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COMPETITIVE ABILITY OF *ALLIARIA PETIOLATA* (GARLIC MUSTARD, BRASSICACEAE), AN INVASIVE, NONINDIGENOUS FOREST HERB

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Alliaria petiolata (Bieb.) Cavara & Grande (garlic mustard, Brassicaceae) is a Eurasian herb that is currently invading forested areas throughout portions of the northern United States and southern Canada. *Alliaria petiolata* enters plant communities in an aggressive fashion, often displacing resident understory species. One possible mechanism that may enable garlic mustard to successfully invade these areas is hypothesized superiority as a competitor. In order to determine the competitive potential of *A. petiolata*, a multiple deWit replacement series was conducted in the greenhouse between *A. petiolata* and three native species: *Impatiens capensis*, an herbaceous annual, and *Acer negundo* and *Quercus prinus*, two woody perennials. Each target species was grown in mixture with *A. petiolata*, and all species were grown in monoculture. After 21 wk, plants were harvested and dried. Aboveground dry-weight biomass (yield) was then used to calculate the relative yield per plant, relative yield total, and mean aggressivity index. *Impatiens capensis* and *A. negundo* experienced greater intraspecific competition than interspecific competition with *A. petiolata*, while *A. petiolata* grown with *A. negundo* experienced more interspecific competition. *Impatiens capensis* and *A. petiolata* were approximately equal in aggressivity, while *A. negundo* was more aggressive than *A. petiolata*. In contrast, *Q. prinus* experienced more interspecific competition when grown with *A. petiolata* and had a lower aggressivity value. *Alliaria petiolata* rosettes had a greater competitive ability and aggressivity than *Q. prinus*, indicating that oak forest understories may be more vulnerable to *A. petiolata* invasion and that *A. petiolata* may negatively affect oak regeneration.

Keywords: ecology, *Acer*, *Impatiens*, *Quercus*, competition, deWit replacement series, relative yield.

Introduction

A growing concern of scientists, nature preserve managers, and conservationists is the phenomenon of biological invasions (Huenneke 1988). A biological invasion occurs any time an organism is introduced to a new area outside of its current range. Often these invasions are linked with anthropogenic disturbance of the environment (Whitney 1994), but pristine natural habitats may also be susceptible to invasion. While many of these invasions are either not successful or have negligible consequences, some invasive species can become serious pests in the habitats they invade (Williamson 1996).

Although some plant communities seem especially prone to invasion, all communities are vulnerable (Crawley 1987; Binggeli 1996). Invasive species may negatively affect a community by leading to decreases in population numbers, increases in species extinctions, or alterations in ecosystem function (Mooney and Drake 1986; Vitousek et al. 1996). These effects may be accomplished by a variety of factors, including competition, predation, disease, or amensalism (Williamson 1996).

Among biological invasions, one problem that stands out is the ever-increasing spread of nonindigenous plants. Often called exotics or weeds, these invasive nonindigenous plants can have harmful effects on the new ecosystems to which they

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are introduced, often displacing and even extirpating the native species in the invaded areas (Cronk and Fuller 1995). Although ca. 10% of the flora worldwide are nonindigenous (Heywood 1989), and 25% of the plants in North America are not native (McKnight 1993), it is only recently that scientists have begun to identify and study some of the more problematic nonindigenous plants.

One nonindigenous plant that is currently receiving much attention because it is invading forested natural areas in the northern United States and southern areas of Canada is *Alliaria petiolata* (Bieb.) Cavara & Grande (Gleason and Cronquist 1991). *Alliaria petiolata* is commonly called garlic mustard because of the strong garlic odor the plant produces when crushed. It is a biennial herb that was first introduced to North America in the mid-1800s (Nuzzo 1993), possibly by colonists who planted it in their gardens for use as a medicinal and edible herb (Grieve 1959). *Alliaria petiolata* is of particular interest experimentally because it has the ability not only to invade mature second-growth forests, habitats that are typically considered to be relatively resistant to many invasives, especially herbaceous plants, but also to displace the native vegetation in these invaded areas (McCarthy 1997). Previous research has shown that when *A. petiolata* is experimentally removed from a forested area, the richness and abundance of understory species, especially annuals and woody perennials including tree seedlings, increase (McCarthy 1997). Thus, significant community-level interference by *A. petiolata* is likely and may be caused by either competition or allelopathy. A

subsequent study by McCarthy and Hanson (1998) ruled out allelopathy as the probable method of interference. Therefore, competition is a mechanism of interference that still needs exploration.

