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EFFECT OF ENVIRONMENTAL VARIATION ON THE INVASIVE SUCCESS OF A NONINDIGENOUS FOREST HERB

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Abstract. With the ever-burgeoning spread of nonindigenous plants, often facilitated by human activities, it is imperative to conduct case studies of particular invasive plants and the sites they invade in order to develop effective and efficient habitat management strategies. *Alliaria petiolata* is a native European biennial mustard that has become a serious invasive pest in many North American forests. In order to better characterize habitat vulnerability to invasion by *A. petiolata*, we conducted an experiment to test the effects of environmental heterogeneity in the form of habitat, microenvironment, and small-scale litter disturbance on *A. petiolata* germination, survival, growth, and reproduction. Treatments consisted of two habitats (upland and lowland), two microenvironments (forest edge and forest interior), and three small-scale litter disturbance treatments (control, litter completely removed, and litter partially removed). Seeds were sown into plots in November, and plots were monitored for two years. Lowland plots had greater soil moisture and less litter per unit area than upland plots. In general, forest edge plots had greater understory cover and light availability and lower overstory cover than forest interior plots. Rosette survival, mature plant survival, plant biomass, height, and fruit and seed production were significantly greater for plants in the lowland compared with plants in the upland. Germination, rosette survival, mature plant survival, and reproduction were significantly greater in the forest edge plots when compared with interior plots. Litter disturbance had no significant effect on germination, growth, or reproduction. It is apparent that site colonization by *A. petiolata* was not dependent on the creation of patches of bare soil by disturbance, since plants were capable of invading sites with an intact litter layer. *Alliaria petiolata* growth and reproduction was greatest in plots with adequate soil moisture and increased light availability. Therefore, mesic forests with a more open canopy structure and forest trails or edges may be the most vulnerable to invasion and the most difficult sites to manage. Drier upland forest interiors, which were more resistant to invasion, may be more responsive to management techniques.

Key words: *Alliaria petiolata*; colonizing ability; edge effects; exotic; garlic mustard; habitat; litter disturbance; microenvironment; upland vs. lowland plant survival.

INTRODUCTION

As scientific attention continues to focus on the ever-expanding spread of species into new regions, it has become apparent that detailed experiments to document the factors contributing to the establishment and proliferation of these species need to be conducted as part of our effort to predict the success of an invasion (Mooney and Drake 1986). The issue of invasive species has been approached from two angles: the idea that certain characteristics of the organism give it an advantage in particular environments and contribute to its invasiveness and the idea that certain habitats are more susceptible to invasion (Baker 1965, Bazzaz 1986, Crawley 1987, Heywood 1989, Hobbs 1989, Lonsdale 1999).

Many characteristics have been associated with invasiveness or weediness of plant species, including

high population growth rates, short generation times (Bazzaz 1986), production of small seeds (Bunting 1960), and a seed bank (Templeton and Levin 1979), no special environmental conditions needed for germination, fast seedling growth, a high degree of phenotypic plasticity, rapid attainment of reproductive maturity, self-compatibility or generalized pollination syndrome, quick flowering times, high seed yield, effective long-range dispersal ability, vegetative reproduction, and high competitive ability (Baker 1965). These attributes are thought to give an invasive plant an advantage in colonizing a new habitat and proliferating once established (Baker 1965, Bazzaz 1986), potentially to the detriment of other species within the community (Crawley 1987). However, invasion success also depends on propagule pressure (Lonsdale 1999), environmental characteristics, and the interaction between the organism and its recipient environment; therefore, species traits alone probably cannot be used to predict whether a particular species will be invasive (Williamson 1996).

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It is likely that all communities are invasible (Crawley 1987, Usher et al. 1988), although susceptibility may vary. Attributes commonly associated with habitat invasibility include low species richness, location near a source of potential immigrants, and habitat similarity between source and colonized areas (Crawley 1987). Species-poor communities are assumed to be more prone to invasion than those that are species rich (Elton 1958, Lodge 1993). However, communities with high species richness may actually be more vulnerable to invasion because these habitats have plentiful resources (Knops et al. 1995, Robinson et al. 1995, Wisser et al. 1998, Lonsdale 1999). In addition, the physical characteristics of a habitat such as light availability (Maule et al. 1995) and soil fertility can contribute to its invasibility (Hobbs 1989, Huenneke et al. 1990, Pyšek and Pyšek 1995).

Another aspect of habitats linked with, and often considered to be a prerequisite of, invasion is disturbance (Oriens 1986, Crawley 1987, Nuzzo 1993), the "sudden change in the resource base in a habitat that is expressed as a readily detectable change in population response" (Bazzaz 1996). Disturbance may affect relationships among community members, soil topography, and plant biomass (Oriens 1986). It may be natural or anthropogenic in origin, and its impact is determined by its frequency and intensity (Westman 1990). Often, human perturbation of a habitat through the removal of the native vegetation is implicated as the major causal factor in an invasion (Heywood 1989), and invasive plants may have special adaptations that enhance their ability to grow in areas subject to anthropogenic disturbance (Barbour et al. 1999). However, even mature forests with infrequent disturbance can be invaded by some nonindigenous species (Saunders et al. 1991, McCarthy 1997).

Often, studies of invasions are conducted after the invasion has occurred (Wisser et al. 1998), making it difficult to determine which factors facilitated the initial entry of the species into the new habitat. In addition, due to dispersal limitation an invasive organism may only occupy a subset of suitable sites, but as the area becomes more saturated with the invader, suitable sites may become more fully occupied (Wisser et al. 1998). Therefore, it is necessary to conduct experiments in which the invasive species is introduced into a variety of the environments that it is likely to encounter in its non-native range.

Alliaria petiolata (Bieb.) Cavara & Grande is an herbaceous mustard native to Europe that was introduced to North America (Gleason and Cronquist 1993), possibly by European colonists who valued its medicinal and edible properties (Grieve 1985). It was first documented in North America in New York in 1868 and is now a prevalent invader across the continent (Nuzzo 1993). *Alliaria petiolata* is a strict biennial; rosettes formed the first year bolt and produce flowers the second year, then senesce by autumn (Baskin and Baskin

1992, Byers and Quinn 1998). It has broad ecological amplitude, invading both forested upland and lowland communities (Nuzzo 1993, McCarthy 1997), where it commonly displaces native species (McCarthy 1997).

