

Comparison of the Effect of Early and Late Removal of Second-Year Garlic Mustard (*Alliaria petiolata*) on First-Year Plants and Deciduous Forest Spring and Summer Dominant Herbaceous Groundlayer Species in Central Illinois, USA

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ABSTRACT

Garlic mustard, a biennial Eurasian species, has extensively invaded eastern North American deciduous forests. We studied effects of 3 years (2005–2007) of annual removal of second-year garlic mustard plants on first-year plants and native spring herbaceous species in upland and lowland woods. Treatments compared removal of second-year plants in mid-March (early treatment) or mid-May (late treatment) to a control. We recorded first- and second-year plants and native herbaceous species percent cover on April 19 and 20. First-year plant cover was higher on control than treatment plots; however, in the upland woods only control and late treatment plots differed significantly. First-year plant cover was less in removal than control plots, indicating reduced seed input; however, we found no difference in cover of second-year plants between late treatment and control plots. Results suggest second-year plants strongly compete with younger conspecifics, and their removal decreases first-year plant mortality. Removal of second-year garlic mustard did not significantly affect total cover of native herbaceous species. Second-year plants complete vegetative growth before late May and might impact early developing native species more than later growing species. We tested effect of removal of garlic mustard on native species in 2 phenological categories: spring- and summer-dominant species. We found no treatment effects on summer-dominant species. However, early treatment plots had significantly more cover of spring-dominant plants than late treatment and control in the upland woods. Indicator Species Analysis indicated a majority of spring (75%) and summer (50%) dominant species maximized performance in the early treatment.

Keywords: deciduous forest, herbaceous groundlayer, invasive species, management control, spring and summer dominants

Garlic mustard (*Alliaria petiolata*), a Eurasian native, is an invasive, biennial plant species in deciduous forests of northeastern and mid-western United States (Nuzzo 1991, Blossey et al. 2001). Currently, the plant occurs in at least 37 states in the USA and 5 Canadian provinces (USDA, NRCS 2011). As a shade

tolerant species, it is more common in mesic lowland semi-shaded forest edges than dry mature forest interiors, but it can invade either (Cavers et al. 1979, Meekins and McCarthy 2001, Carlson and Gorchov 2004, Hochstedler et al. 2007) and invades both disturbed and undisturbed sites (Brothers and Spingarn 1992, Nuzzo 1993).

The plant forms a basal rosette during its first year and bolts in March of its second year, producing flowers between mid-March and late May.

Fruits mature from late May into June, and siliques dehisce in mid-July to early October with peak seed rain occurring in August and September (Anderson et al. 1996). Early seed germination and bolting of second-year plants may give garlic mustard a competitive advantage over many native species for light, space, and nutrients (Myers and Anderson 2003).

Garlic mustard has a high seed output compared to most native woodland species. Individual plants can produce hundreds to thousands of

seeds, and annual seed rains of 9,500 to over 100,000 seeds per m² have been reported (Cavers et al. 1979, Anderson et al. 1996, Pardini et al. 2008, Rodgers et al. 2008). Seeds remain viable in soil for up to 10 years (Rodgers et al. 2008); however, most (70% or more) seeds germinate the year following their production (Baskin and Baskin 1992, Raghu and Post 2008). In unmanipulated areas, mortality of first-year plants is high (92–98%), followed by low mortality the second year (Anderson et al. 1996, Byers and Quinn 1998).

Studies of garlic mustard include its effect on native plant communities, competitive abilities, and methods of control (Nuzzo 1991, Meekins and McCarthy 1999, Carlson and Gorchoff 2004, Hochstedler et al. 2007, Bauer et al. 2010), but evidence for garlic mustard's ability to negatively impact the native plant community is mixed. Carlson and Gorchoff (2004) predicted that garlic mustard competes with natives, especially in the spring when its density is high and before the tree canopy is well developed. However, spot herbicide treatment of garlic mustard during the autumn dormant season did not change species richness or diversity. Cover of spring ephemerals increased, but only following the first year of treatment (Carlson and Gorchoff 2004, Hochstedler et al. 2007). McCarthy (1997) found that garlic mustard negatively affected native vegetation, but species diversity between sites with and without garlic mustard differed little. A greenhouse experiment by Meekins and McCarthy (1999) showed that garlic mustard's competitive success varied depending upon the plant species with which it competed. Stinson et al. (2007) found that garlic mustard removal did not change abundance of native functional groups (herbaceous plants, tree seedlings, and shrubs) 2 growing seasons after removal. Species richness was unaffected by variation in natural or experimental density of garlic mustard, but the Shannon

diversity and equitability indices decreased with increasing densities of garlic mustard.