Competition among plants is a common natural phenomenon. Plants often grow in close proximity to one another, placing demands on the same resources within the community and leading to a negative interaction among and within species (Aarssen and Epp 1990). Competitive ability encompasses those traits that allow one plant to exclude another from an area through monopolizing resources (Aarssen 1992). Neighbor removal experiments have shown that biomass and reproductive output of individual plants increases substantially in the absence of competition from neighbors (Aarssen 1992).

Approaches to the study of competition may be descriptive or experimental in nature. However, descriptive studies do not effectively address the importance and consequences of competitive interactions among plants (Aarssen and Epp 1990). Experimental approaches to the study of competition may involve field or greenhouse experiments. Field experiments typically are neighbor-manipulation experiments in which either plants of the same or other species are planted in varying densities near a target plant or the natural vegetation around the target plant is removed. The resulting effect on the biomass or reproductive output of the target plant and its competitors can then be examined (DiTommaso and Aarssen 1991; Wilson and Tilman 1991; McLellan et al. 1997). Greenhouse studies often employ additive or replacement designs (Hamilton 1994). These designs are used to answer different types of questions regarding competition. Additive designs can be used to quantify competition between species without regard to competition within species, e.g., weed-crop experiments. Replacement designs involve planting target species together in varying proportions (and sometimes in varying densities) to examine the effect one species has on the growth of another, and they can be used to answer questions about intra- and interspecific competition and the similarity of competing taxa (Hamilton 1994).

The objective of this study was to examine the competitive ability of A. petiolata relative to the competitive abilities of three native plant species that often occur in habitats in the northeastern United States invaded by A. petiolata. Two woody plants, Acer negundo L. (box elder), a tree typically found in habitats characterized by wet or moist soils, and Quercus prinus L. (rock chestnut oak), an upland tree species, and one herbaceous plant, Impatiens capensis Meerb. (orange touch-me-not), an herbaceous annual abundant in wet habitats, were chosen as target species. Alliaria petiolata has been reported to grow in association with I. capensis (Byers 1988; Pyle 1995) and A. negundo in moist habitats (Cavers et al. 1979; McCarthy 1997) and Quercus species in drier habitats (Nuzzo 1991; McCarthy 1997).

Material and Methods

Seeds of Alliaria petiolata and the three target species, Acer negundo, Impatiens capensis, and Quercus prinus, were collected in the summer and autumn of 1994 in Athens County, Ohio. Alliaria petiolata seeds were stratified for 105 d on moist filter paper in a seed germinator at 4°C. Seeds of A. negundo

and I. capensis were stratified on moist Sunshine Mix potting medium (70%–80% sphagnum peat moss with perlite and trace quantities of dolomitic limestone and gypsum) at 4°C in a coldroom for 75 and 135 d, respectively. Seeds of Q. prinus were germinated on moist Sunshine Mix potting medium, allowed to grow for 21 d to establish a root system, then cold stratified at 4°C in a coldroom for 90 d. After stratification, trays of A. negundo, I. capensis, and Q. prinus were removed from the cold and placed in a warm greenhouse to stimulate germination or shoot emergence, as appropriate. Alliaria petiolata seedlings emerged in the germinator at 4°C. In April 1995, seedlings of all four species were transferred to black plastic pots (2650 cm^3) filled with a mixture of Sunshine Mix and 240 cm^3 of field soil from a local forest. The field soil served to inoculate the potting medium with native fungal symbionts. Seedlings were planted equidistant from each other in a circular design at the appropriate densities and proportions. Pots were randomly assigned to spaces on a greenhouse bench and were rerandomized every 2 wk in order to avoid any possible position effects within the greenhouse.

Experimental Design

A multiple deWit replacement design (sensu Snyder et al. 1994) was used to test for competition between Alliaria petiolata and each of the target species. Unlike the typical deWit (1960) replacement design, in which plants are grown at various proportions over one constant density, the multiple deWit design is an addition series, varying both density and proportion. The original deWit design has been severely criticized for holding density constant, since the total density selected affects the outcome of the competition experiment (Marshall and Jain 1969; Firbank and Watkinson 1985). Therefore, it is impossible to extrapolate from one density to other densities or to other generations of plants (Law and Watkinson 1987). Each of the species in this experiment was grown in monoculture and in mixture with A. petiolata. Plants were grown in monoculture densities of 1, 2, 3, 4, 6, 8, 9, 12, and 16 plants per pot (ca. 44–711 plants per m^2) and in mixture densities of 2, 4, 8, 12, and 16 total plants per pot. At all mixture densities, except two plants per pot, the two species were grown at three different proportions: 25% A : 75% B, 50% A : 50% B, and 75% A : 25% B. Monoculture densities were replicated four times and mixture densities eight times for a total of 144 monoculture pots and 312 mixture pots.

