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Competitive Interactions among First-Year and Second-Year Plants of the Invasive, Biennial Garlic Mustard (*Alliaria petiolata*) and Native Ground Layer Vegetation

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Abstract

We studied the effects of hand weeding of second-year plants of the biennial garlic mustard (*Alliaria petiolata*) on first-year plants (seedlings) and native ground layer vegetation. Garlic mustard is a Eurasian species that has invaded deciduous forest ground layers in eastern North America. Treatments consisted of a control and an early or late weeding of second-year garlic mustard. The early treatment (early March) was applied before garlic mustard seeds had germinated and when most native species were dormant. The late treatment (mid-May) occurred after plants had bolted, flowering was occurring, and most native species and new garlic mustard seedlings were actively growing. Pre-treatment data were obtained in 2004 and treated and control plots were sampled in 2005, 2006, and 2007. No significant treatment effects were observed in 2004 or 2005. In 2006, mean cover of first-year plants was higher in the early weeding treatment than in the late weeding treatment and control. In 2007, mean cover of first-year garlic mustard was higher in the control than in either of the two weeding treatments. There were no significant treatment effects in any year on native vegetation cover, bare ground, or the five most abundant native species. Our data indicate that (1) late weeding of garlic mustard provided more effective control than early weeding because late weeding allows second-year plants to compete with garlic mustard seedlings for a longer period of time and (2) competition between first- and second-year plants is responsible for alternating dominance of first-year and second-year garlic mustard plants.

Key words: ***Alliaria petiolata*, eastern deciduous forest, intraspecific competition, invasive plant, native plants.**

Introduction

Garlic mustard (*Alliaria petiolata*) (Brassicaceae) is a biennial herb native to Eurasia that was first recorded in the United States on Long Island, New York, in 1868. Several authors consider it to be a species of concern as an invader of the ground layer in the deciduous forests of eastern North America (McCarthy 1997; Carlson & Gorchov 2004; Slaughter et al. 2007). In central Illinois, garlic mustard seeds germinate in mid-February to March depending upon spring temperatures. The plant spends its first year as a basal rosette. During the second year, the plant bolts and rapidly elongates its shoot in March, flowers from March to late May, develops fruits in May and June, and disperses seeds in August and September (Anderson et al. 1996). The plant is a strict biennial in North American (Nuzzo 1991; Anderson et al. 1996; Byers & Quinn 1998); however, it may be a winter annual or biennial in Europe (Clapman et al. 1952). Under suitable conditions, 70% of the seeds germinate in the first year after they mature, but some seeds can germinate at least 4 years after they are shed by the plant (Baskin & Baskin 1992). Baskin and Baskin (1992) reported 4, 0.1, and 3% of seeds germinating 2, 3, or 4 years after maturing, respectively. Seedling density can be high, 8.3–18.0 seedlings/dm^2 (Anderson et al. 1996; Byers & Quinn 1998). However, only 2–7.5% of seedlings survive to maturity (Anderson et al. 1996; Byers & Quinn 1998). Although mortality is high among first-year plants (Anderson et al. 1996), it is low for second-year plants (Nuzzo 1991; Anderson et al. 1996).

Several authors have reported alternating dominance of first-year and second-year garlic mustard plants in areas that were observed over several years suggesting competitive interactions between first- and second-year garlic mustard plants (Baskin & Baskin 1992; McCarthy 1997). McCarthy (1997) found that garlic mustard seedling establishment was greater when all garlic mustard was removed from plots than in unmanipulated plots. Winterer et al. (2005) reported that patches of garlic mustard consisted of nearly exclusively first-year plants or mixed first- and second-year plants. Patches alternated yearly between dominance of first-year plants and a mixture of first- and

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second-year plants. First-year plants that grew in patches of first-year plants or mixed patches where second-year plants had been removed had a higher probability of survival than first-year plants from mixed plots. This suggests that patch types alternate because first-year plants are negatively impacted by the presence of adults (Winterer et al. 2005). The biennial Pale-flowered leaf cup (*Polymnia canadensis*) showed a similar pattern with small individuals dying when they compete with larger plants. This competition leads to a cycle of "mass seeding and senescence" followed by establishment of a large number of seedlings (Bender et al. 2002).