First-year and second-year garlic mustard plants exhibit alternating abundances (Baskin and Baskin 1992, Anderson et al. 1996, Winterer et al. 2005, Bauer et al. 2010). These alternating cycles of abundance have been attributed to the competitive effects of second-year plants on first-year plants (Winterer et al. 2005, Bauer et al. 2010). Pardini and colleagues (2008) reported that presence of adult garlic mustard plants reduced survival of juvenile plants to less than 1% and suggested that management-induced mortality of adult plants may favor juvenile plants.

In this study, we examined competition between garlic mustard and native spring-dominant species including spring ephemerals, and between first- and second-year garlic mustard. Following the experimental procedures of Bauer and others (2010), we experimentally tested the effect of hand removal of second-year garlic mustard on first-year plants and native herbaceous species. Although Bauer and others (2010) showed no effect of garlic mustard removal on native herbaceous species between 2005 and 2007, their sampling occurred in late May and early June, and so primarily examined native species that are dominant in the summer. Because garlic mustard has an early phenology, we hypothesized that second-year garlic mustard would negatively impact: 1) native species that complete most or all of their growth and flower by mid-May; and 2) first-year garlic mustard. We predicted that: 1) cover of spring-dominant native species would be greater with early removal treatment (early to mid-March) than either late removal treatment (mid-May) or control treatment; 2) summer-dominant species would exhibit no treatment effects; and 3) first-year garlic mustard would have less cover in early and late treatments due to reduced seed input than in control treatments, but survivorship of first-year garlic mustard

to maturity would be greater in late treatment plots than in control plots.

Methods

We conducted research at the Park-Lands Foundation 300-ha Merwin Nature Preserve located in McLean County, Illinois, 30 km northeast of Normal, IL. Prior to acquisition by the Foundation, the land was selectively logged and grazed. Since 2005, second-year garlic mustard has been hand removed annually from experimental plots, and data has been collected on garlic mustard and native vegetation from 2004 (pretreatment data) to 2007. We followed the methods of Bauer et al. (2010) on the same study plots.

Within the Merwin Preserve, we selected 2 study sites, an upland woods and a lowland woods located in a low-lying area near a creek. Portions of the lowland woods occasionally flood. Within both woods, 2 blocks, each approximately 23 m by 30 m contained 60 plots laid on parallel transects 5 m apart. There were 5 transects in both upland woods blocks, and in the lowland woods there were 5 transects in Block 2 and 7 transects in Block 1. Permanent treatment plots were located along transects at 2.5-m intervals and randomly 0 to 50 cm to the left or right of the transects. A 50-cm by 50-cm sampling plot was located in the center of each 2.5 m by 2.5 m treatment plot, and the center of the plot was marked with a 10-cm galvanized nail that was pushed through a 1.5-cm washer.

One-third of the plots within each block were randomly assigned to the control, early, or late treatment. A pretreatment sample of the plots taken in 2004 yielded no significant differences among plots assigned to treatments for cover of native species or first- or second-year garlic mustard. Beginning in 2005, we carefully pulled from the soil second-year plants in early and late treatment plots to minimize disturbance and removed them from the site. We removed second-year plants

from early treatment plots on March 14 and on May 13 2008 for late treatment plots. We did not remove second-year plants from control plots.