Plants were kept moist and fertilized monthly with Alaska fish fertilizer (an organic fish emulsion, 5-1-1). Aboveground plant parts were harvested after 147 d, oven-dried at 80°C for 3 d, and weighed with a Mettler AE200 analytical balance. Because of the difficulty of separating the roots from individual plants in each pot for analysis, only shoot biomass was examined.

Data Analysis

Relative yield per plant (RY), relative yield total (RYT), and aggressivity (A) were calculated based on the total dry weight biomass (yield) of each species in each pot at each density and proportion combination. These synthetic values use data concerning the growth of plants in pure stands compared with

their growth in mixtures to provide information about the nature of the competitive interaction among plants of the same and different species. Relative values are used in order to compensate for absolute differences in biomass between different species and to allow interspecies comparisons to be made (Fowler 1982).

Relative yield expresses the relationship between the yield of species A when grown in a mixture containing species B with the yield of species A when grown in monoculture. Assuming total density to be constant, RY can be calculated as

$$RY_{ij} = Y_{ij}/(pY_i) \tag{1}$$

and

$$RY_{ji} = Y_{ji}/(qY_j), \tag{2}$$

where Y_{ij} is the yield of species i when grown in mixture with species j, Y_{ji} is the yield of species j when grown in mixture with species i, Y_i is the yield of species i when grown in monoculture, Y_j is the yield of species j when grown in monoculture, p is the proportion of species i in the mixture, and q is the proportion of species j in the mixture. All yield values are on a per pot basis, while relative yields are on a per plant basis (Fowler 1982). The value of RY indicates the type of competition experienced by the species. If RY is less than 1.0, interspecific competition is assumed to be greater; i.e., competition is greater between plants of different species. If RY is greater than 1.0, the species is assumed to be experiencing greater intraspecific competition; i.e., competition is greater between plants of the same species. An RY value of 1.0 indicates that the species competes equally well in both mixture and monoculture.

The relative yield total (RYT) can then be computed based on the relative yield values as follows:

$$RYT = pRY_{ij} + qRY_{ji} \tag{3}$$

(Fowler 1982). An RYT value of less than 1.0 implies that the two species are mutually antagonistic. If the RYT is greater than 1.0, the two species are not competing. When RYT = 1.0, the species may exclude one another via competition for the same resource (Harper 1977; Radosevich 1988). This value provides additional information about the nature of the interaction between the species.

The RYs can also be used to determine the mean aggressivity index (A; McGilchrist and Trenbath 1971). This index indicates how interspecific competition influences the biomass of the species involved (Roush and Radosevich 1985) and is calculated as

$$A_i = RY_{ij} - RY_{ji} \tag{4}$$

and

$$A_j = RY_{ji} - RY_{ij}. \tag{5}$$

When two species are grown together in a pot, the more

aggressive species will have the higher A value. The plant with the higher aggressivity value is assumed to be the stronger competitor.

The effects of species, density, and proportion on plant growth were examined using relative yield data as the dependent variable. Relativized data were used so that comparisons could be made between species that naturally differ from each other in their absolute biomass. Data were analyzed with SAS (version 6.12) by performing a three-way GLM ANOVA procedure using Type IV sums of squares to correct for the two missing treatment cells at the two-plants-per-pot density level (SAS 1990; Shaw and Mitchell-Olds 1993). All treatment factors were considered fixed.

Multiple t-tests using a Bonferroni correction were used to compare each relative yield value with a value of 1.0, the value expected when a species is grown in monoculture. Each relative yield total value was also compared by multiple t-tests using a Bonferroni correction with 1.0, the value obtained when the expected yields for each species grown in the mixture are summed (Hintze 1995). Since 13 nonindependent comparisons were made, a Bonferroni correction was used for each t-test ($a = 0.05/13$). Data were transformed as necessary to meet the assumptions for homogeneity of variances and normality prerequisite for parametric statistical tests.

Results

The yield of *Impatiens capensis* when grown in mixture with *Alliaria petiolata* was 11.7% higher than the yield of *I. capensis* when grown in monoculture. The yield of *A. petiolata* when grown in mixture with *I. capensis* was 17.4% lower than the yield of *A. petiolata* when grown in monoculture. In all of the five density treatments, the actual yield of *I. capensis* was higher than the expected yield, while the yield of *A. petiolata* was lower than expected in the three lowest treatment densities and higher than expected at only the two highest densities (fig. 1). The yield of *Acer negundo* was 37.0% higher when grown in mixture with *A. petiolata* than in monoculture. The yield of *A. petiolata* was 36.2% lower when grown in mixture with *A. negundo*. At all densities, the yield of *A. negundo* when grown in mixture with *A. petiolata* was higher than expected. The yield of *A. petiolata* was lower than expected for all mixture densities except four plants per pot (fig. 1). The yield of *Quercus prinus* was 34.8% lower in mixture with *A. petiolata* than in monoculture, while the yield of *A. petiolata* was 21.6% higher in mixture with *Q. prinus*. The yield of *Q. prinus* was lower than expected at all five mixture densities. The yield of *A. petiolata* was higher than the expected yield at all mixture densities (fig. 1). There were occasional deaths across treatments, but there were no species-, density-, or proportion-related deaths for any of the four species in the study.