Alliaria petiolata is a fast-growing (Cavers et al. 1979), self-compatible herb (Anderson et al. 1996, Cruden et al. 1996) that produces numerous small dormant seeds (Trimbur 1973, Baskin and Baskin 1992) and a short-lived seed bank (Baskin and Baskin 1992); therefore, just one or a few individuals can quickly establish a new population (Cruden et al. 1996). It has been characterized as a competitive-ruderal species (Grime et al. 1988), able to exploit areas with low stress conditions and high disturbance (Grime 1979, Grime et al. 1988). It can competitively interfere with neighboring species (McCarthy 1997, Meekins and McCarthy 1999) and shows great phenotypic plasticity in response to habitat variation (Byers and Quinn 1998) and light environment (Dhillon and Anderson 1999, Meekins and McCarthy 2000).

Alliaria petiolata invasion is purportedly disturbance mediated, with plants commonly invading habitats subjected to either natural disturbance, such as riverbanks and floodplains, or to anthropogenic disturbance, such as trailsides, roadways, and forest edges (Cavers et al. 1979, Nuzzo 1993). Disturbance, which can remove litter and the extant vegetation, may provide an entry point into a new habitat and can also facilitate spread of established populations. It is not known whether continued disturbance is necessary for the expansion of an extant *A. petiolata* population (Nuzzo 1993).

The purpose of this experiment was to examine the effect on plant performance in response to some of the factors commonly associated with habitat invasion by nonindigenous plants including environmental characteristics and disturbance. In particular, we were interested in the role of fine scale environmental heterogeneity, in the form of disturbance to the leaf litter present on the forest floor, and coarser scale environmental heterogeneity, in the form of forest edge effects and abiotic and biotic variation due to slope position, on the germination, growth, survival, and reproductive capacity of the invasive forest herb, *Alliaria petiolata*. Information concerning the susceptibility of particular sites to invasion by a specified nonindigenous invasive species is critical to developing a management intervention strategy. The results of this experiment, in conjunction with demographic data, will be useful in determining which communities to target for *A. petiolata* monitoring and eradication programs.

METHODS

Study site

The experiment was conducted within the Ridges Land Laboratory (39°19'30" N, 82°07'05" W; United States Geological Survey 1995), a second-growth hardwood forest in Athens County in southeastern Ohio,

USA. This area is part of the unglaciated Allegheny Plateau Region and is characterized by highly dissected topography with rolling hills (Peacefull 1996). The lowlands and north- and east-facing slopes within the Ridges Land Lab are predominately mesic beech-maple forests, while the uplands and south- and west-facing slopes are more xeric oak-hickory forests.

Site elevations range from ~200 m to 249 m (United States Geological Survey 1995). Soils in the study sites are classified as Westmoreland-Guernsey silt loams with 25–40% slopes, some dissected by drainageways and are generally moderately well to well drained, acidic or alkaline, and of medium to low fertility (Lucht et al. 1985, Nash and Gerber 1996). Climate is classified as continental (Lucht et al. 1985). Total annual precipitation is 96.5 cm, with ~35 cm falling as snow. The growing season extends from April through September with a mean of 52.5 cm of precipitation falling during this period. Precipitation is evenly distributed throughout the year. The mean winter temperature is 0°C, with a mean minimum of -6.1°C, and the mean summer temperature is 21.7°C, with a mean maximum of 29.4°C.

Experimental design

Plots were established in two upland ridgetop sites and two lowland stream bottom sites, separated by drainageways. Although some small naturalized populations of *A. petiolata* exist within the Ridges Land Lab, no *A. petiolata* plants were naturally occurring in the plot sites. All sites had a southeast orientation. The overstories of the upland sites were dominated by *Quercus alba*, *Q. velutina*, *Fraxinus* spp., and *Acer saccharum*, while the understories were dominated by *A. saccharum* saplings. Common species of the herb layer included *A. saccharum* and *Fraxinus* spp. seedlings, *Claytonia virginica*, and *Galium* spp. *Quercus alba*, *Q. rubra*, *A. saccharum*, *Aesculus flava*, and *Liriodendron tulipifera* were canopy dominants in the lowland sites. *Asimina triloba* and *A. saccharum* were the most common understory woody plants. *Viola pubescens*, *Claytonia virginica*, *Polygonum virginiana*, and *Pilea pumila* were the most dominant herbs in the lowland sites.

Fifteen plots were located at each of the four sites. Five plots at each site were located in the forest edge microenvironment within 1 m of the forest boundary, and the remaining 10 plots were located under the closed forest canopy (forest interior) at least 20 m from the forest edge. The forested areas were contiguous and surrounded by annually mowed fields. Edge plots were randomly located along a transect following the forest edge, with a minimum of 2 m between adjacent plots. Originally, five forest sites were to be located under canopy gaps and five under closed canopy, but the gaps present in this forest were of such a small diameter that there were no detectable differences in light, moisture, or species composition in patches under small

gaps and under closed canopy; therefore, ten plots were instead located randomly within the forest at a minimum distance of 2 m. Each plot was 1.5 × 0.5 m and was divided into three contiguous 0.5 × 0.5 m subplots. Three litter treatments were used to test for the effect of microhabitat disturbance on *A. petiolata* performance. All of the leaf litter was removed from one subplot (litter absent), half of the litter was removed from the second subplot (low litter), and the third subplot was left undisturbed (control). Each of these three litter disturbance treatments was randomly assigned to the subplots within a plot and implemented. On 8 November 1996, 100 *A. petiolata* seeds that had been collected in Athens, Ohio, in July were sown into each subplot. The number of seeds used was chosen to simulate potential seed production by one or a few invading *A. petiolata* plants and was based on data collected from naturalized populations within the Ridges Land Lab (J. Meekins, unpublished data). Sown seed was allowed to stratify over the winter months and germinate naturally the following spring. Seed viability for seed to be sown was ascertained in the laboratory via a germination experiment. Six replicate glass petri dishes each containing 25 seeds and 5 mL distilled water were placed in darkness in a seed germinator at 4°C for 4 mo and germination was monitored. These conditions have been shown to be optimal for promoting germination (Baskin and Baskin 1992). Seed germination was 95.3% ± 1.9 (mean ± 1 SE).

In Ohio, seeds typically begin to germinate in late February (Trimbur 1973), so plots were monitored weekly beginning in mid-February 1997, and germination, denoted by the emergence of the cotyledons, and subsequent survival were scored on a weekly basis until June, when germination is typically complete (Trimbur 1973, Cavers et al. 1979). Survival of plants was then monitored every 2 wk until November 1997 and again from March until June 1998, by which time plants had flowered and produced seeds and begun to senesce. On 2 June 1998, all plants were harvested before seeds were released, dried at 80°C for 72 h, separated into roots, stems and leaves, and fruits, and weighed on a Mettler 200 AE balance (Mettler Toledo, Im Langacher, Switzerland). Plant height (height of the tallest stem if multiple stems were present), number of mature fruits with seeds, number of fruits without seeds, and number of seeds produced per fruit and per plant were also determined. Since some plots had several *A. petiolata* plants present at the time of harvest, a plot mean was calculated.

