAS Institute, 2002–2004)

EFFECTS OF ADULT MANAGEMENT ON CO-OCCURRING JUVENILES

To quantify effects of management on target adult plants and co-occurring juveniles, we established an experiment in which combinations of different types of management were applied to a single target adult versus all neighboring (non-target) adult plants within 80 1–m^2 quadrats. Forty randomly selected quadrats were treated early in the season (9 Apr. 2006) and the other 40 quadrats were treated late in the season (9 May 2006). In each quadrat, a target adult plant was left unmanaged, clipped at the base or clipped at midheight; all non-target adults were then either left unmanaged, clipped at ground level or pulled. At the initiation of the experiment, we individually tagged up to 10 juveniles in each quadrat. We measured survival and fecundity of the target adult plants and survival of the tagged juveniles. Due to low sample sizes of target adult plants, we restricted our analysis of this experiment to consider only effects of quadrat-level treatment (of non-target adults) on juvenile survival. Because we tagged juveniles only at the initiation of the experiment, our analysis was further restricted to the 40 early-application quadrats, which included 15, 5 and 20 quadrats in which non-target adults were unmanaged, clipped at ground level (hereafter, clipped) and pulled, respectively. Treatment replication was uneven because the combinations of target and non-target plant management were originally designed for monitoring effects on target adult plants.

Within the 40 quadrats considered, we individually tagged 149, 195 and 49 juveniles in unmanaged, pulled and clipped quadrats, respectively. We recorded survival of those tagged juveniles after 10 d and at the conclusion of the experiment (23 Jun. 2006). Juvenile survivorship was low, thus we pooled juveniles across all quadrats within a treatment and then performed chi-square analyses to test the null hypothesis that the frequencies of survivors versus deaths was independent of management treatment after 10 d and on the final survey date; we estimated odds ratios for two by two subset contingency tables to summarize any lack of independence among the variables following Agresti (2007) (PROC FREQ; SAS Institute, 2002–2004).

RESULTS

EFFECTS OF MANAGEMENT AND ITS TIMING ON ADULT PLANTS AND THEIR PROGENY

Clipping plants at ground level, regardless of timing, effectively killed them; none of these plants resprouted. Of 50 plants that were clipped at midheight early in the growing season,

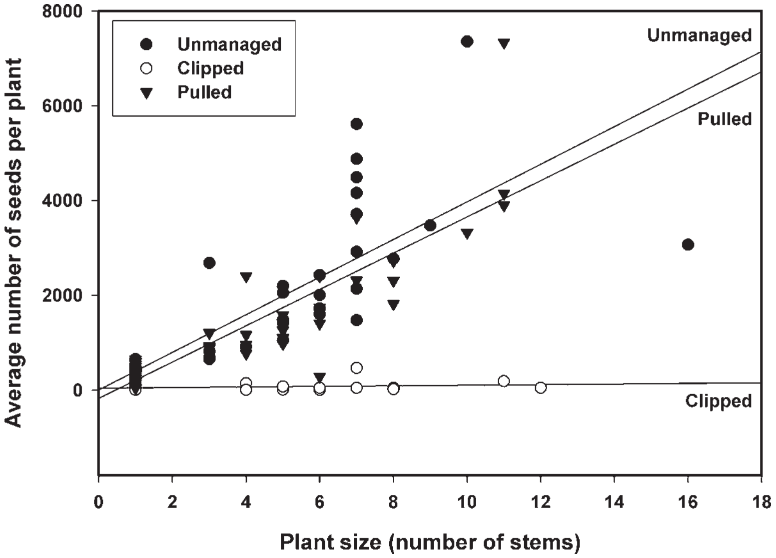

FIG. 1.—A field experiment testing the effects of management type on *Alliaria petiolata* adults demonstrated clipping plants reduced fecundity, and that plant size affected seed production in unmanaged and pulled plants, but not clipped plants. Here, linear regressions on untransformed data within each treatment are presented for ease of visualization