When *I. capensis* and *A. petiolata* were grown together, there was a significant effect of density ($P = 0.006$) and species ($P \leq 0.001$), a density by proportion interaction ($P = 0.005$), and a species by proportion interaction ($P = 0.029$) (table 1). Relative yield increased for both *A. petiolata* and *I. capensis* as the total density of plants per pot increased. The relative yield of *A. petiolata* was greater at all densities when the proportion of *A. petiolata* in the pot was lower (25%). The relative
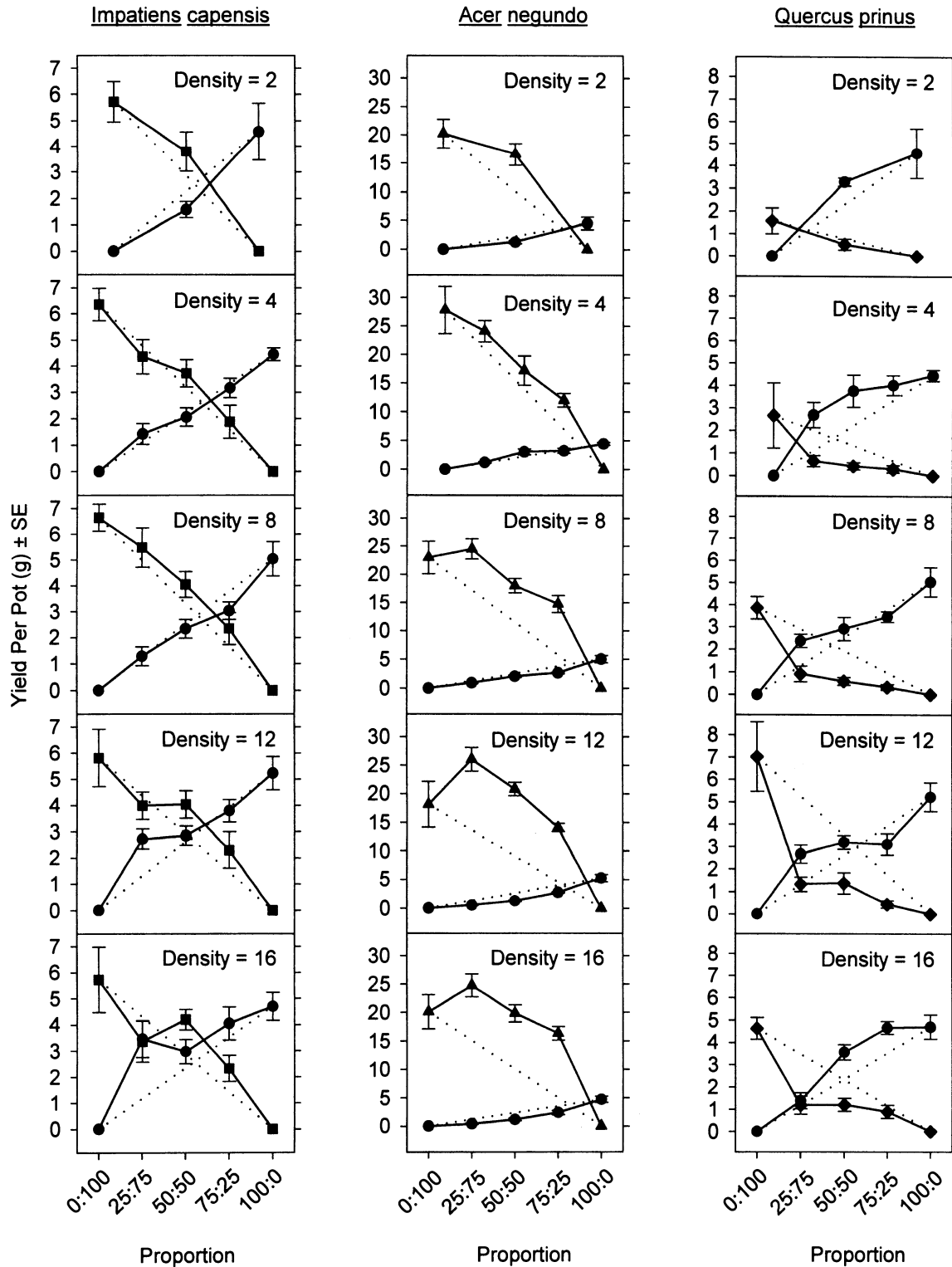
Fig. 1 Yield values (per pot) of *Alliaria petiolata* grown in association with three target species at five proportions over five densities. Black circles indicate the yield of *A. petiolata*. The yields of *Impatiens capensis*, *Acer negundo*, and *Quercus prinus* are indicated by black squares, triangles, and diamonds, respectively. Theoretical yield values are indicated by dashed lines.