To better characterize the study sites, several environmental parameters were measured on a plot or subplot basis at the beginning of the study or throughout the course of the experiment: soil moisture, canopy cover, light, understory cover, litter depth, litter biomass, litter density, soil chemistry, and soil texture. To record subplot moisture levels, a Delmhorst moisture block (Delmhorst Instrument Company, Towaco, New

Jersey, USA) was buried at a depth of 7 cm in each subplot for three randomly selected plots within the forest interior and three plots along the forest edge at each of the four sites. Moisture was measured every two weeks during the growing season (March 1997–October 1997 and March 1998–June 1998). Percentage of canopy cover was monitored bimonthly for each plot during the growing season using a spherical densiometer held at 1 m above the ground. One reading was taken above the center of each subplot. A Li-Cor light meter (LI-1000; Li-Cor, Lincoln, Nebraska, USA) was used to measure solar radiation within each plot. Five readings were taken 20 cm above the ground between 1000 and 1400 within each plot, averaged, and compared with a mean value from five readings taken in an adjacent open field. Readings were taken on sunny days at 2-wk intervals. The identity and percent cover of all herbaceous and woody vegetation within each subplot was monitored on a monthly basis throughout the growing season.

Litter depth of each plot was measured using a pointed stick marked in metric units before litter treatments were instituted. Each plot was divided into 10 sections and litter measurements were taken from two randomly chosen sections and averaged. The approximate amount of litter biomass within each plot was determined by removing an amount of litter equal in area to that of one subplot (0.5×0.5 m) located 0.5 m away from each plot. The litter was dried at 80°C for 72 h and weighed. Litter density was then calculated as the amount of litter biomass (g) per subplot volume (area \times depth, cm³).

To document edaphic differences among sites, soil texture and chemistry were analyzed. Soil samples were collected from the A horizon of three forest interior plots and three forest edge plots at each of the four sites and sent to the Ohio Agricultural Research and Development Center in Wooster, Ohio, for analysis. The pH, cation exchange capacity (CEC), and quantity of potassium (K), phosphorus (P), magnesium (Mg), calcium (Ca), and nitrate nitrogen (NO₃N) in the soil samples were determined. Soil texture was analyzed using the hydrometer method to determine the percent of sand, silt, and clay for each soil sample (Sheldrick and Wang 1993).

Data analysis

Environmental differences in light availability, canopy cover, herb layer cover, and soil moisture among habitats and microenvironments were monitored for the duration of the experiment. We did not test for significant differences among these environmental variables since our objective in measuring these variables was simply to provide a baseline description of the sites and to indicate differences among these variables with respect to our treatments.

Site was considered a random effect in all preliminary statistical analyses but was not a significant term

so it was removed from subsequent analyses. Variation in litter depth, biomass, and density in relation to habitat and microenvironment was explored using a two-way general linear model (GLM) analysis of variance (ANOVA). Differences in ten soil variables among plots in relation to habitat and microenvironment were analyzed using a two-way multivariate analysis of variance (MANOVA). Main effects were considered fixed. Bonferroni tests were used to elucidate significant differences among treatment groups. Statistical procedures were performed using Number Cruncher Statistical Systems 97 (Hintze 1997).

Germination and survival data were analyzed separately with three-way GLM ANOVAs to test for the effects of habitat, microenvironment, and litter disturbance using Number Cruncher Statistical Systems 97 (Hintze 1997). Since we were specifically interested in *A. petiolata* performance in upland vs. lowland habitats, forest edge vs. forest interior environments, and litter removal, the three main effects were considered fixed. Reproductive and morphometric data were analyzed using a three-way multivariate analysis of covariance (MANCOVA) to test for the effects of habitat, microenvironment, and litter treatment with litter density as a covariate (SAS Institute 1990). Shoot biomass was removed from the analysis due to significant autocorrelation with the other variables included in the analysis (Hintze 1997). Litter density was not a significant factor in the MANCOVA (Wilks' lambda = 0.8638, $P = 0.7184$), so the data were then analyzed with a three-way MANOVA (SAS Institute 1990). Our experimental question is a multivariate one, so we chose a multivariate analysis to examine the response of reproductive and morphometric data to the independent variables studied because we wanted to examine the effects of these variables on *A. petiolata* growth and reproduction overall and also on each separate dependent variable measured. To investigate the effects of the treatments on each individual dependent variable measured, separate three-way protected GLM ANOVAs were performed, followed by Bonferroni tests adjusted for the number of tests we performed (Scheiner and Gurevitch 1993). Data for all statistical tests were log₁₀ transformed as necessary to meet the assumptions of normality and homogeneity of variances implicit in parametric statistical procedures.

In addition, to better understand the invasive potential of *A. petiolata*, reproductive rate (R) was determined using the formula

$$R = (S_{t+2})/S_t = gsF$$

where S_t was the number of seeds sown into the plots in 1996, S_{t+2} was the number of seeds produced by mature plants in 1998, g was the germination probability, s was survival of seedlings to reproductive plants in June 1998, and F was the mean seed production in June 1998 (Barbour et al. 1999). Data for R , g , s , F , and the survival of seedlings to rosettes in October