Various investigators (Nuzzo 1991; McCarthy 1997; Meekins & McCarthy 1999; Carlson & Gorchov 2004; Hochstedler et al. 2007) have studied the competitive effects of garlic mustard on native vegetation and methods of control of this species. However, results from these studies are mixed and the effect of garlic mustard on native ground layer species and its control are not well understood. Greenhouse experiments suggested that garlic mustard can be an effective competitor against oak seedlings, Chestnut oak (*Quercus prinus*), but is less competitive against Jewelweed (*Impatiens capensis*) or Boxelder (*Acer negundo*) (Meekins & McCarthy 1999). Garlic mustard reduced the growth of Sugar maple (*A. saccharum*), Red maple (*A. rubrum*), and White ash (*Fraxinus americana*) by disrupting associations with arbuscular mycorrhizal fungi in another greenhouse experiment (Stinson et al. 2006). In addition, garlic mustard has been shown to reduce the biomass of ectomycorrhizal fungi in the field and in greenhouse experiments (Wolfe et al. 2008). Experiments by Roberts and Anderson (2001) and Prati and Bossdorf (2004) have also demonstrated potential allelopathic abilities in garlic mustard.

Herbicide treatments applied to garlic mustard after leaf fall resulted in decreased garlic mustard density and increased cover of spring ephemerals in the first year after treatment. Increased reproduction was also documented in Lopseed (*Phryma leptostachya*) (Carlson & Gorchov 2004). There was a reduction in first-year garlic mustard during the second-year after treatment, likely as a result of reduced seed input from second-year plants in the year following treatment (Carlson & Gorchov 2004). However, Hochstedler et al. (2007) found few changes in the forest understory after 5 years of herbicide treatments to control garlic mustard. Removal of garlic mustard increased relative cover of species with high vegetative growth including vines, annuals, such as impatiens, and tree seedlings but not perennial herbs, graminoids, or shrubs (McCarthy 1997). Stinson et al. (2007) reported that as garlic mustard density declined under natural or experimental conditions, there was no effect on species richness of native herbaceous plants. However, there was an increase in the number of tree seedlings and diversity (H′) and evenness (J) of herbaceous species as measured by the Shannon index. Nuzzo (1991) tested the effectiveness of mid-intensity fires, herbicide applications, and cutting to control garlic mustard. Although all treatments except low-intensity fire reduced garlic mustard density, the response of native vegetation to these control methods was not documented. Additionally, treating garlic mustard by hand weeding, a common control method, was not investigated (Nuzzo 1991). Only one study experimentally investigated the impact of native species on garlic mustard. Murphy (2005) found that plantings of Bloodroot (*Sanguinaria canadensis*) at densities of 9 or 11 ramets/m^2 within garlic mustard patches reduced the success of garlic mustard by lowering the numbers of late spring seedlings, flowering individuals, and fruits.

In this study, we examined the competitive interactions among first-year garlic mustard, second-year garlic mustard, and native vegetation. Specifically, we experimentally examined the response of native vegetation and first-year garlic mustard plants to removal of second-year garlic mustard. Second-year plants potentially compete with first-year plants during the spring and early summer of their first year and with native vegetation. Removal of second-year plants should initially encourage the growth of first-year plants because of reduced competition. In subsequent years, first-year plants should decline because of reduced seed input with repeated removal of second-year plants and this should favor native vegetation (McCarthy 1997; Winterer et al. 2005). We manipulated the abundance of second-year plants by hand weeding. First-year plants were not removed and this allowed us to determine the effect of removal of second-year plants on first-year plants and native vegetation.

We tested the following hypotheses: (1) Second-year garlic mustard plants are strong competitors with first-year plants, which leads to alternating dominance of first- and second-year plants and (2) garlic mustard is a good competitor with native plants and is displacing native species. Based on these hypotheses, we made the following predictions: (1) In the first year, removal of second-year garlic mustard plants will increase the abundance of first-year plants and native vegetation; (2) repeated removal of second-year garlic mustard will cause a decline in first-year garlic mustard plants, because of decreasing seed input, and an increased abundance of native ground layer species; and (3) early spring (March) removal of second-year garlic mustard will positively affect first-year plants more than late removal (May) because first-year plants will compete with second-year plants for a shorter period of time.