Data Collection

We conducted sampling of percent cover on April 19–20 2008. We chose the earlier sampling date to determine effect of removal of second-year garlic mustard on dominant spring native species. We recorded plants by species, except for *Carex* and *Viola*, which were grouped by genus. We included only plants rooted in the sampling plot. We divided the 50 cm x 50 cm plot into 4 quadrants with two 50-cm wooden dowels to facilitate cover estimates. In earlier sampling, we usually estimated cover down to 1% using a square decimeter ($\text{dm}^2 = 100 \text{ cm}^2$) quadrat that was placed over single plants or small clusters of plants as a guide. The dm^2 quadrat had an area equal to 4% of the sampling plot. We recorded cover less than $\frac{1}{4}$ of the area of the dm^2 quadrat as <1% and coded in the data as 0.5% cover. Because of the small size of first-year garlic mustard plants at the time of sampling, we estimated percent cover of first-year garlic mustard to the nearest 0.125%, which was equivalent to an area of about 3 cm^2 in our 50 cm x 50 cm sampling plot. This area was the approximate size of a first-year garlic mustard plant at the time we sampled. We counted scattered individuals of first-year garlic mustard plants in each plot, and we multiplied total number of plants by 0.125% to estimate total cover for these plants. Because of overlapping crowns of herbaceous species, total estimated cover can exceed 100%, even when there is bare ground, which we estimated separately.

We made counts of second-year plants in the 50 cm x 50 cm sample plots, and we counted first-year plants in 2 1- dm^2 quadrats nested in the northeast and southeast corners of the sample plot. For data analyses, we summed the counts in the 2 1- dm^2 quadrats for each plot.

Data Analysis

We used 2-way MANOVA (SAS 2004) with treatment, woods, and treatment*woods as factors to test for treatment differences in cover of first-year garlic mustard and all native herbaceous ground layer (41 species) combined. A second MANOVA tested for treatment effects on 23 native herbaceous species that had at least a total of 5% cover summed across all plots separated into 2 functional groups: spring- and summer-dominant species. Spring-dominant species reached most or all of their maximum cover and flowered before May 15 and included some species that persisted throughout the summer and evergreen species. Spring-dominant species (7) and summer-dominant species (15) are listed in Table 1. For second-year garlic mustard, we eliminated early treatment plots from analysis because the second-year plants were removed from the early treatment plots before cover data were collected. We used 1-way ANOVA to test the effect of late removal on cover of second-year garlic mustard using data from late removal and control plots. We analyzed count data for first- and second-year garlic mustard using 2-way MANOVA. For all of these analyses, we considered woods as a random effect and treatment as a fixed effect.

Log transformed data best met the assumptions of MANOVA. We used LSMEANS tests with a Bonferroni correction for mean separations when appropriate. Means are back transformed in text, tables, and figures.

To determine if the performance of spring- and summer-dominant species was maximized within a treatment group, we used indicator species analysis in PCORD (McCune and Mefford 1999, McCune and Grace 2002). Indicator value is based on a species' relative abundance and relative frequency within a group. We conducted this analysis by combining the treatment data across woods (3 groups) and in a separate analysis considering the treatments in each

woods as a separate group (6 groups). We excluded wild ginger (*Asarum canadense*) from this analysis because it occurred in less than 10 plots. To test the significance of the observed maximum indicator value (IV_{max}) for each species (McCune and Mefford 1999, McCune and Grace 2002), we used the Monte Carlo Method with 1000 randomized runs. We considered the results for a species maximum group to be significant at $p < 0.10$ level of probability (i.e. 10% of the indicator values for randomized trials exceeded the observed value IV_{max}).

Results

First-year Garlic Mustard and Native Species Cover

First-year garlic mustard and native species cover were significantly affected by treatment (Wilks' lambda = 0.7281, $F_{4,448} = 19.25$, $p < 0.0001$) and woods*treatment interaction (Wilks' lambda = 0.9026, $F_{4,448} = 5.89$, $p = 0.0001$), but not woods (Wilks' lambda = 0.9996, $F_{2,244} = 0.04$, $p = 0.9637$). Standard canonical coefficients indicated that treatment had a greater effect on cover of first-year garlic mustard (1.1647) and a smaller and opposite effect on combined cover of natives (-0.2795). Similarly, standard canonical coefficients indicated the significant treatment*woods interaction was mostly due to the response of first-year garlic mustard (1.0942) which was larger than and opposite to that of native herbaceous cover (-0.4672).