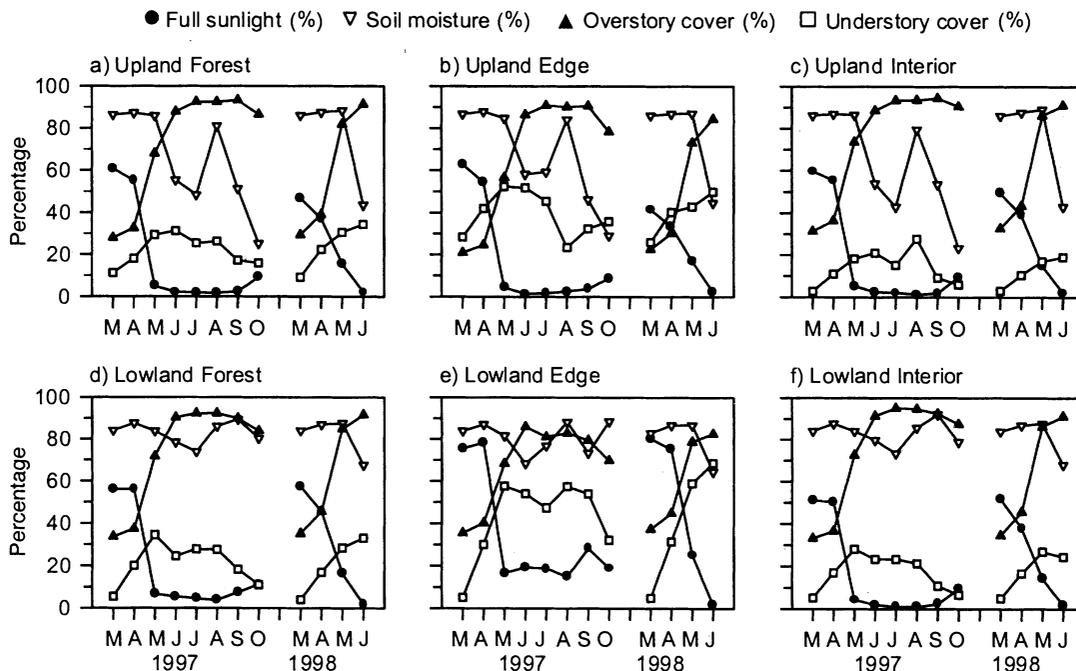


FIG. 1. Mean percentage of full sunlight, soil moisture, understory vegetation cover, and canopy cover measured monthly over the growing season from March 1997 to June 1998 in upland, lowland, forest interior, and forest edge plots in a forest in southeastern Ohio. Months included are March (M), April (A), May (M), June (J), July (J), August (A), September (S), and October (O). Data are pooled across all microenvironment and litter removal treatments within the upland for panel (a) and within the lowland for panel (d).

1997 were \log_{10} transformed and analyzed using a three-way GLM ANOVA to test for the effects of habitat, microenvironment, and litter disturbance.

RESULTS

Habitat description

There were clear differences among the upland and lowland habitats and the forest interior and forest edge microenvironments throughout the growing season (Fig. 1). Plots in the lowland had greater soil moisture levels than upland plots through the summer and autumn months, although there was no difference in soil moisture between upland and lowland plots in the moist spring months (Fig. 1a, d). Rainfall for the period during which the experiment was conducted ranged from 22.1 to 3.1 cm/mo (Scalia Laboratory for Atmospheric Analysis, Athens, Ohio, USA). These values fall within the slightly wet to extremely wet classification of the Palmer Drought Severity Index, which is used to classify soil moisture conditions (Palmer 1965).

Within the upland, forest edge plots had greater understory vegetation cover than forest interior plots, ranging from 26% at the beginning of the growing season to 50% in early summer, while understory cover for forest interior plots ranged from 3% to 21% (Fig. 1b, c). Within the lowland, forest edge plots had greater light levels, lower overstory cover, and greater understory cover than plots in the forest interior (Fig. 1e, f). Light measurements for forest edge plots ranged from

80% ($1440 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) of full sunlight before trees produced leaves in the spring to <15% ($270 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) after trees had produced fully expanded leaves. Light measurements for forest interior plots ranged from 50% ($900 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) of full sunlight at the beginning of the growing season to <1% ($18 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) over the summer months. Concomitant with the decrease in light reaching the forest understory was the increase in canopy cover with leaf out. On the forest edge, overhead cover ranged from 35% to 85%, while in the forest interior, overhead cover ranged from 35% to 95%.

There were 93 different species encountered overall, 67 in the upland plots and 77 in the lowland plots, with 49 species common to both upland and lowland sites. There were 70 species in forest edge plots and 67 in forest interior plots, with 44 species common to both habitat types. Maximum understory cover during the summer months was >50% in edge plots and 23% in forest interior plots. Percentage cover of *A. petiolata* was fairly low, ranging from 0.9% in March 1997 to 4.0% in June 1997 in upland plots (overall mean cover from germination to harvest 2.1%) and from 1.1% in March 1997 to 5.2% in June 1997 in lowland plots (overall mean 3.2%). Overall mean percentage of cover for forest edge (2.7%) and forest interior (2.7%) plots was very similar. Although some *A. petiolata* plants had already invaded a small portion of the Ridges Land Lab, the only *A. petiolata* plants that were found in the

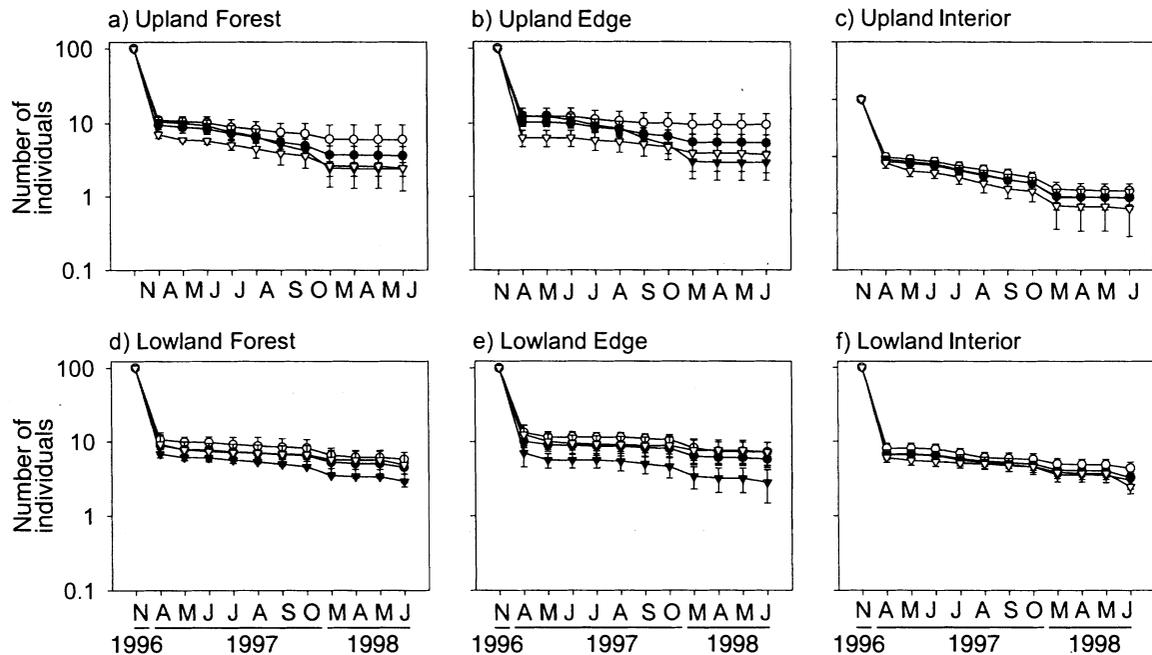


FIG. 2. Survival curves (mean \pm 1 SE) for *Alliaria petiolata* plants growing in lowland and upland plots and forest interior and forest edge plots measured monthly throughout the growing season. Cumulative survival for plants growing in all plots (filled circles), plants growing in control plots (open circles), plants growing in low-litter plots (filled triangles), and plants growing in litter-absent plots (open triangles) are shown. Months included are March (M), April (A), May (M), June (J), July (J), August (A), September (S), October (O), and November (N). Note \log_{10} scale on y-axes.

experimental sites for this study were those that germinated as a result of sowing by the researchers.

