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Response of *Alliaria petiolata* (garlic mustard) to five years of fall herbicide application in a southern Ohio deciduous forest[1]

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Slaughter, B. S., W. W. Hochstedler, D. L. Gorchov and A. M. Carlson (Department of Botany, Miami University, Oxford, OH 45056). Response of *Alliaria petiolata* (Garlic Mustard) to Five Years of Fall Herbicide Application in a Southern Ohio Deciduous Forest. J. Torrey Bot. Soc. 134: 18–26. 2007.—*Alliaria petiolata* is an invasive herb impacting forests throughout the eastern United States. We studied the impacts of glyphosate, bare ground, and summer precipitation on *A. petiolata* cover and density in two forest stands of different ages at Hueston Woods State Park, Preble and Butler Cos., OH. Fifty 1 × 1 m plots were established in each stand and 25 plots per stand were treated with glyphosate each November 2000–2004. Cover and density of *A. petiolata* rosettes and adults were measured multiple times each year from 2000 through 2005. Percent bare ground was estimated using a point frame in May 2003.

Adult cover in May was significantly lower in sprayed vs. unsprayed plots in three of five years; in the other two years adult cover was very low in both sprayed and unsprayed plots. However, spray treatment did not significantly affect May rosette cover across years. ANCOVA revealed that May 2003 bare ground positively associated with density of *A. petiolata* rosettes in May 2003, but bare ground was not significantly associated with October 2003 rosette density. Variation across years in both October rosette density and May adult density of *A. petiolata* was significantly associated with precipitation the previous June; wetter Junes were followed by higher densities.

Despite sustained suppression of adult *A. petiolata* in plots sprayed with glyphosate, new rosettes appeared each spring at densities comparable to unsprayed plots, which we attribute to seed dispersal from outside of the plots. Bare ground had minimal effect on *A. petiolata* populations. Evidence that *A. petiolata* density was positively affected by June precipitation suggests that management efforts should be focused in years of wet summers.

Key words: alien species, Brassicaceae, competition, deciduous forests, exotic species, glyphosate, invasive species, precipitation.

Alliaria petiolata (M. Bieb) Cavara and Grande (Brassicaceae), garlic mustard, is an invasive non-native herb impacting deciduous forests in the midwestern and northeastern United States (McCarthy 1997, Luken 2003). *A. petiolata* is considered a significant threat to forested natural areas in this region (Nuzzo 1991) and has been shown to alter community composition and structure by competing with native plants (McCarthy 1997, Meekins and McCarthy 1999, Carlson and Gorchov 2004).

A. petiolata is a biennial, and, as such, forms populations comprised of two cohorts (in addition to seeds). In spring, newly germinated seedlings coexist with flowering-age plants that germinated the previous spring. In summer, the flowering-age plants senesce after setting seed while seedlings have grown into rosettes (Nuzzo 1991). By fall, the *A. petiolata* population consists of rosettes, in addition to seeds, including those deposited by plants that flowered a few months earlier.

Because *Alliaria petiolata* seeds remain viable in soil for approximately five years (Baskin and Baskin 1992), long-term management is necessary to eliminate established

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populations. Application of glyphosate herbicide appears to be an effective control strategy (Nuzzo 1991, 1996, Carlson and Gorchov 2004). Spring herbicide application is advantageous to fall application because it affects both cohorts (flowering-age plants and seedlings), while fall herbicide application affects only rosettes. However, glyphosate is a nonselective herbicide, affecting most photosynthetic vegetation (Monsanto 2002). Since many affected forest communities are characterized by a rich early spring flora, dormant-season fall spraying is desirable to minimize damage to native plants. Since fall spraying affects only one cohort, herbicide application must be repeated in successive years to eliminate newly germinated plants, as seeds are not affected by glyphosate (Nuzzo 1991). Nuzzo (1991) tested the efficacy of three herbicides in reducing *A. petiolata* cover and minimizing impacts on native species. Glyphosate, applied at 1% and 2% concentration, was found to be superior to bentazon and acifluorfen in this regard.