Table 1

Analysis of Variance Results for Relative Yields of *Acer negundo, Impatiens capensis,* and *Quercus prinus* Plants When Grown in Mixture with *Alliaria petiolata* under Varying Densities and Proportions

Mixture and source of variation	df	SS	F	P
A. petiolata and *A. negundo*:				
Density	4	0.93	2.54	0.040
Proportion	4	97.11	265.73	<0.001
Density × proportion	14	1.97	1.54	0.096
Species	1	45.67	499.92	<0.001
Density × species	4	12.95	35.45	<0.001
Proportion × species	4	45.07	123.33	<0.001
Density × proportion × species	14	11.05	8.64	<0.001
A. petiolata and *I. capensis*:				
Density	4	4.46	3.68	0.006
Proportion	4	91.77	75.77	<0.001
Density × proportion	14	9.72	2.29	0.005
Species	1	<0.00	0.00	0.998
Density × species	4	2.66	2.19	0.069
Proportion × species	4	3.32	2.74	0.029
Density × proportion × species	14	5.01	1.18	0.287
A. petiolata and *Q. prinus*:				
Density	4	1.32	1.77	0.136
Proportion	4	51.83	69.52	<0.001
Density × proportion	14	2.78	1.06	0.390
Species	1	31.34	168.11	<0.001
Density × species	4	1.80	2.41	0.049
Proportion × species	4	24.81	33.27	<0.001
Density × proportion × species	14	5.58	2.14	0.010

Note. Type IV sums of squares were used in the analysis to account for the incomplete density effect. SS = sums of squares.

yield of *I. capensis* at each density was greater when the proportion of *I. capensis* per pot was lower. The lack of any significant species effect indicates that there was no significant effect of interspecific competition on *A. petiolata* or *I. capensis* when the two were grown in mixture.

When *A. negundo* and *A. petiolata* were grown together, there was a significant effect of density ($P = 0.040$), species ($P \leq 0.001$), and proportion ($P \leq 0.001$), a density by species interaction ($P \leq 0.001$), a proportion by species interaction ($P \leq 0.001$), and a density by species by proportion interaction ($P \leq 0.001$) (table 1). The relative yield of *A. petiolata* decreased with increasing density, while the relative yield of *A. negundo* increased as the number of plants per pot increased. The relative yield of *A. negundo* was greater than that of *A. petiolata* at all densities, indicating a significant effect of interspecific competition on the growth of *A. petiolata* by *A. negundo*. As the proportion of *A. negundo* plants per pot increased, the relative yield of *A. negundo* decreased. As the proportion of *A. petiolata* plants per pot increased, the relative yield of *A. petiolata* increased.

When *Q. prinus* and *A. petiolata* were grown in mixture, there was a significant effect of proportion ($P \leq 0.001$) and species ($P \leq 0.001$), a density by species interaction ($P = 0.049$), a proportion by species interaction ($P \leq 0.001$), and a density by species by proportion interaction ($P = 0.010$) (table 1). The relative yield of *A. petiolata* increased with decreasing proportions of *A. petiolata* per pot. The relative yield of *A. petiolata* was greater across all treatments than that of *Q.*

prinus, indicating a significant effect of interspecific competition on the growth of *Q. prinus*.

The relative yields of *A. petiolata* and *I. capensis* when grown together in mixture did not differ significantly from 1.0, except in two treatments (table 2). The relative yield of *A. negundo* was significantly greater than 1.0 in 11 of the 13 total treatments, including all nine treatments at densities of 8, 12, and 16 plants per pot. The relative yield of *A. petiolata* was significantly lower than 1.0 for eight of the 13 treatments and for all proportions at densities of 12 and 16. The relative yield of *Q. prinus* was significantly lower than 1.0 in 11 of the 13 comparisons, including almost every proportion at densities greater than two plants per pot. The relative yield of *A. petiolata* was significantly greater than 1.0 in four of the 13 total comparisons.