There were also litter differences among plots. Upland plots had significantly more litter (204.5 ± 16.3 g, mean \pm 1 SE) than lowland plots (96.4 ± 10.2 g, $P < 0.001$) and forest interior plots had significantly more litter (178.9 ± 14.6 g) than forest edge plots (92.6 ± 14.1 g, $P < 0.001$). Similarly, upland plots had significantly greater litter density (0.026 ± 0.002 g/cm³) than lowland plots (0.014 ± 0.002 g/cm³, $P < 0.001$) and forest interior plots had significantly greater litter density (0.046 ± 0.004 g/cm³) than edge plots (0.025 ± 0.005 g/cm³, $P < 0.001$). There were no significant interaction terms and no significant differences in litter depth among plots due to habitat ($P = 0.223$) or microenvironment ($P = 0.161$).

The two-way MANOVA indicated that there was no significant effect of habitat ($P = 0.396$), microenvironment ($P = 0.225$), or an interaction of the two ($P = 0.076$) on the soil texture and chemistry variables measured. Across all plots, the soil was moderately sandy ($28.0 \pm 0.4\%$) with a large proportion of silt ($62.2 \pm 0.7\%$) and a small proportion of clay ($9.7 \pm 0.4\%$), slightly acidic (pH 5.4 ± 0.1), and low to moderate in fertility (available phosphorus 11.3 ± 1.2 μ g/g, potassium 139.3 ± 5.4 μ g/g, calcium 1880.0 ± 164.0 μ g/g, magnesium 194.7 ± 18.6 μ g/g, nitrate 2.8 ± 0.1 mg/kg, and cation exchange capacity 19.5 ± 0.1 cmol/kg). Since there were no significant edaphic differences among plots, but there were differences in soil moisture

availability, light levels, and plant cover, it is likely these latter microenvironmental differences played important roles in distinguishing habitats and microenvironments.

Survival, growth, and reproduction

Germination within plots was fairly low (Fig. 2). The three-way ANOVA results for the germination and survival data indicated that microenvironment significantly affected both how many seeds germinated and how many plants survived (Table 1). Germination was significantly greater in the edge plots (11.4 ± 0.8) than in the forest interior plots (8.7 ± 0.4 , Fig. 3). Survival until October 1997 (rosettes) and June 1998 (mature plants) was significantly greater in forest edge plots (October, 7.0 ± 0.7 ; June, 5.5 ± 0.8) than in interior plots (October, 4.1 ± 0.3 ; June, 2.6 ± 0.2 ; Fig. 3). Survival was also significantly affected by habitat (Table 1). There were more plants alive in the lowland plots in both October 1997 (5.5 ± 0.4) and June 1998 (3.8 ± 0.3) when compared with the upland plots (October, 4.5 ± 0.4 ; June, 3.0 ± 0.4 ; Fig. 4). In addition, the number of mature plants present in June 1998 was significantly affected by litter treatment (Table 1). There were more plants alive in the control subplots (5.9 ± 1.5) than in either the litter removed (2.7 ± 0.3) or low litter (3.6 ± 1.3) treatment subplots. There were no significant interaction terms.

The three-way MANOVA to test the effects of habitat, microenvironment, and litter disturbance showed

TABLE 1. Three-factor GLM analysis of variance results for growth, reproduction, germination, and survival variables measured for mature *Alliaria petiolata* plants grown in varying habitats, microenvironments, and litter treatments. Numbers in the table are *F* ratios.

Dependent variable	Habitat	Micro-environment	H × M	Litter disturbance	H × L	M × L	H × M × L
Plant height	19.85**	0.28	0.01	2.63	1.09	0.22	0.29
Root biomass	12.89**	1.47	0.19	1.78	0.13	0.34	0.05
Total biomass	19.93**	1.36	0.09	2.51	0.22	0.39	0.14
Fruit biomass	13.98**	3.53†	0.28	3.17	0.58	0.40	0.34
No. mature fruits	15.01**	2.70	0.13	3.06	0.37	0.41	0.27
No. immature fruits	9.73*	0.44	0.23	1.69	0.49	0.74	0.74
No. seeds/fruit	16.56**	5.45†	0.02	1.44	1.22	0.72	0.86
No. seeds/plant	17.31**	3.64†	0.07	2.38	0.31	0.64	0.35
No. germinated	0.15	6.29*	0.61	0.99	2.78	0.36	1.41
No. rosettes	6.57*	9.35**	0.00	2.72	0.82	0.84	0.30
No. mature plants	16.67**	18.83***	0.63	6.88**	1.77	3.30	0.99
df	1, 82	1, 82	1, 82	2, 82	2, 82	2, 82	2, 82

Notes: For germination and survival data: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. A Bonferroni correction was used to adjust for experiment-wise error for morphometric and reproductive variables by dividing by 8: * $P < 0.0063$, ** $P < 0.0013$, † $P < 0.1$.

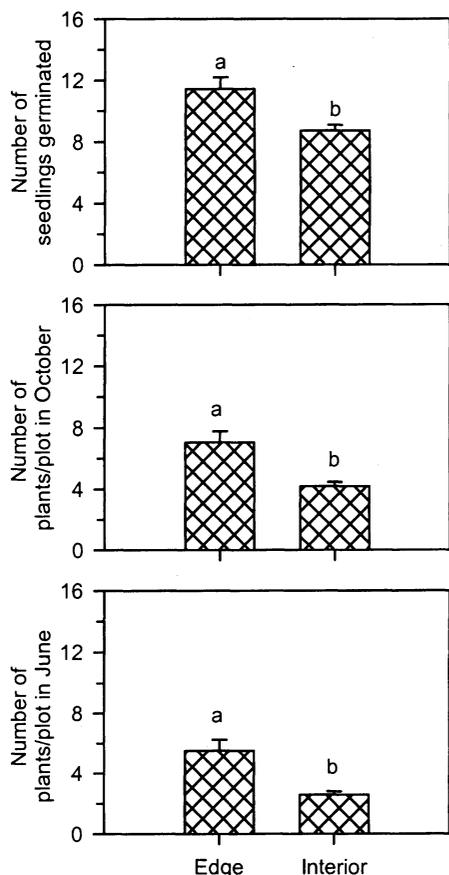


FIG. 3. Mean (+1 SE) number of *Alliaria petiolata* seedlings emerging and number of plants surviving until October 1997 and June 1998 in plots in forest edge and interior microenvironments. Different letters above the bars indicate significant differences between microenvironments based on Bonferroni tests.