34 plants produced new shoots and 27 of these produced fruits. Of 50 plants that were clipped at mid-height late in the growing season, 1 plant produced new shoots, but died before producing fruits. Among plants that were pulled and left on the ground, none rerooted, but all of them produced seeds, presumably drawing resources from the uprooted taproot. Only plants that were unmanaged, pulled and left on the ground and clipped at midheight early in the season (hereafter, clipped) produced seeds. Unmanaged plants produced an average of 1529.9 seeds (range 138.2 to 7355.1), pulled plants produced an average of 1280.7 seeds (range 39.9 to 7338.1) and clipped plants produced an average of 72.1 seeds (range 2.1 to 467.8). There was a significant interaction between treatment and stem number ($F_{2,120} = 10.93$, $P < 0.001$), indicated by heterogeneous slopes between the unmanaged and pulled treatments versus the clipped treatment (Fig. 1). Comparison of least squares mean fecundity at plant sizes of 1, 5 and 10 stems indicated that unmanaged and pulled plants produced more seeds than clipped plants at all compared plant sizes (Table 1). Plant size (STEMS) explained a significant proportion of variation in total fecundity for both unmanaged and pulled plants (unmanaged, adjusted $R^2 = 0.725$, $F_{1,48} = 130.22$, $P < 0.001$; pulled, adjusted $R^2 = 0.732$, $F_{1,48} = 134.89$, $P < 0.001$; Fig. 1). There was no difference between these two treatments (all comparisons between unmanaged and pulled plants least squares mean fecundity at 1, 5 and 10, stems had *P*-values > 0.5). Linear regression revealed no effect of plant size on fecundity in clipped plants (adjusted $R^2 = -0.016$, $F_{1,24} = 0.61$, $P = 0.442$, Fig. 1).

The weight of seeds produced by adult plants differed among the management treatments ($F_{2,297} = 385.55$, $P < 0.001$). Seeds produced by unmanaged plants weighed almost twice as much as those produced by plants in the pulled and left or clipped at mid-height early in the season treatments (Table 2). The first seed germinated on Feb. 2nd (day

TABLE 1.—Effects of adult management on fecundity (number of seeds). Fecundity was natural log-transformed prior to analysis; least squares means were evaluated at three levels of the covariate, stem number. Back-transformed least squares means are presented here for ease of interpretation. Letters indicate significant differences ($P < 0.001$) among treatments in the least squares means of the transformed data

Treatment	Plant size (number of stems)		
	1	5	10
Unmanaged	357.8[a]	1200.0[a]	5377.6[a]
Clipped	27.9[b]	35.2[b]	47.5[b]
Pulled	330.2[a]	1085.7[a]	4769.5[a]

1) and peak germination across all treatments was on Feb. 8th (day 6). Eleven individuals germinated on 23 Mar. after a late freeze; 10 of these were from clipped plants and one was from a pulled plant. The percent of germination within treatments in the first phase ranged from 23% to 48%; the total percent of germination recorded in the experiment ranged from 24% to 50%. Considering total germination (both phases), chi-square analysis revealed a significant association between management treatment and the frequency of germinants versus non-germinants ($\chi^2_2 = 17.35$, $P < 0.001$). Odds ratio analysis revealed that seeds from unmanaged plants were 2.9 ($\chi^2_1 = 12.50$, $P < 0.001$; 95% CI 1.6–5.3) times as likely to germinate as seeds from pulled plants and seeds from clipped plants were 3.2 ($\chi^2_1 = 14.50$, $P < 0.001$; 95% CI 1.7–5.8) times as likely to germinate as seeds from pulled plants; there was no difference in frequency of germinants between seeds from unmanaged versus clipped plants (Table 2).

Considering only those individuals in the first germination phase, ANOVA indicated there were no significant differences among the management treatments in the number of days to germination (Table 2). The differences in biomass among treatments were not statistically significant (ANCOVA, TREATMENT effect, $F_{2,99} = 2.33$, $P = 0.102$; Table 2). The number of days to germination had a significant effect on juvenile biomass (ANCOVA, DAYS effect, $F_{1,99} = 5.07$, $P = 0.027$); individuals that germinated earlier were larger than those that germinated later (Fig. 2). The regression of biomass against the number of days to germination was significant for seeds from unmanaged plants (adjusted $R^2 = 0.231$, $F_{1,37} = 12.40$, $P < 0.005$) and from clipped plants (adjusted $R^2 = 0.324$, $F_{1,44} = 22.55$, $P < 0.001$), but was not significant for seeds from pulled plants (Fig. 2).