Protected univariate ANOVA indicated significant treatment effects ($F_{2,225} = 38.41$, $p < 0.0001$) and a 2-way interaction ($F_{2,225} = 8.92$, $p < 0.001$) between treatments and woods for first-year garlic mustard.

Follow-up tests for first-year garlic mustard were done separately for each woods. In the upland woods, the control had significantly higher cover than the 2 removal treatments ($p < 0.0001$), which were not significantly different from each other. For

Table 1. Indicator analysis for treatment groups for spring (SPR) and summer (SUM) dominant species. MaxGrp numbers indicate treatment and woods of maximum performance. Group numbers 1, 2, and 3 indicate control, early, and late treatments, respectively, in the upland woods, and 4, 5, and 6 indicate the same treatments, respectively, in the lowland woods. The *p*-value is the proportion of 1000 randomized trials with indicator values < the observed indicator value (IV). Statistical significance was accepted at $p < 0.10$.

Species	Observed		Randomized Groups			Phenology
	MaxGrp	IV	Mean	SD	<i>p</i>	Group
<i>Dentaria laciniata</i>	3	25.3	13.4	2.47	0.001	SPR
<i>Floerkea proserpinacoides</i>	2	34.2	11.9	2.20	0.001	SPR
<i>Claytonia virginica</i>	2	27.9	18.2	1.84	0.001	SPR
<i>Geranium maculatum</i>	3	13.6	3.8	1.70	0.002	SPR
<i>Trillium recurvatum</i>	2	14.6	6.1	1.97	0.003	SPR
<i>Hydrophyllum virginianum</i>	2	6.5	3.5	1.61	0.059	SPR
<i>Geum canadense</i>	5	12.3	9.1	1.97	0.065	SPR
<i>Mertensia virginica</i>	2	6.4	3.6	1.73	0.087	SPR
<i>Sanicula gregaria</i>	5	19.5	18.0	1.73	0.172	SPR
<i>Podophyllum peltatum</i>	2	4.4	4.0	1.66	0.321	SPR
<i>Chaerophyllum procumbens</i>	6	13.2	13.0	2.14	0.422	SPR
<i>Dicentra cucullaria</i>	1	3.2	3.7	1.95	0.427	SPR
<i>Phlox divaricata</i>	1	7.5	8.9	2.61	0.674	SPR
<i>Erythronium americanum</i>	1	3.1	4.4	1.75	0.747	SPR
<i>Allium tricoccum</i>	3	1.5	3.6	1.91	0.892	SPR
<i>Cryptotaenia canadensis</i>	5	25.0	10.2	2.00	0.001	SUM
<i>Elymus virginicus</i>	4	22.1	16.3	2.16	0.016	SUM
<i>Laportea canadensis</i>	3	11.0	6.9	1.85	0.038	SUM
<i>Polygonum virginianum</i>	5	9.6	6.2	2.33	0.085	SUM
<i>Osmorhiza longistylus</i>	5	5.4	3.5	1.69	0.12	SUM
<i>Festuca obtusa</i>	6	10.5	12.4	2.39	0.783	SUM
<i>Galium triflorum</i>	6	7.8	9.7	2.31	0.807	SUM

the lowland woods, the control had significantly higher cover of first-year garlic mustard than the late treatment ($p = 0.004$), but not the early treatment ($p = 0.087$) (Figure 1). Percent cover of total herbaceous native species showed no significant effects (mean cover = 18.06 ± 1.06 and 18.36 ± 1.05 in the upland and lowland woods, respectively).

Second-year Garlic Mustard Cover

Neither treatment ($F_{1,47} = 0.00$, $p = 0.9677$) nor treatment*woods interaction ($F_{1,149} = 0.42$, $p = 0.5187$) significantly affected second-year garlic mustard cover. However, there were marginally significant effects due to woods ($F_{1,149} = 3.79$, $p = 0.0534$) for second-year plants in the late treatment and control plots. The upland woods had greater percent cover (0.70 ± 0.20) than the lowland woods (0.29 ± 0.07).