For a management treatment to be effective, herbicide must not only kill the treated plants, but eradicate populations or reduce them sufficiently so that the treatment does not need to be repeated indefinitely. Carlson and Gorchov (2004) found that two consecutive fall-season glyphosate applications in 2000 and 2001 significantly reduced *Alliaria petiolata* density in sprayed plots compared to unsprayed plots. However, *A. petiolata* density declined over the same period in the unsprayed plots as well. One possible explanation for the decline may be a lack of disturbance in these plots. Nuzzo (1999) found that *A. petiolata* invasion was facilitated by disturbance, ranging from windthrow to flooding. In the absence of disturbance, cover of *A. petiolata* declined (Nuzzo 1999). Anderson et al. (1996) proposed that micro-site disturbances might facilitate establishment by providing small sites with reduced competition. Meekins and McCarthy (2001), on the other hand, found no effects of leaf litter removal on *A. petiolata* survival, growth, or reproduction. These findings warrant further investigation of the importance of leaf litter disturbance on *A. petiolata* populations.

Variation in *Alliaria petiolata* cover and density among years could also be due to intrinsic factors such as previous year's seed production and inter-cohort competition or extrinsic factors such as weather. *A. petiolata* not only shows substantial within-cohort density-dependence in growth and survival (Meekins and McCarthy 2000, 2002), but also intraspecific competition between the adult and rosette cohort (Winterer et al. 2005). Rosette plants growing in association with adult plants died at a higher rate than rosette plants growing in patches lacking adult plants, and rosettes achieved much higher densities in patches lacking adults than in mixed patches of rosettes and adults (Winterer et al. 2005). These findings warrant further investigation of the effects of inter-cohort competition on *A. petiolata* populations. We focused on late spring and summer precipitation as a possibly important extrinsic factor affecting *A. petiolata* populations because we hypothesized that precipitation may impact survival of rosettes over the growing season and the number of surviving adults the following spring, since this species is associated with moist sites (Grime et al. 1987) and demographic rates are typically higher in forested floodplains than upland forests (Byers and Quinn 1998, Meekins and McCarthy 2001).

The objective of our research was to assess the effectiveness of herbicide application in reducing *Alliaria petiolata* populations and to evaluate other factors possibly affecting *A. petiolata* population fluctuation. We extended the experiment established by Carlson and Gorchov (2004) an additional three years in order to answer three main questions: 1) Does fall glyphosate application, repeated over several years, reduce *A. petiolata* cover over time? 2) Is *A. petiolata* density correlated with the percentage of the forest floor characterized by bare ground? 3) Is *A. petiolata* density affected by inter-cohort competition and/or summer precipitation?

Methods. STUDY SITE. Experiments were carried out in two forest stands at Hueston Woods State Nature Preserve, a forested natural area occupying portions of Preble and Butler Counties in southwestern Ohio, USA. Most of the nature preserve is dominated by old-growth beech (*Fagus grandifolia* Ehrh.)-sugar maple (*Acer saccharum* Marsh.) forest, with those species comprising nearly 90% of the canopy (Runkle et al. 1984). The forest is underlain by soils of the Russell-Xenia association, well-drained and moderately well-drained deep soils underlain by calcareous till (Lerch et al. 1969). Areas with slightly- to moderately-sloping topography are underlain by Russell Silt Loam, while Cosco, Rodman, and Fox soils occupy portions of the preserve with steeper, more eroded topography (Lerch et al. 1969). The site lies approximately 20 miles north of the southern limit of the Wisconsinan glaciation and is situated near the southern limit of the beech-maple forest region (Braun 1950).

Experimental Design. In May 2000, Carlson and Gorchov (2004) established 50 1 × 1 m plots in each of two forest stands, one a 20-ha *Fagus-Acer* old-growth (many canopy trees > 200 years old) stand (39° 34′ 07″ to 39° 34′ 00″ N, 84° 45′ 10″ to 84° 45′ 02″ W), and the other a 16-ha second-growth (trees ca. 50–100 years old) stand dominated by *Liriodendron tulipifera* L. (tulip-tree) (39° 34′ 33″ to 39° 34′ 31″ N, 84° 45′ 41″ to 84° 45′ 37″ W). Plots were placed in areas of high *Alliaria petiolata* density with the stipulation that plots were spaced at least 5 m apart and situated away from drainages, trails, and treefall gaps. Within each stand, 25 plots were randomly assigned to receive yearly herbicide applications, and the other 25 plots were assigned to an unsprayed control group. Each November 2000–2004, after leaf-fall, *A. petiolata* individuals within 2 m of the center (≈ 12.6 m^2) of each sprayed plot were spot-sprayed using backpack sprayers with a 1% glyphosate solution. The glyphosate solution was prepared by dilution of 0.08 L Roundup© PRO (41% glyphosate, in the form of isopropylamine salt) with 7.6 L water. To prevent repeated spraying, the herbicide contained blue coloring. Leaf litter within the plots was not manipulated, so *A. petiolata* individuals covered by leaves were not sprayed unless visible in the absence of manipulation.