TABLE 2.—Effects of adult management treatment (unmanaged, clipped at midheight early in the season or pulled and left on the ground early in the season) on offspring seed weight, germination and juvenile biomass. For seed weight, $n = 100$ for each treatment and letters indicate significant differences among least squares means for treatments ($P < 0.05$, adjusted for multiple comparisons). For frequency of germinants (of 100 seeds planted in each treatment), letters summarize significant differences ($P < 0.001$) in odds ratios between treatments. There were no significant differences among treatments for days to germination (ANOVA) or juvenile biomass (ANCOVA); treatment means and standard errors are presented and sample sizes for analysis are indicated in brackets

Treatment	Seed weight (mg) (SE)	Frequency of germinants (both phases)	Days to germination (SE)	Above-ground juvenile biomass (mg) (SE)
Unmanaged	1.91 (0.03)[a]	48[a]	6.5 (0.3) [n = 46]	84.5 (5.4) [n = 47]
Clipped	1.09 (0.03)[b]	50[a]	6.2 (0.4) [n = 39]	72.3 (5.1) [n = 41]
Pulled	1.00 (0.03)[c]	24[b]	5.1 (0.3) [n = 21]	71.7 (7.6) [n = 22]

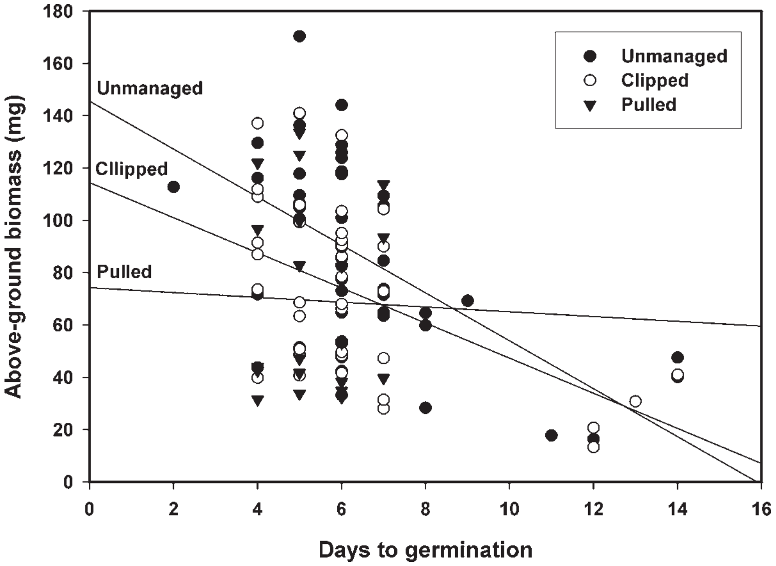

FIG. 2.—Effects of adult management type on offspring traits from an early growth experiment conducted in the cold room and greenhouse. Juvenile biomass was not significantly different among treatments, but juveniles that germinated earlier were larger than those seeds that germinated later. Linear regressions of biomass against the number of days to germination were significant for seeds from unmanaged and clipped plants

EFFECTS OF ADULT MANAGEMENT ON CO-OCCURRING JUVENILES

Frequency of survivorship of co-occurring juveniles after 10 d was independent of management type ($\chi^2_2 = 1.59$, $P = 0.453$), but there was a significant association between management type and total juvenile survival over the course of the entire experiment ($\chi^2_2 = 12.55$, $P = 0.002$; Fig. 3). Odds ratio analysis of total survival revealed that juveniles in quadrats where adults were clipped were 20.3 times as likely ($\chi^2_1 = 14.70$, $P < 0.001$; 95% CI 2.4–168.3) to survive, and in quadrats where adults were pulled were 11.0 times as likely ($\chi^2_1 = 8.31$, $P = 0.004$; 95% CI 1.4–84.5) to survive than juveniles in quadrats where adults were unmanaged (Fig. 3).

DISCUSSION

The goal of invasive species management is to significantly reduce the abundance and distribution of the invasive species, often from natural areas, agricultural fields or transportation corridors. The success of management depends on the particular method used for control, the timing of its use and its effect on the fitness of individuals within all stage classes. One important complication for stage-structured invasive species is that management might harm one life stage but facilitate another. Indeed, in *Alliaria petiolata*, we find that the type of control and its timing significantly differ in reducing the reproduction of adult plants. Further, the most effective treatment for adults (clipping plants at the base) was also the treatment that most facilitated the survival of juveniles in the population. Our results highlight the importance of considering the timing of management strategies and implementing a broad management plan that encompasses all stage classes and multiple years.