Methods

Study Site

The study site is located in second-growth hardwood forest in the ParkLands Foundation's Merwin Nature Preserve located 30 km northeast of Normal, Illinois, U.S.A. The site was subject to selective logging and grazing prior to acquisition of the property by the Foundation in 1970. Study plots are located in areas with established populations of garlic mustard. One area is an upland site, and the other is located in a low-lying site near a creek. Wood nettle (*Laportea canadensis*), Cluster sanicle (*Sanicula gregaria*), and Wingstem (*Verbesina alternifolia*) were dominant ground layer species.

Experimental Design

The experimental design is a randomized complete block design with blocks nested within woods. Both study areas (woods) have two blocks (approximately 23 × 30 m) containing 60 plots for a total of 240 study plots. Each plot consists of a treatment area (2.5 × 2.5 m), with a sampling plot (50 × 50 cm) located in the center. In each block, parallel transects were located 5 m apart. Plots were placed at 2.5-m intervals along each transect at a random distance of up to 50 cm to the right or left of the transects. This placement of plots resulted in a minimum buffer strip of 1.5 m between rows of plots. One-third of the plots in each block (20) were randomly assigned to one of the two treatments (early or late hand weeding of second-year plants) or a control. In early-treatment plots, all second-year garlic mustard plants were removed from the treatment plot between 4 March and 9 March, before garlic mustard seeds had germinated and nearly all native species were dormant. In late-treatment plots, all second-year plants were removed between 15 May and 18 May after second-year garlic mustard plants had bolted, flowering was occurring, and native species were actively growing. Treatments were applied in 2005, 2006, and 2007, following a pre-treatment sample of the plots in 2004. Care was taken to avoid trampling and to minimize disturbance to the sampling area when applying treatments and sampling.

Data Collection

Within the sampling plots, percent aerial cover of all plants rooted within the plot was estimated by species or by genus for Sedges (*Carex*) and Violets (*Viola*). Nomenclature follows Gleason and Cronquist (1991). Cover of first- and second-year garlic mustard and bare ground was also determined. The numbers of second-year garlic mustard plants within each 50 × 50–cm sampling plot were tallied. First-year plants were counted in decimeter-square quadrats located in the northeast and southeast corners of the sampling plots. The plots were established and sampled in May and early June of 2004 and sampled again in late May of 2005, 2006, and 2007.

Data Analysis

Treatment Effects Across Years on First-Year Garlic Mustard, Bare Ground, and Native Species. Data were analyzed using SAS 9.1 (SAS Institute Inc. 2004). To determine treatment effects across years on percent cover of first-year garlic mustard, bare ground, and the total cover of all native species, multivariate analysis of variance with repeated measures (MANOVAR) was used. Fixed effects were treatment, year, woods, block nested within woods in this model, and those described below. Cover of second-year garlic mustard was not included in the analysis because these plants were removed in the treatment plots. The effect of treatment on number of first-year garlic mustard plants within the decimeter quadrats was analyzed with repeated measures analysis of variance (ANOVA). In all analyses, the number of first-year plants in each decimeter quadrat within plots was added together, which reduced the number of zero values and improved the distribution of the data to meet assumptions of the statistical tests. Separately, MANOVAR was also used to analyze the effect of treatment over time on the five most abundant native species, *Carex* spp., Wild rye (*Elymus* sp.), *L. canadensis*, *S. gregaria*, and *V. alternifolia*.