Data Collection. *Alliaria petiolata* adult density was counted each February or March, as well as May and June, 2001–2005. Rosette density was counted in May, June, and October, 2000–2005. Rosettes represented new plants that emerged following the previous fall's herbicide application. Percent cover of adults and rosettes was estimated using a point frame in May and June of each year, 2000–2005. Each plot was sampled with 50 pin drops, with each pin touch corresponding to 2% cover. In 2003, three unsprayed plots and two sprayed plots in the old-growth stand, and two sprayed plots in the second-growth stand, were severely impacted by tip-up mounds or fallen limbs, and were therefore dropped from the analyses. In 2004, two additional unsprayed plots and one sprayed plot in the old-growth stand were lost and dropped from the analyses, leaving 20 unsprayed plots and 22 sprayed plots. In 2005, one of the lost unsprayed plots in the old-growth stand was relocated, but two additional sprayed plots were lost and dropped from the analyses. All 50 plots in the second-growth stand were analyzed in 2005.

The percent of each plot comprised of bare ground (as opposed to leaf litter) was estimated visually prior to leaf fall in October 2002 and was quantified with the point frame sampling in May 2003. Monthly precipitation values (cm) for the years 2000–2005 were obtained from the Ohio Agricultural Research and Development Center (OARDC) weather station at the Ecology Research Center (ERC) of Miami University, Butler County, Ohio, ca. 5 km SE of the study sites.

Data Analysis. All analyses were performed using the SAS Statistical Package, version 9.1.3 for Microsoft® Windows (SAS Institute, Inc. 2001). The effect of fall application of glyphosate over five successive years on *A. petiolata* adult cover each May was assessed with non-parametric tests, because cover was 0% in many plots, particularly in the later years of the study. We used Friedman's method for randomized blocks (Sokal and Rohlf 1995) with stands as blocks, using SAS PROC FREQ.

We tested the effect of glyphosate on May *Alliaria petiolata* rosette cover across years, with a univariate repeated measures ANOVA with a split-plot design with stands as the split plots, in SAS PROC GLM. To meet the assumptions of homogeneity of variance, cover values were arcsine square root transformed (Littell et al. 1991). In this analysis the appropriate *F*-test for the effect of treatment uses, as the denominator, the mean square of the plot (stand*treatment) term, to account for the correlated response (in rosette cover) within plots among years.

To assess whether leaf litter disturbance explained variance among plots in *Alliaria petiolata* density, analyses of covariance (ANCOVAs) with Type III sums of squares were used to test effects of May 2003 percent bare ground on May 2003 and October 2003 *A. petiolata* rosette density. Stand and spray treatment were treated as factors and percent bare ground was assigned as the covariate. To account for differences among plots in adult cover, we included log-transformed May 2002 adult cover as an additional covariate. Significance level was adjusted to $\alpha = 0.025$ using the Bonferroni correction to account for multiple tests. The interaction of bare ground and herbicide was not significant for either May or October rosette density, so the data were analyzed using simplified ANCOVA models with no interaction terms.

To assess whether rosette density of *Alliaria petiolata* is negatively affected by competition with adults, we analyzed data from unsprayed plots each year (2001–2005) with an ANCOVA with Type III sums of squares. The response variable in each ANCOVA was log-transformed May rosette density, the factor was stand, and the covariate was May adult density. We did not include sprayed plots, because these mostly had zero or very low densities of adults. For each of the five ANCOVAs the interaction between stand and adult density was not significant ($P >$ 0.16), indicating that the relationship between rosette and adult density did not differ between the stands. Therefore each year's data was reanalyzed with a reduced ANCOVA model that did not include the interaction term.