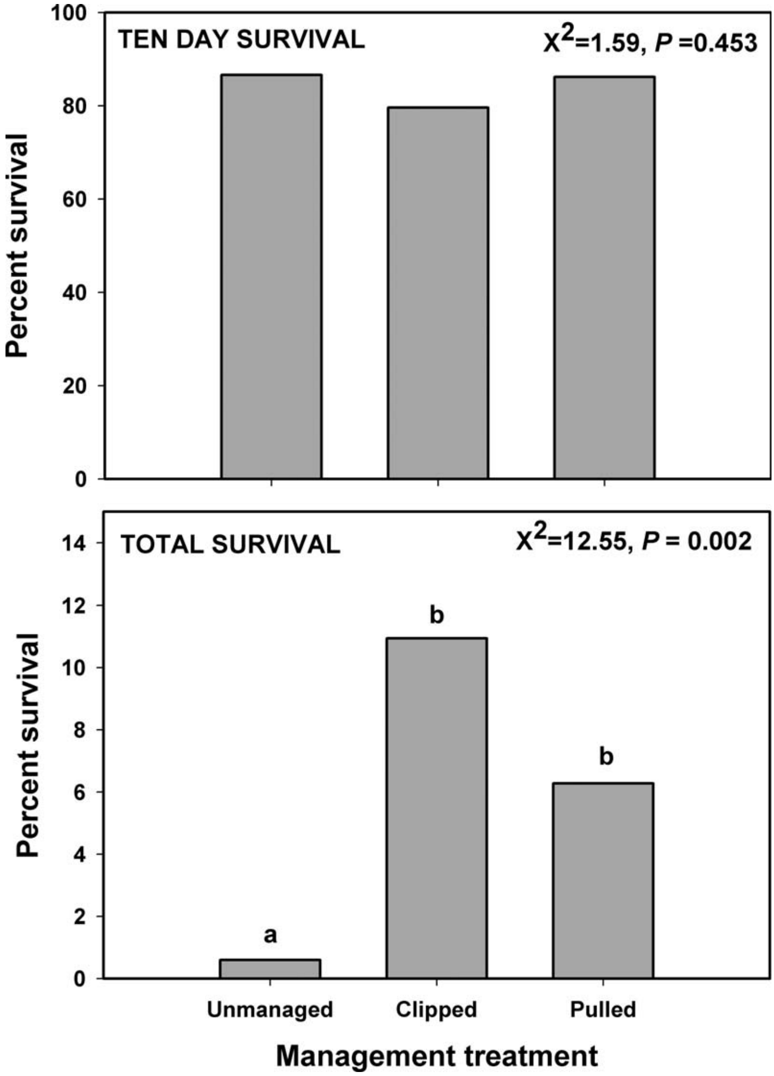

FIG. 3.—Survival of *Alliaria petiolata* juveniles in 40 1-m^2 quadrats where adult plants were unmanaged, clipped at ground level, or pulled. Juvenile survival was low so juveniles were pooled across all quadrats within each treatment. The top panel indicates survival of tagged juveniles 10 d after treatments were applied; the bottom panel indicates total survival of tagged juveniles to end of the experiment. Letters indicate results of odds ratio analysis summarizing the associations between treatment and frequency of total survivors versus deaths. Total juvenile survival was higher in quadrats where adults were removed by clipping or pulling

Adult plants are often targeted for *Alliaria petiolata* management because this species is monocarpic (individuals flower in their second year and then die), and, therefore, if all reproduction in the population can be prevented for several years (to exhaust the seed bank), complete eradication should be possible (Baskin and Baskin, 1992; Nuzzo, 1991;

Nuzzo, 2000). We find that the most effective strategy is clipping plants at their base, which results in complete reproductive failure for adult plants. Our result concurs with that found by Nuzzo (1991), in which clipping at the base resulted in 99% mortality. However, this method is also quite labor intensive, because it requires hand clipping plants. Clipping plants 15 cm above the base is an easier strategy because it can be achieved using a string trimmer. However, as plants clipped early in the season will resprout and produce viable seeds, we find this technique is only successful if applied late in the season. Because at this time fruits are almost fully developed, the clipped stem portions must be collected and removed from the site to prevent seed dispersal; thus, this technique is labor-intensive, as well. Further, the string trimmer is likely to harm other native plant species in the forest understory. Pulling plants and leaving them on the ground does not successfully prevent seed set, even when applied early in the season when plants possess only flowers and immature fruits. We found that pulling plants and leaving them on the ground resulted in no difference in the number of seeds produced relative to unmanaged plants, indicating that this management approach would be wasteful in terms of finances and time. This result may also apply to other short lived perennials and annuals where stored resources of pulled plants result in reproductive success. Our result concurs with that of Solis (1998) which concluded that bagging plants is the only way to effectively prevent pulled adults from successfully reproducing.