First- and Second-year Counts for Control and Late Treatment

Two-way MANOVA for counts of first- and second-year garlic mustard in control and late treatment plots indicated significant effects owing to treatment (Wilks' lambda = 0.7359, $F_{2,148} = 26.55$, $p < 0.0001$) but not woods (Wilks' lambda = 0.9854, $F_{2,148} = 1.09$, $p = 0.3374$) or treatment*woods interaction (Wilks' lambda = 0.9763, $F_{2,148} = 1.79$, $p = 0.1699$). Standard canonical coefficients indicated counts of first-year plants (1.1745) were more important in causing treatment differences than counts of second-year plants (0.1569). Protected univariate ANOVAs results were significant only for treatment effect on counts of first-year plants ($F_{1,152} = 52.16$, $p < 0.001$). Control plots had significantly greater counts for first-year plants ($9.8 \pm 1.3/\text{dm}^2$) than late treatment plots ($1.3 \pm 0.3/\text{dm}^2$), but not second-year plants ($0.5 \pm 0.1/0.25 \text{ m}^2$ and $0.45 \pm$

$0.09/0.25 \text{ m}^2$ for late treatment and control plots, respectively).

Dominant Native Spring and Summer Species

Treatment did not significantly affect dominant spring and summer native species (Wilks' lambda = 0.9684, $F_{4,448} = 1.81$, $p = 0.1259$). However, woods (Wilks' lambda = 0.6428, $F_{2,224} = 62.24$, $p < 0.0001$) and treatment*woods interaction (Wilks' lambda = 0.9304, $F_{4,448} = 4.11$, $p = 0.0028$) were significant effects. Summer natives accounted for a greater amount of the variance in the differences between woods (standardized canonical coefficient = 1.0237), and the response was opposite to that of spring natives (-0.6000). Spring natives had greater effect (1.0899) on the interaction than summer-dominant plants (-0.2499).

Univariate ANOVAs indicated significant treatment ($F_{2,225} = 3.33$,

$p < 0.0377$), woods ($F_{1,225} = 29.48$, $p < 0.0001$), and treatment*woods interaction ($F_{2,225} = 7.95$, $p < 0.0005$) effects for spring-dominant natives (Figure 2a); however, summer-dominant species showed only significant woods effects ($F_{1,225} = 107.55$, $p < 0.0001$), 1.58 ± 1.11 and 6.20 ± 1.09 percent cover for the upland and lowland woods, respectively), Figure 2b.

In the upland woods, spring-dominant species cover was significantly greater in early treatment plots than in either the control or late treatment plots. There were no significant differences among treatments in the lowland woods for spring native species percent cover (Figure 2a), which was overall less than in the upland woods (11.88 ± 1.06 vs. 7.76 ± 1.05 , for the upland and lowland woods, respectively).

Indicator Species Analysis

When indicator analysis was carried out with 3 groups (control, early, and late treatments) considered across both woods, only 1 species, spotted geranium (*Geranium maculatum*), had a significant ($p = 0.0390$) maximum indicator value (IV_{max}), which occurred in the late treatment. However, when each treatment within a woods was considered to be a separate group, 12 of the 22 species met the minimum threshold probability level (Table 1). Of these 12 species, 8 were spring-dominant species (53% of the 15 spring-dominant species used in the analysis) and 4 were summer-dominant (57% of all summer-dominant species). The early treatment had the largest number (8) of the significant IV_{max} values (67% of all significant IV_{max}), followed by the late treatment (3) (25% of all IV_{max}). Only 1 species (virginia wildrye, *Elymus virginicus*) had its highest IV_{max} in a control (8% of all significant IV_{max}).

Of species having a significant IV_{max} , spring-dominant species had a larger proportion of the species achieve their greatest IV_{max} in the early treatment than the summer-dominant species. One of the 4 summer-dominant