To reduce the number of variables in the native species' dataset, nonmetric multidimensional scaling (NMS) was used to ordinate the plots using percent cover of all native species, and the axis scores were analyzed with MANOVAR to determine if there was an effect of treatment over years (McCune & Mefford 1999; Beals 2006). Dimensionality was assessed using the scree plot from an NMS ordination with 20 runs of real data and six axes. Based on the scree plot, the ordination was conducted with three axes. A Sorensen (Bray–Curtis) distance measure was used, with the starting configuration set from the axis scores of a Bray–Curtis ordination. One run was conducted with real data, a maximum number of iterations set to 200, and the stability criterion set at 0.0005. The first, second, and third axes accounted for 29.0, 22.5, and 16.4% of the variance, respectively. Monte Carlo tests indicated that the NMS ordination was significantly different from random data ($p = 0.0476$).

Year Effects on First- and Second-Year Garlic Mustard. To determine the effects of year on percent cover and number of first- and second-year garlic mustard in control plots, we used multivariate analyses of variance (MANOVA) with year, woods, and block nested within woods as fixed effects. Linear regressions were performed to analyze the association between cover of first-year garlic mustard, second-year garlic mustard, and native vegetation within plots. In 2004, the pre-treatment data from all plots were used for the regression analysis, but in subsequent years, only the data from the control plots were used because second-year plants were removed from treatment plots.

Follow-up Tests. The repeated measures ANOVA, MANOVA, and MANOVARs were followed up with univariate ANOVAs and least square (LS) means tests when appropriate. All data were log transformed to meet assumptions of the statistical tests. After transformations, the data of the top five most abundant species still violated the assumption of normality; however, transformations improved the distribution of this data.

Results

Treatment Effects Across Years on First-Year Garlic Mustard, Bare Ground, and Native Species

There was a significant time × treatment × woods × block within woods interaction for percent cover of first-year garlic mustard, bare ground, and total native vegetation. This interaction was due to trends in differences for cover of first-year garlic mustard plants among treatments in blocks within the low-lying woods during 2006, which were the same as for blocks in the upland woods but were not significant. However, there was no significant time × treatment × woods interaction, meaning that the effect of treatment was consistent across woods. Consequently, both interactions remained in the model, but we only discuss the time × treatment interaction (Table 1). Standardized canonical coefficients did not reveal any interpretable trends or patterns. No effects of treatment were observed in 2004 or 2005.

Treatment Effects on First-Year Plants. Univariate follow-up ANOVAs (Scheiner 1993) indicated that for first-year garlic mustard, there were significant treatment effects in 2006 and 2007. In 2006, mean cover of first-year garlic mustard was higher in the early weeding treatment than in the late weeding treatment and control ($F = 21.82$, $df = 2$, $p < 0.0001$; Fig. 1). In 2007, the mean cover of first-year garlic mustard was higher in the control treatment than in either the early or late weeding treatments ($F = 87.95$, $df = 2$, $p < 0.0001$; Fig. 2). The numbers and percent cover of first-year garlic mustard showed a similar response to treatments, and only cover data are discussed in this article (Table 2; Bauer 2007).

Treatment Effects on Native Vegetation and Bare Ground. Univariate ANOVAs indicated no significant effect of treatment in any year on percent cover of native vegetation; however, there were significant ($F = 3.21$, $df = 2$, $p = 0.0423$) treatment effects on bare ground in 2006. Nevertheless, LS means tests showed no significant differences in bare ground among treatments ($p > 0.0557$, in all cases). There were no significant effects of treatment over time for any of the five most abundant native species in the study plots (MANOVAR, $F_{[30,\ 448]} = 1.01$, $p = 0.4561$). No significant effect of treatment over time was found on any of the three NMS axes scores (MANOVAR, $F_{[18,\ 460]} = 1.21$, $p = 0.2499$).

Year Effects on First- and Second-Year Garlic Mustard

In the control plots, there was a significant year × woods × block within woods interaction on percent cover of first-year and second-year garlic mustard in control plots with two significant eigenvectors. MANOVA indicated a significant main effect of year on percent cover of first-year and second-year garlic mustard in control plots with two significant eigenvectors. First- and second-year garlic mustard showed opposite responses along the first eigenvector, shown by opposite signs of standard canonical

Table 1. MANOVAR summary table for effects and interactions of time, treatment, block, and block within woods on first-year garlic mustard, native vegetation, and bare ground.