Our results from field and greenhouse experiments provide the first quantitative estimates of the effects of different adult management strategies on the number and performance of progeny produced per adult plant. Seeds from pulled and clipped plants weighed half as much as seeds from unmanaged plants, but a lower proportion of seeds from pulled plants germinated relative to clipped and unmanaged plants, which both had about 50% germination. This suggests that pulling had a detrimental effect on seed development. It was interesting to note that about 40% of the seeds from clipped plants germinated in the first phase of germination, followed by 10% germination in the second phase. Seeds of this species display developmental dormancy and require cold stratification for germination (Baskin and Baskin, 1992; Cavers *et al.*, 1979; Lhotska, 1975). Seeds produced by clipped plants were born on stems that resprouted after the early management treatment was applied on 26 Apr.; if these seeds were developmentally delayed, additional cold stratification may have been required, which would have been consistent with a late bout of germination. If these seeds have higher levels of dormancy, they may also result in a longer persistence of the seed bank. While plants that are clipped at ground level or clipped at midheight late in the season will not produce any seeds, plants that are clipped at midheight early in the season can still produce tens of viable seeds. In all, these results demonstrate that management of adult plants must have the goal of preventing any seed production because control strategies that result in significant decreases in seed number and seed weight still allow for high numbers of juveniles in the following year.

Our results demonstrate that *Alliaria petiolata* juvenile fitness is negatively affected by the presence of adult plants, and that the removal of these adult plants increased juvenile survivorship. When adults are not managed, juvenile survivorship is less than 1%. These results concur with those of Anderson *et al.* (1996), Byers and Quinn (1998), Nuzzo (1993b) and Winterer *et al.* (2005). Juvenile survivorship is increased more than six-fold when adult plants are pulled, and more than 10-fold when adult plants are clipped at the base. One possible reason that juvenile survivorship is higher when neighboring adults are clipped rather than pulled could be that pulling causes significant soil disturbance, resulting in mortality of small juveniles.

The mechanism that results in density dependence in *Alliaria petiolata* is not known, and future experiments are necessary to determine whether or not intraspecific competition causes the observed patterns in density dependence. In *A. petiolata* it is possible that plants negatively affect each other through exploitative competition for soil nutrients, water, light or space or through interference competition via their allelopathic chemical production; previous studies suggest that both forms of competition might be important. Juveniles may compete with adult plants for light, since *A. petiolata* is known to have greater photosynthetic rates (Myers and Anderson, 2003), faster growth (Meekins and McCarthy, 2001) and more biomass (Meekins and McCarthy, 2000) in forest edge habitats or experimental treatments with higher light (but see Winterer *et al.*, 2005). In addition, studies have shown that *A. petiolata* fitness may depend on soil moisture (Meekins and McCarthy, 2001) and nutrient availability (Meekins and McCarthy, 2000), suggesting that competition for water and nutrients may be important. The allelopathic chemicals produced by *A. petiolata* have been shown to have direct negative consequences on other plant species (Aminidehaghi *et al.*, 2006; Prati and Bossdorf, 2004) and indirect consequences through alteration of belowground arbuscular mycorrhizal fungi (Stinson *et al.*, 2006); it is possible that these same chemicals result in intraspecific competition.

Successful management of garlic mustard may require focusing simultaneously on both adult and juvenile plants. Juvenile garlic mustard can be successfully managed with chemicals, such as glyphosate (Nuzzo, 1991; Nuzzo *et al.*, 1996). Glyphosate is a non-selective herbicide and will kill native species, particularly when applied in spring. However, because pre-reproductive garlic mustard rosettes emerge from leaf litter earlier in the spring than most native plants species and photosynthesize later in the fall than most native plant species, there may be a window of time in which garlic mustard can be managed with minimal damage to the native flora. The combined effects of chemical and mechanical control with a focus on both life stages of *Alliaria petiolata*, and effects of these treatments on native plant species should be the focus of future research on this plant species.

Our study experimentally demonstrates that management-induced mortality of adult plants may benefit juvenile plants. A similar problem has been considered by Buckley *et al.* (2001) for the annual invasive plant species, *Tripleurospermum perforatum*. They found evidence for strong density dependence among similarly-sized plants in their survivorship and fecundity, and used population models to show that such density dependence means that stronger control measures are necessary to provide significant decreases in the abundance of the species. Many invasive species occur at high densities where individuals likely suffer from strong density dependence. It is likely that one unanticipated effect of invasive species management in this scenario may be a release of surviving individuals from density dependence. Best management practices should broadly include methods that target individuals in multiple life stages in structured populations of invasive plants.

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