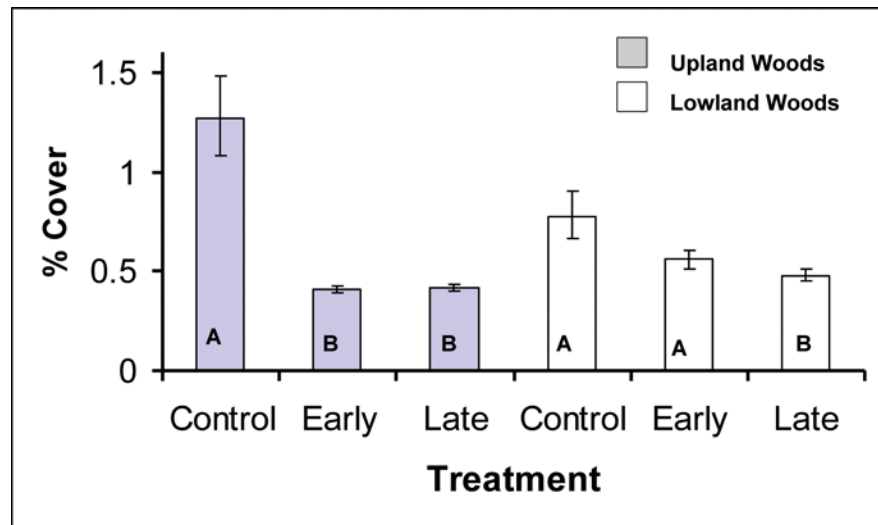


Figure 1. Back-transformed mean \pm SE percent cover of first-year garlic mustard following 4 years of treatments. Second-year plants were removed from early treatment plots on March 14 and on May 13 2008 for late treatment plots. Second-year plants were not removed from control plots. Within woods, treatments with same letter are not significantly different.

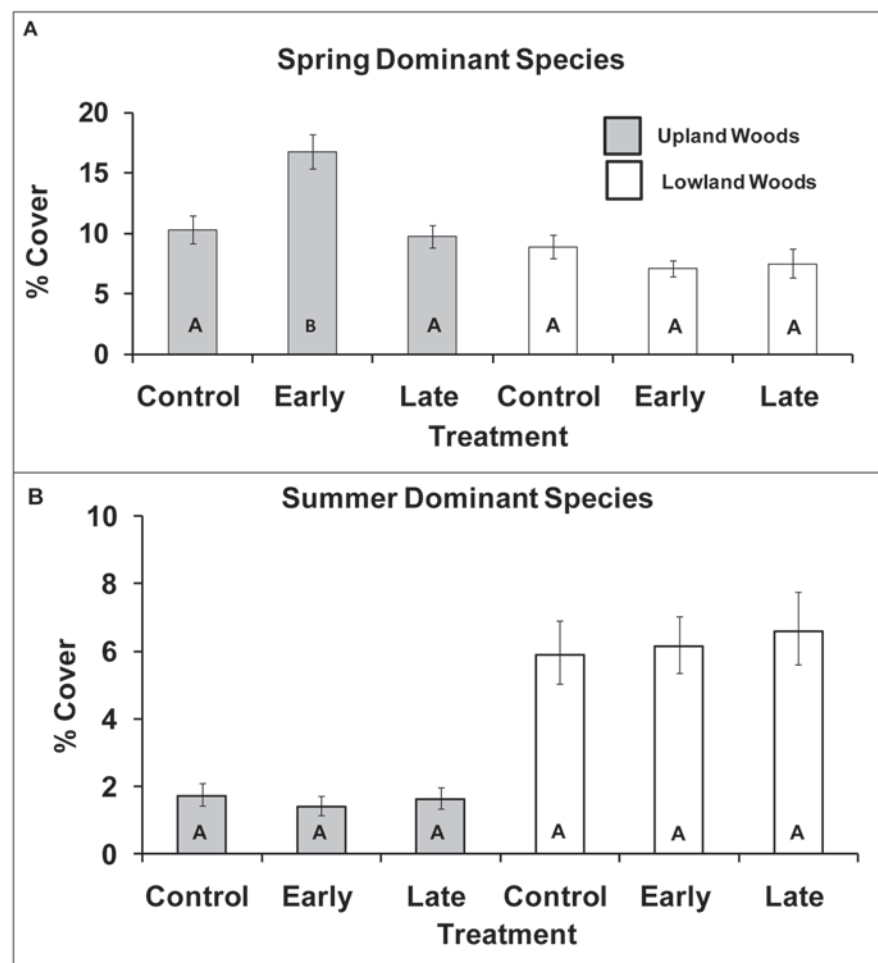


Figure 2. Back-transformed mean \pm SE percent cover of (A) spring-dominant native herbaceous species and (B) summer-dominant herbaceous plants. Second-year plants were removed from early treatment plots on March 14 and on May 13 2008 for late treatment plots. Second-year plants were not removed from control plots. Within woods, treatment with the same letter for summer- or spring-dominant species are not significantly different.

species, virginia wildrye, had its IV_{\max} in the control, 2 species (50%) had their greatest IV_{\max} in the early treatment, and 1 in the late treatment. By comparison, 75% of spring-dominant species (6 of 8) had their IV_{\max} species in the early treatment, and the remaining 2 species achieved their greatest IV_{\max} in the late treatment.