The relative yield totals of *I. capensis* when grown in mixture with *A. petiolata* were not significantly different from 1.0. The relative yield totals of *A. negundo* when grown in mixture with *A. petiolata* were significantly greater than 1.0 in five of the 13 comparisons made, all of these at densities greater than eight. The relative yield totals of *Q. prinus* were less than 1.0 in all but two of the comparisons made but were significantly less than 1.0 in only two of the 13 comparisons made, both of these at densities greater than eight.

Impatiens capensis ($A = 0.0003 \pm 0.13$) and *A. petiolata* ($A = -0.0003 \pm 0.13$), when grown together, had aggressivity values approaching zero. When grown in mixture together, *A. negundo* ($A = 1.13 \pm 0.10$) had a greater aggressivity value

Table 2

Mean Relative Yield Values Per Plant (RY) ± Standard Error (SE) for *Alliaria petiolata* and the Three Target Species, *Impatiens capensis*, *Acer negundo*, and *Quercus prinus*, When Grown in Mixture at Several Proportions over Five Densities

Density and proportion	Mean RY ± SE		Mean RY ± SE		Mean RY ± SE	
	Alliaria petiolata	Impatiens capensis	A. petiolata	Acer negundo	A. petiolata	Quercus prinus
2:						
50 : 50	0.69 ± 0.13	1.33 ± 0.27	0.56 ± 0.13*	1.64 ± 0.19*	1.44 ± 0.08**	0.67 ± 0.30
4:						
25 : 75	1.27 ± 0.35	0.91 ± 0.14	1.06 ± 0.14	1.15 ± 0.09	2.42 ± 0.50	0.32 ± 0.12**
50 : 50	0.92 ± 0.16	1.17 ± 0.16	1.36 ± 0.23	1.23 ± 0.18	1.69 ± 0.32	0.32 ± 0.12*
75 : 25	0.95 ± 0.11	1.19 ± 0.39	0.97 ± 0.14	1.73 ± 0.17*	1.20 ± 0.13	0.45 ± 0.23*
8:						
25 : 75	1.02 ± 0.29	1.10 ± 0.15	0.73 ± 0.11	1.42 ± 0.10*	1.88 ± 0.23*	0.31 ± 0.12**
50 : 50	0.93 ± 0.14	1.22 ± 0.15	0.81 ± 0.09	1.56 ± 0.11**	1.15 ± 0.21	0.31 ± 0.09**
75 : 25	0.80 ± 0.09	1.41 ± 0.37	0.71 ± 0.04**	2.56 ± 0.26**	0.91 ± 0.06	0.34 ± 0.13**
12:						
25 : 75	2.08 ± 0.29*	0.92 ± 0.12	0.39 ± 0.06**	1.91 ± 0.15**	1.93 ± 0.31	0.25 ± 0.06**
50 : 50	1.09 ± 0.14	1.39 ± 0.18	0.49 ± 0.05**	2.30 ± 0.13**	1.23 ± 0.12	0.39 ± 0.13*
75 : 25	0.97 ± 0.11	1.58 ± 0.48	0.70 ± 0.02**	3.11 ± 0.16**	0.79 ± 0.12	0.25 ± 0.10**
16:						
25 : 75	2.94 ± 0.60	0.78 ± 0.18	0.35 ± 0.08**	1.64 ± 0.14*	1.18 ± 0.31	0.34 ± 0.12*
50 : 50	1.27 ± 0.20	1.46 ± 0.14*	0.49 ± 0.10**	1.97 ± 0.15**	1.52 ± 0.15*	0.52 ± 0.13*
75 : 25	1.15 ± 0.18	1.62 ± 0.35	0.67 ± 0.11*	3.25 ± 0.24**	1.32 ± 0.08*	0.76 ± 0.25

Note. The proportion is the ratio of the percentage of *A. petiolata* plants to the target species in a pot. A *t*-test was used to compare each relative yield value with 1.0, the relative yield of a species in monoculture. Indications of statistical significance are based on a Bonferroni correction for multiple tests with $a = 0.05$.

* $P < 0.01$.

** $P < 0.001$.

than *A. petiolata* ($A = -1.13 \pm 0.10$), while *A. petiolata* ($A = 1.03 \pm 0.09$) had a greater aggressivity value than *Q. prinus* ($A = -1.03 \pm 0.09$) when these species were grown in mixture.