	Pillai's Trace	*F*	*Numerator df*	*Denominator df*	*p > F*
Response	1.00	53108.1	3	226	<0.0001
Response × treatment	0.12	5.0	6	454	<0.0001
Response × woods	0.08	6.3	3	226	0.0004
Response × treatment × woods	0.005	0.17	6	454	0.9836
Response × treatment × woods × block (woods)	0.47	7.1	18	684	<0.0001
Response × time	0.83	122.8	9	220	<0.0001
Response × time × treatment	0.58	10.1	18	442	<0.0001
Response × time × woods	0.39	15.6	9	220	<0.0001
Response × time × treatment × woods	0.08	1.0	18	442	0.4154
Response × time × treatment × woods × block (woods)	0.71	3.3	54	1,350	<0.0001
Between Subjects Effects	*df*	*Type III SS*	*MS*	*F*	*p > F*
Treatment	2	5.7	2.86	4.03	0.191
Woods	1	0.3	0.28	0.39	0.533
Treatment × woods	2	0.4	0.21	0.30	0.7399
Treatment × woods × block (woods)	9	31.5	3.50	4.94	<0.0001
Error	228	161.7	0.71		

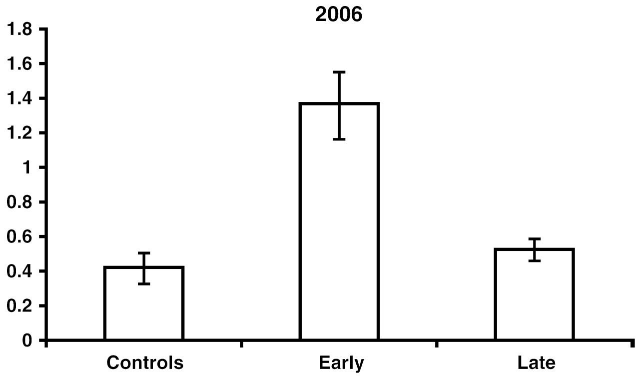

Figure 1. Back transformed mean ± SE percent cover of first-year garlic mustard in early and late weeding treatments and control in 2006. The early weeding treatment is significantly different from the control and late weeding treatment.

coefficients, but similar responses along the second eigenvector (Table 3). In all years, cover of first-year garlic mustard was significantly different from all other years (Fig. 3). Cover of second-year plants was not significantly different in 2005 and 2007, but all other comparisons between years were significantly different. Years of high abundance of first- and second-year plants alternated annually. First-year plants had high abundance in 2005 and 2007, whereas second-year plants had high abundance in 2004 and 2006 (Fig. 3). Woods × block within woods interactions were due to significant differences in cover of first- or second-year plants between the 2 years of high abundance. In all cases, the trend of alternating high and low abundance was consistent.

Relationships Between First- and Second-Year Garlic Mustard Plants and Native Vegetation

Using the pre-treatment data from all plots in 2004, significant negative regressions were observed between first-year garlic mustard (y) and second-year garlic mustard (x)

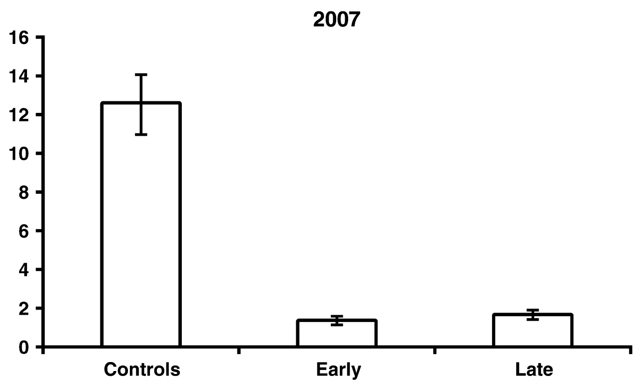

Figure 2. Back transformed mean ± SE percent cover of first-year garlic mustard in early and late weeding treatments and control in 2007. The control is significantly different from the early and late weeding treatments.