that only habitat ($\lambda = 4.29$, $P < 0.001$) and micro-environment ($\lambda = 4.14$, $P < 0.001$) significantly influenced the *A. petiolata* morphometric and reproductive variables measured. Litter disturbance did not significantly affect the variables measured ($\lambda = 1.10$, $P = 0.358$), and there were no significant interaction terms (habitat \times microenvironment, $\lambda = 0.63$, $P = 0.751$; habitat \times litter disturbance, $\lambda = 1.37$, $P = 0.162$; microenvironment \times litter disturbance, $\lambda = 0.66$, $P = 0.829$; habitat \times microenvironment \times litter disturbance, $\lambda = 0.75$, $P = 0.739$). Analysis of variance results indicated that all morphometric variables were significantly influenced by habitat (Table 1). Mature *A. petiolata* plants growing in the lowland plots were taller (41.5 ± 2.4 cm); had greater root biomass (89.4 ± 12.3 mg), total biomass (425.5 ± 61.1 mg), and fruit biomass (139.3 ± 20.0 mg); and produced more mature fruits per plant (6.4 ± 0.7) and more seeds per plant (59.7 ± 8.4) than plants in the upland plots (height, 23.0 ± 2.5 cm; root biomass, 46.3 ± 9.3 g; total biomass, 168.5 ± 35.1 mg; fruit biomass, 79.9 ± 19.9 mg; number of fruits, 3.3 ± 0.6 ; number of seeds, 29.7 ± 7.5 ; Fig. 4). In addition, fruit biomass, the number of seeds per fruit, and the number of seeds per plant were marginally significantly affected by habitat (Table 1). Plants in forest edge plots had greater fruit biomass (167.2 ± 39.7 mg) and seed production per fruit (71.3 ± 14.9) and per plant (59.6 ± 13.4) than plants in forest interior plots (fruit biomass, 93.7 ± 12.5 mg; number of seeds per fruit, 37.6 ± 8.7 ; number of seeds per plant, 42.1 ± 6.4).

Habitat and microenvironment significantly affected three of the five reproductive rate variables examined. Plants in the lowland had a greater probability of surviving to become rosettes (0.65 ± 0.04 , $P < 0.001$), had greater mean seed production (41.6 ± 6.8 , $P < 0.001$), and a greater reproductive rate (1.98 ± 0.33 ,

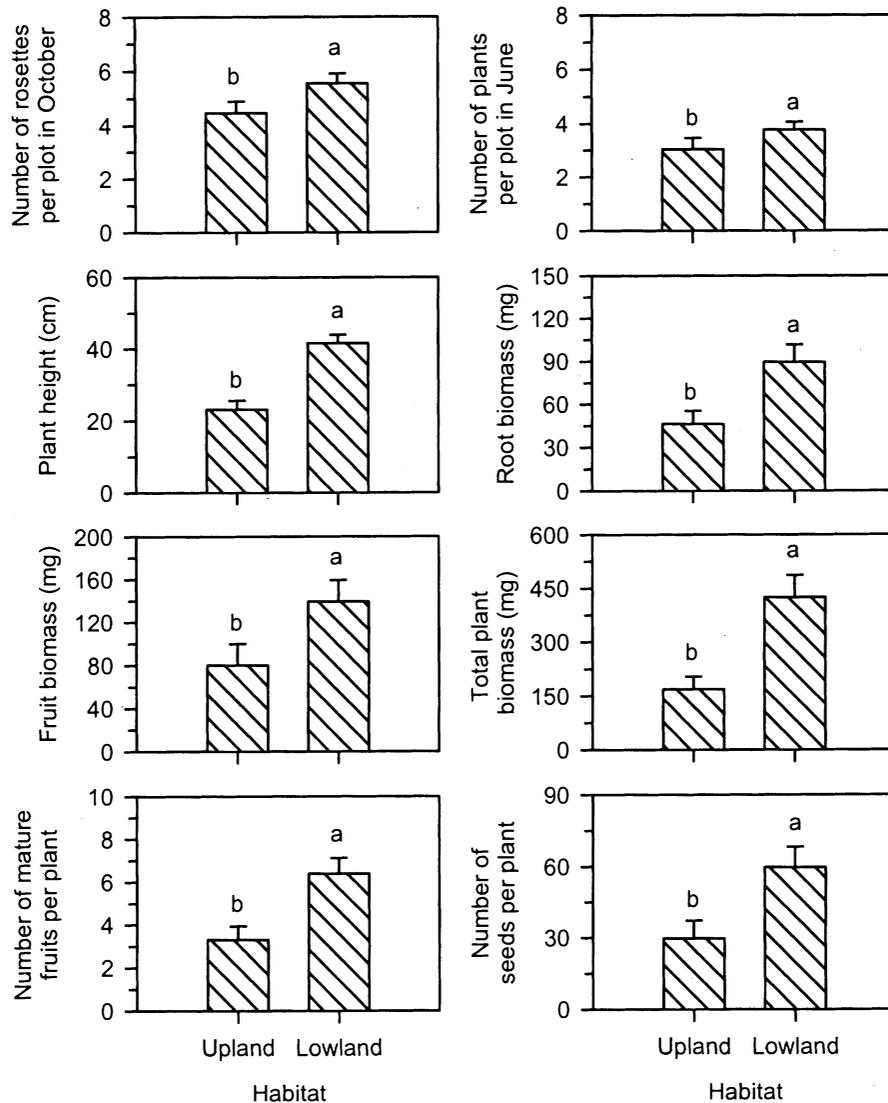


FIG. 4. Mean (± 1 SE) height, biomass, survival, and reproductive output of mature *Alliaria petiolata* plants growing in upland and lowland plots. Values presented are means for all plants that germinated in the two different habitats. Different letters above the bars indicate significant differences between habitats based on Bonferroni tests.