Discussion

The ability of *Alliaria petiolata* to compete as well as or better than some understory plants could contribute to its success as an invasive plant in North America. The results of this study indicate that, in some instances, *A. petiolata* rosettes may be capable of outcompeting neighboring species and reducing their growth, but, in other situations, *A. petiolata* may itself be the poorer competitor. In general, *Impatiens capensis* and *A. petiolata* experienced similar levels of intraspecific and interspecific competition when grown together. *Acer negundo* experienced more intraspecific competition than interspecific competition when grown in mixture with *A. petiolata*. For *A. petiolata*, at least at higher densities, interspecific competition was greater than intraspecific competition. *Quercus prinus* was the species most negatively affected by the presence of *A. petiolata*. At most densities, *Q. prinus* experienced greater interspecific competition than intraspecific competition, while *A. petiolata* experienced more intraspecific competition. Overall, relative yield and aggressivity values indicate that *A. petiolata* was a moderate to poor competitor with *I. capensis* and a poor competitor with *A. negundo* but was a superior competitor with *Q. prinus*. These results indicate that high densities of *A. negundo* may interfere with *A. petiolata* invasion into moist riparian zones, while *Q. prinus*, which is already ex-

periencing regeneration declines throughout much of its range, may facilitate invasion into drier upland forests.

From the ecological literature, it is axiomatic that competition with neighbors can significantly affect the survival, growth (Aarssen and Epp 1990), and reproduction of terrestrial plants (Begon et al. 1986). Plants often grow in close proximity to one another and, over space and time, certain resources, including light, water, and nutrients, can become limiting. Plants, therefore, may have to compete with each other, either within or among species, for those resources (Aarssen and Epp 1990). In particular, interspecific competition can exert considerable influence on plant distribution and abundance across a range of habitat types (Schoener 1983) and environmental gradients (Gurevitch et al. 1992; Kadmon 1995). Often, plants that are similar taxonomically or morphologically are considered to be strong competitors (Goldberg and Werner 1983). When two such species with overlapping niches are grown together, their mean yield is determined by both the density and proportion at which the species are growing (Harper 1977). However, competition does not just occur among similar species; since all plants utilize the same basic set of resources, all plant species in a given community can be considered potential competitors (Goldberg and Werner 1983).

Literature concerning the presence of competition and its effect on plant communities abounds. Researchers have investigated such diverse topics as the effects of competition over space and time (Keddy 1989; Grace and Tilman 1990; Gurevitch et al. 1990; Goldberg and Barton 1992), competition among woody and herbaceous plants (Keddy et al. 1994; Huenneke and Thomson 1995; Gould 1996; Trisel 1997), and

competition along productivity and environmental gradients (Gurevitch et al. 1990; DiTommaso and Aarssen 1991; Kadmon 1995). More recently, the focus has shifted to the potential competitive interactions between nonindigenous, invasive plants and the native plants present in the invaded areas (Walker and Vitousek 1991; Huenneke and Thomson 1995; Trisel 1997).

Invasive plants in particular are often considered to be competitively superior (Baker 1965). One hypothesis to explain this enhanced competitive ability is that when plants are introduced to new areas that are free from native herbivores, they reallocate biomass previously used for herbivore defense toward growth and reproduction. This reallocation leads to an increase in the competitive ability of the introduced (nonindigenous) plant and may provide a partial explanation of why some nonindigenous species are so successful in their new habitats (Blossey and Nötzold 1995). Preliminary studies with *Lythrum salicaria* showed that biomass of plants in a nonnative habitat, where herbivore pressure was low, was greater than biomass in the native habitat (Blossey and Nötzold 1995).

Through the mechanism of competition, invasions can lead to native species displacement and a corresponding loss of local diversity (Herbold and Moyle 1986). *Dipsacus sylvestris*, a nonindigenous invasive thistle, reduced the growth and germination of *Circium vinaceum*, a native New Mexican thistle, when the two were grown in mixture in a greenhouse experiment (Huenneke and Thomson 1995). Braithwaite et al. (1989) studied the effect of the invasive shrub *Mimosa pigra* on Australian plant communities and found that the presence of *M. pigra* was correlated with decreased species richness, herbaceous biomass, and number of tree seedlings. In Hawaii, the invasive tree *Myrica faya* interferes with germination, survival, and growth of *Metrosideros polymorpha*, a native late-successional tree (Walker and Vitousek 1991). Keddy et al. (1994) looked at the competitive affect and response rankings of several wetland plants, including *L. salicaria*, a nonindigenous invasive plant in North America, when grown with three wetland indicator species. They found that when *L. salicaria* was grown in mixture with the indicator species, their yield was reduced by 60%, indicating that *L. salicaria* poses a serious risk to other plant species through competition. Trisel (1997) examined the effects of shoot and root competition with *Lonicera maackii*, a nonindigenous invasive shrub in North America, on seedlings of four native tree species: *Acer saccharum*, *Fraxinus americana*, *Prunus serotina*, and *Quercus rubra*. The presence of *L. maackii*, especially shoots, significantly reduced tree seedling survival, primarily through competition for light. Similarly, *L. maackii* had a negative effect on native herbaceous plants. There was a significant decrease in fitness of *Gallium aparine*, *Impatiens pallida*, and *Pilea pumila* when grown in the presence of *L. maackii*, possibly because of competition for light, water, and nutrients (Gould 1996). Seed germination in the native plant *Calluna vulgaris* was reduced by the presence of *Campylopus introflexus*, an invasive moss that forms a dense carpet (Equihua and Usher 1993).