($y = -0.17x + 8.8$, $p < 0.0001$, $r^2 = 0.063$) and between second-year garlic mustard (y) and total cover of native vegetation (x) ($y = -0.14x + 26.8$, $p < 0.0001$, $r^2 = 0.088$) but not between native vegetation and first-year garlic mustard. In 2005, we found a significant regression relationship between native vegetation (x) and first-year garlic mustard (y) in control plots ($y = -0.28x + 55.3$, $p = 0.007$, $r^2 = 0.089$). In 2006, the pattern observed in control plots was similar to that observed in 2004 with significant negative relationships between first-year garlic mustard (y) and second-year garlic mustard (x) ($y = -0.039x + 1.93$, $p = 0.005$, $r^2 = 0.076$) and between second-year garlic mustard (y) and native vegetation (x) ($y = -0.18x + 31.4$, $p = 0.0011$, $r^2 = 0.13$). In 2007, there were no significant relationships among these variables.

Discussion

We hypothesized that removal of second-year garlic mustard plants would increase cover and density of first-year plants. Lack of significant treatment effects in 2005 is not surprising because few second-year plants occurred in any plots that year so their removal was unlikely to have a substantial influence on first-year plants. Removing second-year plants in years when first-year plants dominate could affect first-year plants the following year by reducing seed input. However, there was not a significant reduction in the number of first-year plants in the late weeding treatment compared to the control in 2006. Nevertheless, by 2007, both treatments had fewer first-year plants than the control.

These results support our prediction that first-year plants would decline over time as second-year plants were removed. However, our results are contrary to those of Slaughter et al. (2007), who found that 5 years of winter herbicide application to garlic mustard rosettes did not decrease the number of first-year rosettes compared to unsprayed control areas. They attribute these results to treatment areas (1 × 1–m sample area with a 1-m buffer area surrounding the sample area) that were too small to prevent movement of seeds into the treatment areas from adjacent unsprayed areas. Our sample plots (50 × 50 cm) are centered within a 2.5 × 2.5–m treatment area and provide slightly more buffer (1.25 m) than theirs. Nevertheless, our results showed a decline in number and cover of spring first-year rosettes with continued removal of second-year plants. Slaughter et al. (2007) did not search for rosettes under litter when herbicide was being applied, and it is possible that some plants were missed and could have input seed into their plots.

The significant treatment effects on cover and counts of first-year plants observed in 2006 between the early and the late weeding treatments indicate that second-year garlic mustard is an important competitor with first-year garlic mustard. By removing second-year plants early in the growing season, first-year plants were released from

Table 2. Mean percent cover and SE by treatment of first-year garlic mustard (GM), second-year GM (controls only after 2004), native vegetation, and bare ground and counts of first-year and second-year GM in each year of the study.

	2004		2005		2006		2007	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1st yr GM cover								
Early	6.54	1.23	36.51	3.48	2.86	0.60	3.75	1.10
Late	6.85	1.22	28.96	2.71	0.79	0.18	4.16	0.99
Control	5.96	1.15	32.52	2.94	1.22	0.27	19.15	1.68
2nd yr GM cover								
Early	13.35	1.54	—		—		—	
Late	12.72	1.56	—		—		—	
Control	16.85	2.23	0.78	0.38	19.83	1.94	0.04	0.04
Native cover								
Early	86.65	3.33	83.44	3.62	83.33	4.03	108.06	3.20
Late	90.43	3.97	90.99	4.04	78.26	3.56	106.69	3.18
Control	86.41	4.02	84.13	3.16	75.99	3.89	101.87	2.90
Bare ground cover								
Early	15.83	1.85	13.39	1.48	29.86	2.49	17.59	1.49
Late	18.38	1.86	13.09	1.18	34.32	2.48	17.74	1.46
Control	17.94	1.91	13.99	1.45	25.21	1.84	16.14	1.50
1st yr GM count								
Early	2.18	0.33	11.50	0.98	1.15	0.25	0.78	0.18
Late	2.58	0.37	9.23	0.85	0.79	0.18	0.95	0.19
Control	2.39	0.44	11.30	1.07	0.65	0.20	6.51	0.55
2nd yr GM count								
Early	4.46	0.43	—		—		—	
Late	4.30	0.53	—		—		—	
Control	4.24	0.50	0.20	0.07	12.41	1.02	0.05	0.02