To explore whether inter-annual *Alliaria petiolata* density was associated with summer precipitation, we plotted the relationship between density of rosettes in unsprayed plots in October 2000–2005 and precipitation the previous April, May, June, July, August, and September. We made similar plots using density of adults the following May (2001–2005) as the dependent variable. Only June precipitation showed strong trends with *A. petiolata* density; therefore we used this as the predictor variable in regressions of October rosette density and the following May adult density. In addition, we regressed the average survival of *A. petiolata* rosettes from May to October on June precipitation. For each of these three regressions stands were treated as replicates, thus we had two values for the *A. petiolata* parameter for each of the six years: the average from old-growth plots and the average from second-growth plots.

Results. May *Alliaria petiolata* adult cover varied greatly across years in unsprayed plots, particularly in the old-growth stand, but in the sprayed plots declined across years and remained very low, averaging less than 1% in each stand each year from 2003 through 2005 (Fig. 1 A, B). Before herbicide application began in November 2000, adult cover (May 2000) was initially similar between treatments, but it differed significantly between treatments in three of five years (2001, 2003, and 2004) (Table 1). In the other two years (2002 and 2005) adult cover was very low ($\leq$ 4%) in unsprayed as well as sprayed plots in both stands (Fig. 1A, B).

May *A. petiolata* rosette cover fluctuated across years, particularly in the old-growth stand, but remained below the initial values of May 2000 (Fig. 1 C, D). However, there was no significant effect of spray treatment, or treatment*year interaction in rosette cover (Table 2).

Adult and rosette densities changed over years across treatments in patterns similar to that found for adult and rosette cover, except that fluctuations were wider, and final (May 2005) rosette density exceeded initial (May 2000) density in unsprayed second-growth plots and both sprayed and unsprayed old-growth plots (Fig. 2).

In May 2003 the density of *A. petiolata* rosettes in plots was positively related to the percent bare ground (Fig. 3). ANCOVA revealed an overall model effect on May 2003 *A. petiolata* rosette density, but the effect of May 2003 percent bare ground was not significant, given the adjusted α of 0.025 (Table 3). Rosette density was marginally reduced by herbicide, positively affected by the plot's May 2002 adult cover, and differed between the stands (Table 3). By October 2003, rosette density was not significantly explained by bare ground, spray treatment, or stand, based on ANCOVA, although it was still positively related to the cover of the previous adult cohort (Slaughter 2005).

Density of *A. petiolata* rosettes was not dependent on the density of adults in the same plot. In one year, 2003, there was a non-significant *positive* relationship between log-transformed May rosette density and adult density the same month (ANCOVA, slope = 0.066, t = 1.72, P = 0.09). For each of the other four years of the study the ANCOVA