$P = 0.011$) than plants in the upland (rosette survival, 0.37 ± 0.03 ; seed production, 13.1 ± 3.7 ; reproductive rate, 1.35 ± 0.42). In edge plots, germination (0.11 ± 0.01 , $P = 0.019$), rosette survival (0.56 ± 0.05 , $P = 0.035$), and reproductive rate (2.89 ± 0.78 , $P = 0.027$) were significantly greater than in forest interior plots (germination, 0.09 ± 0.01 ; rosette survival, 0.48 ± 0.03 ; reproductive rate, 1.16 ± 0.23). There was only one significant interaction term. Survival to reproduction was significantly greater ($P = 0.023$) for plants in the lowland forest (0.44 ± 0.05) and upland edge (0.34 ± 0.07) compared with plants in the upland forest (0.17 ± 0.04).

DISCUSSION

Habitat invasion by nonindigenous plants has increased with the rise in global travel, exotic species

propagule availability, and the proportion of disturbed habitats (Frankel 1977), but our ability to predict the invasive potential of a particular species and the invasibility of a given site is poor (Roughgarden 1986, Williamson 1996, Lonsdale 1999). A successful botanical invasion depends upon the ecological attributes associated with the invaded habitat (Lodge 1993), and their interaction (Williamson 1996). To develop a successful site-monitoring program, it is crucial to study invasive species behavior in relation to habitat characteristics (Luken and Mattimiro 1991), including the ecological limitations of the species, the ability to and rate of spread, demography, response to disturbance, and characteristics leading to persistence in a site (Luken and Mattimiro 1991). It may then be possible to develop a

strategy to monitor areas and manage the invasive species that poses the threat.

In this experiment, the invasibility of several different types of forested environments by *Alliaria petiolata*, a nonindigenous invasive plant in North America, was investigated. Although *A. petiolata* seed germinated and plants persisted under all habitats, micro-environments and litter treatments, there were significant differences in germination, survival, growth, and reproduction in response to environmental variation. This response suggests that subtle variation in habitat, microenvironment, and/or disturbance regime may be an important determinant of site invasibility by *A. petiolata*. The most susceptible plots were those in the lowland and along the forest edge. In general, litter disturbance had little effect on *A. petiolata* germination, growth, or reproduction, although plots did differ in litter quantity.

In order to examine which environmental characteristics may have favored site invasion by *A. petiolata*, we measured several important abiotic and biotic factors. The differences between the lowland and upland plots involved summer and autumn soil moisture and litter biomass and density. There were only minor differences between the two habitats in terms of light or plant cover. The three-way exploratory MANCOVA results indicated that litter density was not a significant factor affecting *A. petiolata* growth and reproduction. In addition, there were no significant differences in soil chemistry among plots, so it is likely that soil moisture played the dominant role in the success of *A. petiolata* germination, survival, and growth in the lowland. Although *Alliaria petiolata* plants can tolerate wide variation in moisture availability ranging from dry upland forests to periodic inundation (Cavers et al. 1979), seeds and rosettes are drought sensitive (MacKenzie 1995). Drought leads to decreased seed germination (Baskin and Baskin 1992, MacKenzie 1995) and increased rosette mortality (Byers and Quinn 1998). In particular, rosette mortality tends to be highest during the drier summer and autumn months (Byers and Quinn 1998).

Riparian areas may be more easily invaded than upland forests because although they may have relatively low light levels, they can also experience frequent disturbance in the form of flooding (Gosselink and Lee 1989, Williams 1993). Flooding can remove humus from the forest floor, increase soil fertility (Grime 1979, Van Cleve and Viereck 1981, Gosselink and Lee 1989, Williams 1993), and bring seeds of nonindigenous plants to new sites from populations growing upstream. *Alliaria petiolata* seed dispersal is often associated with human (Lhotská 1975) and animal activity, and seeds in moist soil may be dispersed by adhesion to an animal's exterior (Cavers et al. 1979). Flooding may also be an important factor in the spread of *A. petiolata* along streambanks (J. Meekins, *personal observation*).

Therefore, spread of *A. petiolata* in riparian areas may be more rapid than in dry upland areas.

In this study, we looked at the implications of two possible types of disturbance on site invasibility: small scale disturbances in the litter layer that expose bare ground and larger scale disturbances that create edge habitats with increased light levels. Disturbance is often associated with site invasion by nonindigenous plants (Mack 1981, Hobbs 1989, Rejmánek 1989, Thompson 1991), and *A. petiolata* can often be found growing in disturbed areas (Cavers et al. 1979, Nuzzo 1993). Habitat disturbance typically results in sites that have an unpredictable nature, are heterogeneous, and change rapidly in terms of environmental attributes and community composition (Barrett and Richardson 1986, Ashton and Mitchell 1989, Bazzaz 1996, Schweitzer and Larson 1999). Plants that are morphologically plastic may be favored under this set of circumstances (Barrett and Richardson 1986, Ashton and Mitchell 1989, Bazzaz 1996, Schweitzer and Larson 1999).

Light availability is an important factor often correlated with habitat colonization by nonindigenous plants (Crawley 1987, Hobbs and Huenneke 1992, Robertson et al. 1994). The creation of forest edges and gaps can result in greater light availability for understory plants (Matlack and Litvaitis 1999). The fragmented nature of contemporary forests means they are surrounded by ruderal and nonindigenous species (Burgess and Sharpe 1981, Hill 1985), so propagules from these species can more easily enter the forest. The edge environment, a boundary area of variable width between communities (Wales 1972, Thomas et al. 1979, Lovejoy et al. 1986, Chen 1991), appears to be favorable for many exotic species (Goldblum and Beatty 1999, Kemper et al. 1999, Matlack and Litvaitis 1999).

Although *A. petiolata* populations can persist both along forest edges and under closed forest canopies, forest edges in our experiment were more invasible. *Alliaria petiolata* germination, survival, and reproductive effort were greater in forest edge plots than in forest interior plots. Several characteristics of *A. petiolata* may be beneficial for invasion and persistence in a forest edge community. Although *Alliaria petiolata* is adapted to grow in low light conditions (Cavers et al. 1979, Dhillion and Anderson 1999), plants grown experimentally in higher light conditions have significantly greater biomass and reproductive output than plants grown in the low light conditions typical of those in a temperate forest interior (Meekins and McCarthy 2000). When Luken et al. (1997) removed *Lonicera maackii* shrubs from an invaded forest understory, they found that in terms of both density and importance value (a synthetic value resulting from the addition of relative density and relative frequency values), *A. petiolata* was one of the most important understory species growing in the newly formed gaps.