In the upland woods, 7 spring-dominant and 1 summer-dominant species had significant IV_{\max} values, and in the lowland woods 3 summer-dominant and 1 spring-dominant species had significant IV_{\max} values.

Discussion

Treatment significantly affected first-year garlic mustard indicating that second-year garlic mustard plants are important competitors of first-year plants. Light availability strongly affects survival of first-year garlic mustard seedlings (Meekins and McCarthy 2000). Second-year garlic mustard plants may shade out first-year plants, leading to an annual alternating of dominance between first- and second-year garlic mustard plants (Winterer et al. 2005, Bauer et al. 2010). Early removal of second-year garlic mustard plants should allow for greater survival of first-year plants than late removal since they receive an earlier release from competition. However, after 3 years of continuous removal of second-year plants, there was a reduction in cover of first-year garlic mustard plants in the early and late treatments, apparently due to a decrease in seed input (Bauer et al. 2010). Therefore, early and late treatments would be expected to converge over time, resulting in non-significant differences, as we observed in our data. Our results on removal of garlic mustard are different than those of Slaughter and colleagues (2007), who reported that after 5 years of fall herbicide application to garlic mustard rosettes, spring rosettes were equally abundant in sprayed and unsprayed plots each spring. They attributed

these results to seed dispersal from outside their treatment plots.

Counts and cover differed significantly between late treatment and control plots for first-year plants, but not second-year plants, supporting our prediction that survivorship of first-year plants would be greater in late treatment plots than in control plots. Thus, even though abundance of first-year plants was initially lower in late treatment than in control plots, once second-year plants were removed, a greater proportion of remaining first-year plants reached maturity in late removal plots than in control plots. These results support the hypothesis that second-year plants are important competitors of first-year plants. Control plots had higher cover of first-year garlic mustard than treatment plots because their seed bank was replenished yearly. Consequently, while second-year plants competed with first-years in control plots, the continued seed input ensured their persistence. These results are consistent with findings of Pardini and others (2008), who reported that management of adult plants increases survival of juvenile plants, and several years of removal of adult plants is required for effective control.

A dense cover of native species can also shade out small garlic mustard plants, resulting in less cover of the invasive species. Bloodroot (*Sanguinaria canadensis*), a spring ephemeral, has been reported to have such an effect (Murphy 2005). However, during our sampling in early spring, cover of native species was relatively low (about 18%) compared to the cover of natives during the summer (75% to 108%), and it is likely that second-year garlic mustard was the strongest competitor of first-year plants (Winterer et al. 2005, Pardini et al. 2008, 2009, Bauer et al. 2010). Native species may have greater impact on garlic mustard later in the summer when their cover is higher and second-year plants are undergoing senescence.

Significant treatment effects on native species were only apparent

among spring-dominant natives occurring in the upland woods where cover was greater in the early removal plots than in either the control or late removal plots. Natives in early treated plots were released from the competition of second-year garlic mustard plants after they were removed on March 14, whereas on the late removal plots second-year plants were present at the time of sampling. Thus control and late treatment had essentially the same effect on the native spring plants prior to the sampling date. In the lowland woods, neither treatment significantly affected spring-dominant species as a functional group, which may be due to differences in relative abundance of spring- and summer-dominant species in the 2 woods. Averaged across treatments, summer-dominants had cover in the lowland woods that was more than 3-fold greater than the cover of these species in the upland woods. Summer-dominants may play a more important role in reducing abundance of spring-dominant species in the lowland than in the upland woods. Consequently, removal of garlic mustard may have less effect on spring-dominant species in the lowland woods than the upland woods.