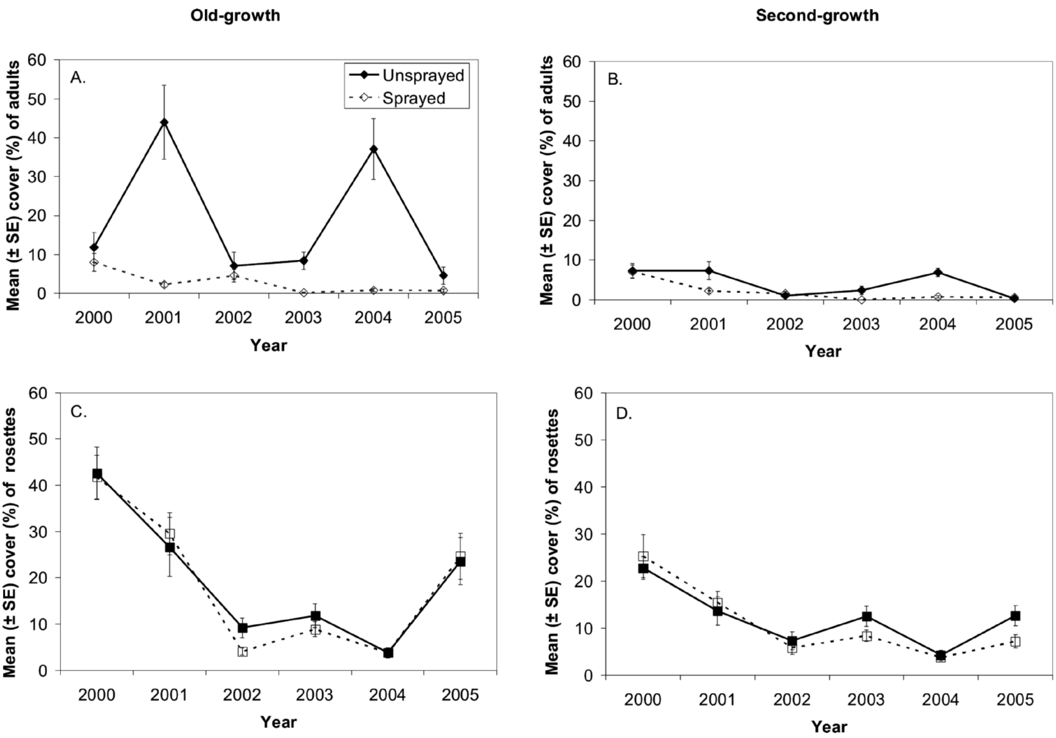

FIG. 1. Mean (± SE) May *A. petiolata* adult and rosette cover in each stand (A: old-growth adult cover, B: second-growth adult cover, C: old-growth rosette cover, D: second-growth rosette cover), 2000–2005. Means based on 25 1 × 1 m plots per treatment, per stand, except as reduced by treefall in 2003–2005.

revealed no dependence of rosette density on adult density (*t*-test of slopes $P > 0.24$).

Variation among years (2000–2005) in survival of *Alliaria petiolata* rosettes from May through October (unsprayed plots only) was positively related to June precipitation (Fig. 4; $F = 9.03$, df = 1, 10, $P = 0.0132$, $R^2 = 0.47$). Density of rosettes in October showed a similar, but not significant, pattern (linear regression $F = 4.24$, df = 1, 10, $P = 0.0664$).

Table 1. Effect of treatment (sprayed vs. unsprayed) on adult *A. petiolata* cover (Fig. 1) on 1 × 1 m plots each May, determined by Friedman's method for randomized blocks. Stands (old-growth, second-growth) were the blocks. CMH is the Cochran-Mantel-Haenszel Statistic determined from the rank scores. **Bold** indicates significance at $\alpha = 0.05$.

Year	*N*	CMH	*P*
2000	100	0.02	0.88
2001	100	11.8	**<0.0001**
2002	100	1.54	0.21
2003	93	24.1	**<0.0001**
2004	90	40.47	**<0.0001**
2005	91	0.13	0.72

May *A. petiolata* adult density across years (2001–2005) was also positively related to the previous June's precipitation (Fig. 5; $F = 9.23$, df = 1, 10, $P = 0.0161$, $R^2 = 0.54$).

Discussion. Over the course of five years, spot-spraying *Alliaria petiolata* with glyphosate in the fall was effective at reducing adult cover. While this herbicide application did not kill all *A. petiolata* individuals, survival was significantly lower in sprayed plots in four out of the five years (unpubl. data). Cover of adults decreased from ca. 8% before herbicide (2000) to less than 1% each year from 2003–2005, when adult *A. petiolata* cover was 0% in > 45% of the plots in each stand. Adult cover was significantly lower in sprayed plots in three of the five years; the lack of statistical significance in the other two years was due to the extremely low cover in unsprayed, as well as sprayed, plots.

Rosette density and cover, on the other hand, were generally not affected by spray treatment. Of course we did not expect the rosette cohort to be directly affected by herbicide, since these individuals were in the

Table 2. Univariate repeated measures ANOVA of May *Alliaria petiolata* rosette cover from 2000 through 2006, analyzed with a split-plot design with stands (old-growth, second-growth) as the split plots. The appropriate *F* test for "Treatment" (sprayed vs. unsprayed) is that given on the bottom line, where the denominator is the mean square of the plot (stand*treatment) term. Cover was arcsine square root transformed to meet assumption of homogeneity of variances. **Bold** indicates significance at $\alpha = 0.05$.

Source term	df	MS	*F*	*P*
Model	109	0.70	5.80	**<0.0001**
Error	460	0.12		
Corrected Total	569			
Stand	1	3.10	25.88	**<0.0001**
Treatment	1	0.10	0.86	0.3550
Year	5	8.65	72.09	**<0.0001**
Treatment*Year	5	0.23	1.89	0.0952
Plot(Stand*Treatment)	97	0.29	2.41	**<0.0001**
Hypothesis test using the MS for Plot (Stand*Treatment) as the Error term				
Treatment	1	0.10	0.36	0.5524

seed stage during fall herbicide application. Nevertheless, we expected the dramatic reduction in adult cover and density due to herbicide would greatly reduce seed production and therefore seedling recruitment in the sprayed plots, and the absence of such an herbicide effect begs explanation.