Counts of second-year garlic mustard are for all plants rooted within the 50 × 50–cm study plot and counts of first-year garlic mustard are the total count of first-year plants within two decimeter-square quadrats located within the 50 × 50–cm study plots.

early competition with second-year plants, allowing them to increase in cover, supporting our prediction. The negative relationship between cover of second-year plants and first-year plants also suggests that second-year plants may be important competitors with first-year plants. It seems unlikely that first-year plants would have a significant effect on the established second-year plants. Even in years of high abundance of first-year plants, second-year plants would have essentially completed their reproductive phase before first-year plants would be effective competitors.

In 2007, cover and counts of first-year garlic mustard in control plots were significantly higher than in early and late weeding treatment plots, but differences between the two treatments were not significant. Consequently,

Table 3. MANOVA table for the effect of year and year × woods × block (woods) interaction on cover of first-year and second-year garlic mustard (GM) in control plots.

	Pillai's Trace	F	Numerator df/denominator df	p
Year	0.83	71.41	6/608	<0.0001
Year × woods × block (woods)	0.33	4.98	24/608	<0.0001

	Year		Year × Woods × Block (Woods)	
	Can 1	Can 2	Can 1	Can 2
Eigenvalue	2.81	0.10	0.27	0.13
Proportion	0.97	0.03	0.67	0.33
F	105.55	14.91	5.02	3.61
Numerator df/denominator df	6/606	2/304	24/606	11/304
p	<0.0001	<0.0001	<0.0001	<0.0001
Standard canonical coefficients				
1st yr GM	0.81	1.32	1.50	0.40
2nd yr GM	−1.36	1.13	−0.21	1.76

Can 1, First canonical coefficients; Can 2, Second canonical coefficients.

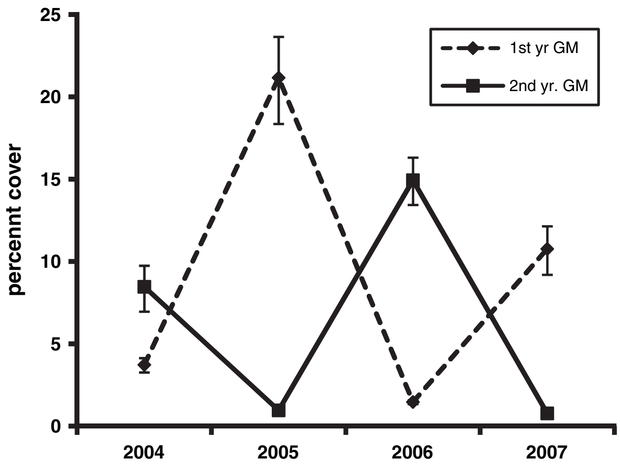

Figure 3. Back transformed mean percent cover ± SE of first-year and second-year garlic mustard in control plots in each year of sampling.

treatment differences may be short lived once the abundance of second-year plants is reduced. Removing all second-year plants during a year when they dominate a site can significantly reduce density and cover of garlic mustard. Reasonable control of garlic mustard will require several years of removal of second-year plants including years when first-year plants dominate because a single second-year plant can produce 13–195 seeds (Byers & Quinn 1998; Susko & Lovett-Doust 2000), and garlic mustard has a seed bank that persists at least 4 years (Baskin & Baskin 1992).

We found no response of native ground layer species to garlic mustard removal. However, native species may recover slowly so that treatment effects were not observable during our study. In addition, garlic mustard reduces mycorrhizal mutualism (Roberts & Anderson 2001; Stinson et al. 2006; Wolfe et al. 2008), which could increase recovery time for native vegetation. In contrast to our study, Carlson and Gorchov (2004) reported increased cover of spring ephemerals in the first year following removal of garlic mustard. However, our sampling was conducted after most spring ephemerals had senesced, so we would not have detected changes in ephemerals. Nevertheless, other studies have suggested that garlic mustard may not be a strong competitor against all native species (McCarthy 1997; Meekins & McCarthy 1999; Murphy 2005; Hochstedler et al. 2007; Slaughter et al. 2007).