Litter can also strongly impact vegetation and there can be much variation in the distribution of litter on

the forest floor (Shure and Phillips 1987, Facelli and Carson 1991, Facelli and Pickett 1991). The amount of litter is often greater in the forest interior compared with the forest edge and in uplands compared with lowlands, where leaf decay and turnover rates are higher. The presence of litter in temperate forests can negatively affect seedling establishment and survival for relatively small-seeded genera, and often these species are restricted to sites with bare mineral soil or on woody debris (Keever 1973, Marks 1983). These types of conditions can be found in association with disturbances that may also increase light level on the forest floor (Robertson et al. 1994). Disturbance in forest leaf litter can open up bare ground for colonization by nonindigenous plants. However, not all plants depend on litter disturbance (e.g., Rose and Frampton 1999). We found no differences in *A. petiolata* germination, rosette survival, growth, or reproduction among litter treatments, indicating that bare ground is not a prerequisite to *A. petiolata* invasion. Interestingly, there was significantly greater survival to maturity for *A. petiolata* plants in control plots compared with litter removal plots, possibly due to slightly greater moisture levels under the leaf litter in control plots. For many plant species, germination requirements are not as restrictive as later requirements for establishment (Turnbull et al. 2000), so seedling and rosette *A. petiolata* plants may be more limited in their ability to persist under less optimal environmental conditions. Although bare ground is not necessary for *A. petiolata* colonization of a new site, *A. petiolata* seed dispersal via animals or water may coincide with site disturbance and litter removal.

Abiotic factors are not the only ones associated with site invasibility. Another factor to consider is species richness. Although conventional wisdom deems species-poor habitats more susceptible to invasion, many studies have shown that they are less susceptible to invasion than species-rich sites (Pickard 1984, Knops et al. 1995, Palmer and Maurer 1997, Wisser et al. 1998, Lonsdale 1999). Many factors may explain the positive correlation between species richness and invasibility including the greater availability of resources in species-rich sites (Pickard 1984, Knops et al. 1995), higher levels of disturbance (Planty-Tabacchi et al. 1996), soil moisture level and site microclimate (Pickard 1984), and greater habitat edginess (Planty-Tabacchi et al. 1996). The higher nutrient availability, in particular, may lead to a surfeit of nutrients available to invaders (Wisser et al. 1998). Higgins et al. (1999) found a positive correlation between species richness and site invasibility in South Africa and concluded that species richness did not provide an adequate indication of site invasibility. It is possible that it is not species richness that drives this pattern, but rather resource availability within a community (Stohlgren et al. 1999a, b). In this study, *A. petiolata* plant performance was best in lowland plots, where species richness was slightly greater

than in upland plots. However, it is unlikely that the greater species richness in the lowland sites enhanced *A. petiolata* survival and growth, rather it is likely that both species richness and *A. petiolata* performance were positively linked with greater resource availability in the lowland compared with the upland sites.

Even when site conditions are favorable, invasion depends on the presence of propagules from potential invaders (Rejmánek 1989, DeFerrari and Naiman 1994). *Alliaria petiolata* produces a copious amount of small seeds (Cavers et al. 1979, Anderson et al. 1996). Under favorable conditions, a dense stand of *A. petiolata* can produce >100 000 seeds/m² (Cavers et al. 1979). This seed may then be dispersed by gravity, in the mud adhering to mammal hooves (e.g., deer), or by ballistic propulsion (Lhotská 1975, Cavers et al. 1979, Nuzzo 1991). Therefore, *A. petiolata* seed can easily spread within a forest, especially if there is a nearby seed source. Although germination was fairly low in this experiment, some seeds in all treatment combinations germinated and eventually produced more seed, so the possibility of new populations becoming established is great. The areas most vulnerable to population spread are the lowland habitat and edge microenvironment, where seed production was highest.

There are a few caveats that apply to the interpretation of the data from this experiment. Germination of *A. petiolata* in the field was low compared with germination in the lab. Low germination does not imply suboptimal conditions for *A. petiolata* growth and proliferation. Field germination is often low, but copious seed production can compensate for this low germination. The fact that germination and establishment did occur implies that the absence of *A. petiolata* in the experimental areas is due to seed limitation and not to an inability to persist in those sites. Seed limitation is commonly found by researchers conducting both seed addition and seed augmentation studies in natural plant communities (Turnbull et al. 2000). Also, several small, but expanding, naturalized populations of *A. petiolata* ($\lambda = 1.26\text{--}1.45$; J. Meekins, unpublished data) were present within the Ridges Land Lab forest, implying that as the populations increase more areas will be invaded.

The years during which the study was conducted were consistent with normal 30-yr climate patterns. Since *A. petiolata* is drought sensitive, a dry year may exacerbate the differences in germination and growth between the moist lowland and drier upland sites. Also, sites may differ in moisture due to slope aspect. In general, air and soil temperature and vapor pressure deficit are higher on south-facing slopes (Cantlon 1953), while soil moisture and relative humidity are highest on northeast-facing slopes (Hutchins et al. 1976). This study was conducted on southeast-facing slopes. Therefore, there is a possibility that *A. petiolata* would react differently on north-facing slopes, perhaps

experiencing less difficulty becoming established in this more mesic environment.

Management implications

In trying to control the spread of nonindigenous plants, it is important to understand the environmental conditions that favor entry of the species into a habitat and its subsequent proliferation and spread. *Alliaria petiolata* has been shown to spread rapidly (Nuzzo 1993) and have a negative impact on understory plant communities and is therefore of great concern to land managers. The plants in this experiment had reproductive rates greater than one under all treatments, meaning that on average more seeds were produced by reproductive plants in plots the second year than were originally sown. Therefore, if plants had not been harvested, it is probable that new plants would have germinated the following spring and new *A. petiolata* populations would have formed in each site. The ability of *A. petiolata* to persist and even thrive after only one introduction event of a limited quantity of seed implies that even a small initial invasion must be considered a serious threat and should be dealt with swiftly. Control of small populations may be best achieved through hand weeding (McCarthy 1997), but larger infestations may require the use of herbicide treatment or dormant season fire for effective control (Nuzzo 1991).

The results of this experiment suggest that a wide range of habitats is vulnerable to *A. petiolata* invasion and colonization including both upland and lowland habitats. However, spread of *A. petiolata* in riparian habitats with increased light availability might be more rapid than in forest interior sites and drier upland sites. As a consequence, closed canopy, upland sites may be potentially easier to manage for *A. petiolata* invasion. In addition, merely removing *A. petiolata* plants within the area to be protected may not eliminate the threat of future invasion by this pernicious plant. Any area that is close to a seed source will be vulnerable to continued reinvasion. It is important to further our understanding of the mechanisms of *A. petiolata* invasion and how these relate to patterns of survival and growth in order to increase our knowledge of *A. petiolata* control and environmental restoration.

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