One possible reason why rosette density failed to decline over five years of herbicide treatment would be release from inter-cohort competition with adults. If such inter-cohort competition is important, as it is in central Pennsylvania (Winterer et al. 2005), then the smaller number of *A. petiolata* seeds that would be expected in sprayed plots would have higher germination, establishment, or early survival than the larger number in unsprayed plots, because sprayed plots consistently had fewer adults. However, we found no evidence for this inter-cohort competition; in no year was there a significant negative slope of May rosette density on May adult density across plots, although there was a trend for a positive slope in one of the five years.

A second potential explanation is that viable *Alliaria petiolata* seeds persisted in the soil. After removing every flowering individual from *A. petiolata* populations for three successive years, Drayton and Primack (1999) found that 25% of these populations persisted and even increased over that timeframe. They concluded that new plants were most likely germinating from a large seed bank. While seeds are thought to be viable in the soil for up to five years, most germinate the first spring, and only very small percentages germinate after two years (Roberts and Boddrell 1983, Baskin and Baskin 1992). If germination from a seed bank was responsible for recruitment of *A. petiolata* in sprayed plots, we would expect ever-decreasing numbers of rosettes over the five years of treatment. Instead, *A. petiolata* rosette density fluctuated in the unsprayed plots, and in the old-growth stand was higher in 2005 (268 individuals/m^2) than it was in any other year (Fig. 2). Therefore, the seed bank is an unlikely explanation for persistence of *A. petiolata* in sprayed plots.

The most likely explanation for the persistence of *Alliaria petiolata* rosettes in sprayed plots is seed dispersal from *A. petiolata* adults growing outside the 2 m diameter treated area. Nuzzo (1999) found that *A. petiolata* populations spread regionally at an average rate of 5.4 m/yr in northern Illinois, primarily through ballistic dispersal of seeds from fruiting adults, but aided by disturbance and seed vectors (including humans). Although off-trail human traffic is prohibited in Hueston Woods State Nature Preserve, seed dispersal is apparently sufficient to spread *A. petiolata* seeds into our sprayed plots from surrounding unsprayed areas. Therefore, in order for fall herbicide application to control this biennial, larger areas need to be treated.

The trend for May 2003 *Alliaria petiolata* rosette density to be positively affected by May 2003 bare ground is consistent with the notion that leaf litter disturbances facilitate *A. petiolata* establishment and growth (Anderson et al. 1996). Nuzzo (1999) found that *A. petiolata* cover declined in the absence of disturbance. Disturbance in the form of leaf litter removal and/or movement, creating