Although several studies have investigated the impact of garlic mustard on native vegetation (McCarthy 1997; Meekins & McCarthy 1999; Carlson & Gorchov 2004; Hochstedler et al. 2007), only Murphy (2005) reported a negative effect on garlic mustard by a native species. We were unable to detect any changes in the native ground layer with removal of garlic mustard; however, we observed a negative relationship between second-year garlic mustard and native vegetation during both years of high abundance of second-year plants. Although Murphy (2005) reported that a spring ephemeral, *Sanguinaria candensis*, had a significant impact on garlic mustard, our results suggest that native vegetation could have a greater effect on first-year garlic mustard plants later in the growing season than it does in the spring. In deciduous forest, most herbaceous species are light limited (Whigham 2004), and light availability strongly effects growth and seed production in garlic mustard (Meekins & McCarthy 2000; Myers et al. 2005). This suggests that safe sites for first-year garlic mustard establishment could be in areas where there is less competition for light, which would occur in areas of relatively low cover of native ground layer species. In the following spring, garlic mustard plants surviving the previous summer and winter would be located in the safe sites, resulting in the negative relationship between native vegetation and second-year plants.

We only observed a significant relationship between cover of first-year garlic mustard and native vegetation in 2005. Although this suggests that competition with native vegetation can effect first-year garlic mustard plants early in the growing season, when we sampled native ground layer, cover was still increasing and dense cover of native species had been in place for a short period of time (Anderson, unpublished). As cover of native plants increases over the growing season and is in place for a longer period, these species are likely to become more important competitors with first-year garlic mustard plants.

Based on our results, the cause of the alternating dominance of first-year and second-year plants in patches of garlic mustard is due to competition between the two cohorts, which supports the findings of other studies (Baskin & Baskin 1992; McCarthy 1997; Winterer et al. 2005). In the early spring (March and early April), second-year garlic mustard plants are likely the strongest competitor of first-year plants because the native ground layer is not well developed at this time (Myers & Anderson 2003). In years when second-year plants are abundant, few of the apparently competitively inferior first-year plants are likely to survive. As a result of high seed input and low competition from second-year plants, first-year plants would be more abundant in the following year. These plants would primarily compete with native vegetation, which would allow more to survive to maturity than when second-year plants are abundant, so that second-year plants would be abundant again in the following year.

Late removal of garlic mustard may be more effective than early removal for managing populations of garlic mustard. If second-year plants compete with first-year plants early in the growing season, then the abundance of first-year plants is reduced and fewer second-year plants would be expected in the following year. This study also suggests that first-year garlic mustard plants are vulnerable to competition from established native vegetation and therefore an intact native understory may limit the establishment of garlic mustard.

Implications for Practice

- First- and second-year garlic mustard plants show a pattern of alternating dominance. Removing second-year garlic mustard plants during a year when they have high abundance can reduce the abundance of a garlic mustard infestation. However, follow-up treatments for at least 4 years and continued monitoring for reinvasion would be necessary to achieve a reasonable level of control of garlic mustard.
- Increasing the time that second-year plants are in direct contact with first-year plants reduces their abundance. Therefore, late removal of second-year plants should promote more effective control of garlic mustard than early removal. Second-year plants that are bearing well-formed green fruits should be removed from the site after they are weeded because, based on our experience, the seeds can continue to mature after the plant is pulled from the ground.
- Hand weeding of garlic mustard could have the unintended result of disturbing native vegetation and thereby increasing the success of garlic mustard. However, our study did not detect any effect of treatment on native vegetation. Consequently, if carried out judiciously, hand weeding of garlic mustard should be an effective method of control in small areas where other methods, such as herbicide application, biocontrol, or fire, might damage native vegetation.
- A healthy native understory may help limit garlic mustard's abundance. Actions that promote a healthy native understory are likely to help decrease garlic mustard's abundance and should be a complementary conservation strategy to weeding of garlic mustard.

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