Indicator analysis revealed only 1 species had a significant IV_{\max} value when treatments were considered across woods. However, at least one-half of spring- and summer-dominant species had a significant IV_{\max} when treatments in each woods were considered to be separate groups. These results show that some species of summer dominants individually showed positive responses to treatment conditions, and that these results were specific to 1 of the 2 woods. Nevertheless, a higher percentage of spring species with significant IV_{\max} values achieved these values in the early treatment than did the summer-dominant species. These results suggest that the early treatment is more favorable for native species than the late treatment as we predicted. However, both phenological groups had more species

achieve their IV_{\max} in the early treatment than either the control or the late treatment, but our prediction was that only the spring dominant species would show this pattern.

Several studies have demonstrated garlic mustard's ability to disrupt native plant species' symbiotic relationship with mycorrhizal fungi, and most of the perennial ground layer herbs form mycorrhizal associations (Roberts and Anderson 2001, Stinson et al. 2006, Callaway et al. 2008, Wolfe et al. 2008). However, since plant species vary in their dependence on mycorrhizal fungi, certain species will be more affected by the invader than others. In the eastern deciduous forests most (70–80%) native plant species form arbuscular mycorrhizal fungal (AMF) associations (Berliner and Torrey 1989, Brundrett 1991), and on our study site nearly all ground layer species are colonized by AMF (Anderson et al. 2010). Loss of the mycorrhizal association can reduce growth, reproductive success, and competitiveness of plant species (Allen 1991, Smith and Read 1997). It is of interest that 3 leading species for IV_{\max} are non-mycorrhizal—spring beauty (*Claytonia virginica*), cutleaf toothwort (*Cardamine concatenata*), and false mermaid (*Floerkea proserpinacoides*). It is possible that these early spring species benefit from removal of garlic mustard sooner than mycorrhizal species because they are affected by direct competition—scramble competition for resources and interference competition resulting from allelopathy—whereas mycorrhizal species also experience indirect competition resulting from disruption of the mycorrhizal association. Consequently, mycorrhizal species may be delayed in their response to garlic mustard removal until after the mycorrhizal community is well established (Anderson et al. 2010).

Some soil microbial communities may mitigate the effect of garlic mustard on the mycorrhizal association by degrading the alleochemicals (Lankau 2010). The greater number

of species having significant IV_{\max} that show positive effects due to removal of garlic mustard in the upland woods than the lowland could be due to differences in the soil microbe communities between the 2 woods, and their ability to mitigate the negative allelopathic effect that garlic mustard has on AMF, as well as the presence of non-mycorrhizal species in the upland site. Of interest to garlic mustard's effect on mycorrhizae is the study of Lankau and others (2009). The authors reported a marked decline in the production of phytochemicals in garlic mustard populations after initial invasion of founder populations. Nevertheless, other direct competitive effects of garlic mustard may ensure its continued success as an invader of deciduous forests, and the secondary compounds also may be important in reducing herbivory (Knight et al. 2009), which could result in selection for retention of high levels of these compounds.

Our results support the conclusions of Pardini and colleagues (2009) that management should focus on adult populations of garlic mustard with concentrated efforts in targeted areas rather than attempting less effective control over large areas. In areas where there is substantial cover of native species, hand removal of garlic mustard in spring is preferable to fall application of herbicide to rosettes. Herbicide application can cause collateral damage to native species that are evergreen and rosettes hidden under fallen leaves may be missed (Slaughter et al. 2007). Removal of adult plants will encourage growth of juvenile first-year plants, but continual removal of second-year plants results in less seed input and depletion of soil seed banks will cause a decline in the species. Early removal of second-year garlic mustard appears to favor early native spring species compared to late removal of second-year plants. Long-term studies are needed to better understand community responses to eradication of invasives due to these slow responses and yearly fluctuations

in composition (Hochstedler et al. 2007). It may take 5 years before these changes become apparent statistically (McCarthy 1997).

Acknowledgements

We thank Geoff Ower, Adam Feltes, Alicia Mullarkey, and Ebony Murrell for assistance with field sampling and data analysis on this study and the ParkLands Foundation for granting us permission to do long-term research on the Merwin Preserve.

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