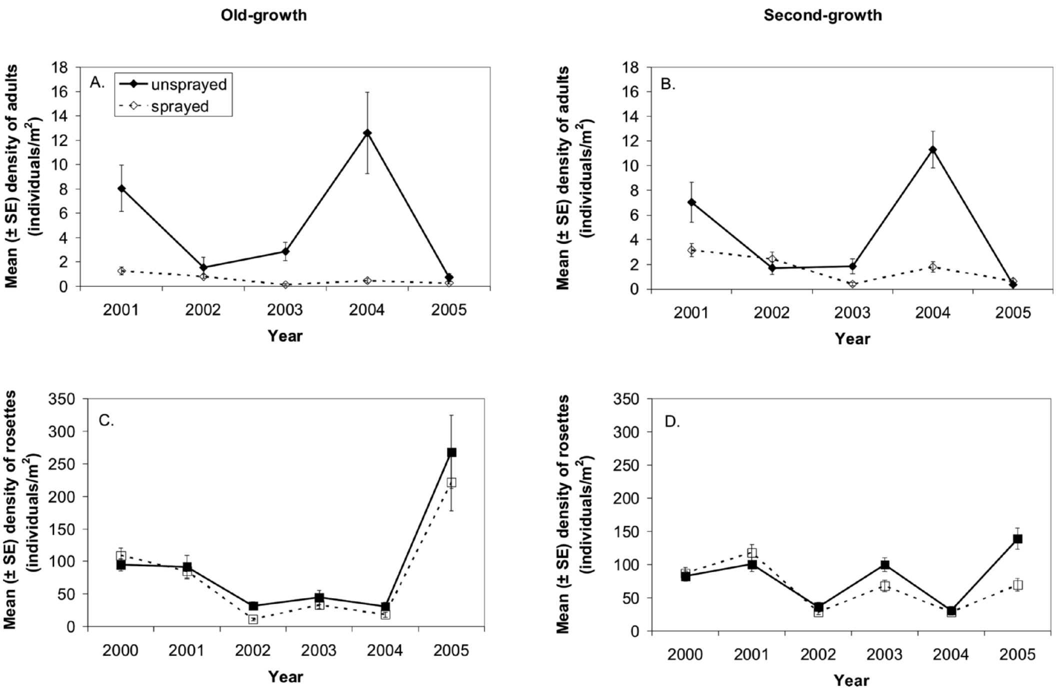

FIG. 2. Mean (± SE) May *Alliaria petiolata* adult (2001–2005) and rosette (2000–2005) density in each stand (A: old-growth adult density, B: second-growth adult density, C: old-growth rosette density, D: second-growth rosette density). Means based on 25 1 × 1 m plots per treatment, per stand, except as reduced by treefall in 2003–2005.

patches of bare ground, may aid in the persistence of *A. petiolata* in our plots. On the other hand, absence of such disturbance may lead to population declines.

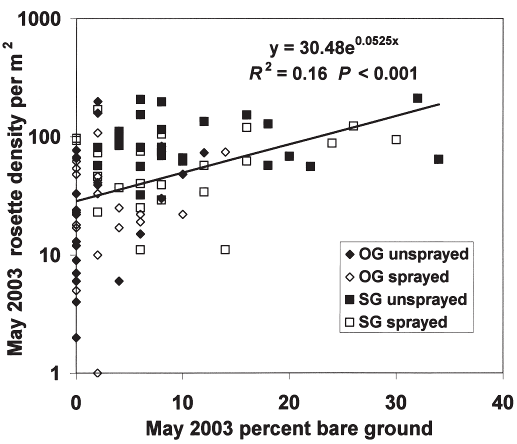

FIG. 3. May 2003 *Alliaria petiolata* rosette density (log scale) vs. May 2003 percent bare ground, both stands, both treatments (93 1 × 1 m plots total). Regression line is based on plots in all stand*treatment combinations, y variable is (density +1).

By October 2003, however, *Alliaria petiolata* rosette density was no longer affected by May bare ground, but it was still correlated with the cover of *A. petiolata* adults the previous May. This effect of the previous *A. petiolata* cohort's cover is presumably due to in situ seed input, since seed production depends on the size of overwintering rosettes (Byers and Quinn 1998) and the height of adults (Smith et al. 2003). Although disturbance or lack thereof may affect *A. petiolata* populations in our plots,

Table 3. ANCOVA of ln(x+1) May 2003 *Alliaria petiolata* rosette density in 1 × 1 m plots on treatment (sprayed vs. unsprayed), stand, May 2003 bare ground, and ln(x+1) May 2002 *A. petiolata* adult percent cover in the same plots. **Bold** indicates significance at α = 0.025.

Source term	df	MS	*F*	*P*
Model	4	9.07	15.06	**<0.0001**
Error	86	0.60		
Corrected Total	90			
Bare ground May 2003	1	2.32	3.85	0.053
Treatment effect	1	2.94	4.89	0.030
Stand	1	15.96	26.50	**<0.0001**
May 2002 *A. petiolata* adult cover	1	8.98	14.92	**0.0002**

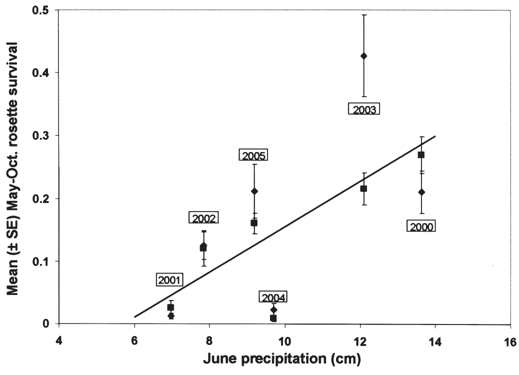

FIG. 4. Mean (± SE) survival of *Alliaria petiolata* rosettes from May to October versus June precipitation, 2000–2005, in old-growth (diamonds) and second-growth (squares) stands. Each point represents the mean of 25 1 × 1 m unsprayed plots within a stand, except as reduced by treefall in 2003–2005. Regression line is $S = 0.036(P) - 0.205$, where S = survival (=October density / May density) and P = June precipitation in cm.

May bare ground does not appear to be a significant predictor of density at the end of the growing season. This is consistent with the findings of Meekins and McCarthy (2001) that leaf litter removal had no significant effect on *A. petiolata* germination, rosette survival, growth, or reproduction. In fact, the benefits of bare ground (e.g., increased availability of sunlight, increased soil temperature, reduced competition) may be outweighed by negative impacts, such as reduced soil moisture (Meekins and McCarthy 2001). Disturbance likely affects *A. petiolata* germination and establishment, but our measure of bare ground may not adequately reflect important disturbance events, and self-thinning may dampen these effects over the life of the cohort.

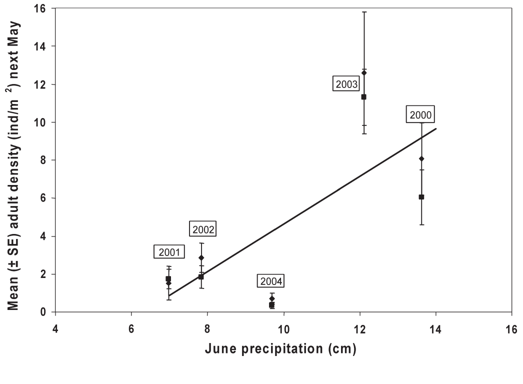

FIG. 5. Mean May *Alliaria petiolata* adult density vs. the previous year's June precipitation, 2001–2005, in old-growth (diamonds) and second-growth (squares) stands. Each point represents the mean (± SE) of 25 1 × 1 m unsprayed plots within a stand, except as reduced by treefall in 2003–2005. Regression line is $A = 1.253(P) - 7.890$, where A = adult density and P = June precipitation in cm.

Annual survival rate of *Alliaria petiolata* rosettes from May through October was strongly correlated with June precipitation, as was adult density the following May, when the rosettes became flowering adults. June precipitation may enhance rosette growth and, in turn, enhance survival through the following summer, fall, and winter months. An alternative explanation for interannual variation in density—the previous year's seed production—can be rejected, since interannual variation in October rosette density was not affected by the previous May's adult cover (unpublished analyses). Precipitation later in the life cycle (November–June of the second year) may also be important to *A. petiolata* demography; winter-spring survival, size, and fecundity of second-year plants was greater in a wet vs. a dry year (Rebek and O'Neil 2006).

While this is the first study to link interannual variation in *A. petiolata* density to precipitation, other studies have shown that spatial variation in soil moisture affects *A. petiolata* establishment, growth, survival, and reproduction. Byers and Quinn (1998) found that *A. petiolata* rosettes died in dry summer months, and mortality was higher in upland forests than in a floodplain forest. Meekins and McCarthy (2001) found that plants growing in lowland forest had a greater probability of surviving to become rosettes, greater survival to reproduction, and had greater mean seed production, than plants growing in upland forest. Our hypothesis that mortality is highest in years with low June precipitation is consistent with these demographic data.

Our findings have several implications for management and control of *A. petiolata*. Although fall herbicide application greatly reduced adult *A. petiolata*, the appearance of new rosettes each year means the population of this invasive species would recover as soon as spraying is terminated. If our inference that recruitment of new rosettes is due to seed dispersal from nearby unsprayed areas is correct, then treatment of larger areas should be much more effective. Application of herbicide earlier in the fall should also be considered, to maximize activity of the herbicide and minimize the number of rosettes that escape spray by virtue of being leafless or covered with leaf litter. Although bare ground appeared to have a minimal effect on *A. petiolata* rosette density, care should be taken to avoid unnecessary disturbance that may aid seed dispersal and subsequent expansion of the population. Park employees or land managers with limited resources should focus on applying herbicide in years of high June precipitation, as soil moisture appears to strongly affect population density.

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