Although all habitats are vulnerable to invasion (Williamson 1996), many plants are geographically, physiologically, or ecologically limited in their abilities to invade certain areas. The results from this experiment indicate that upland oak forests may be more vulnerable to *A. petiolata* invasion than moist, lowland forests with an *A. negundo* overstory and *I. capensis* understory. Before invasion can occur, though, an organism must reach a new region and then establish a viable population there. Propagule pressure, the number of seeds or other reproductive units produced, is important in helping an invasive organism flourish and spread. The more propagules an organism produces, the greater its chances of becoming established (Williamson 1996). Baker (1965) lists several other characteristics that may be important determinants of success for "weedy" or invasive plants: no special germination requirements, rapid seedling growth, quick flowering, and self-compatibility or generalized pollination by wind or insects.

The profound negative effect that *A. petiolata*, a highly successful nonindigenous invasive plant, has been observed to have on North American floral communities could be affiliated with a variety of the aforementioned factors. *Alliaria petiolata* has a broad environmental tolerance and can be found in a wide range of habitats, from partially inundated mesic communities (Cavers et al. 1979) to dry sand forests (Maier 1976) and open fields (Byers 1988). It has also been shown to exhibit phenotypic plasticity, a trait that could enable it to exploit these different types of habitats. Byers and Quinn (1998) transplanted *A. petiolata* seedlings to four different habitats with varying moisture and light regimes. Overall, these seedlings exhibited significant plasticity in biomass allocation patterns, seed size, and mortality in response to the different areas in which they were grown. *Alliaria petiolata* can also adapt to a variety of irradiance levels ranging from 125 to 1125 $\mu E/m^{-2}/s^{-1}$ (Anderson and Dhillion 1991). In addition, *A. petiolata* has a high propagule pressure. It is capable of producing an enormous quantity of seed, over 100,000 seeds per m^2 in dense populations (Cavers et al. 1979), and although only a low percentage of the seedlings arising from these seeds may survive to reproduce (Baskin and Baskin 1992), the plants are self-compatible (Anderson et al. 1996), so only one mature plant is needed to start a population in a new area.

It has also been suggested that *A. petiolata* may be allelopathic, thus allowing it to suppress the vegetation of an area. In one experiment, an extract of *A. petiolata* inhibited the development of seedlings of wheat, radish, lettuce, and tomato (Kelley and Anderson 1990). However, McCarthy and Hanson (1998) found little evidence supporting the claim of allelopathy in *A. petiolata*. They treated both seeds and seedlings of radish, lettuce, hairy vetch, and winter rye with a dilution series of extracts from *A. petiolata* roots and shoots and found only a slight depression of germination and growth at the highest concentrations, which were far greater than the level that would be found in the natural environment.

Competition is generally assumed to be important in productive habitats, although its importance in unproductive habitats is surrounded by controversy (Grime 1979; Tilman 1987, 1988; Goldberg and Novoplansky 1997). Tilman proposes (1987, 1988) that below-ground competition for water and nutrients is more important in unproductive habitats, while above-ground competition for light is more important in productive habitats. Indeed, shading is commonly listed as the major way nonindigenous plants affect plant communities (Webb and Kaunzinger 1993; Woods 1993; Trisel 1997). *Alliaria petiolata* commonly invades productive forested habitats

in the United States where shading may be an important issue. In the present experiment, *A. petiolata* rosettes were about as tall as *Q. prinus* seedlings; therefore, *A. petiolata* may have been competing with *Q. prinus* mainly for light. *Impatiens capensis* and *A. negundo* were taller than *A. petiolata* rosettes, and *A. negundo* seedlings had a dense crown of leaves, which would have produced more shade than *I. capensis* for *A. petiolata* rosettes, possibly resulting in the greater success of *A. negundo* when grown with *A. petiolata*.

Since *A. petiolata* is a biennial in North America (Cavers et al. 1979), it is also important to consider the competitive effect of mature plants as well as rosettes on native vegetation. Rosettes bolt in early spring, producing a tall flowering stalk that easily overtops any herbaceous or small woody seedlings in an area. Often, larger plants are competitively superior (Tripathi and Harper 1973), and in many communities plant interactions occur between individuals of varying sizes and ages (Grubb 1977). Therefore, the potential competitive superiority of mature *A. petiolata* plants may compensate for any inferior competitive interactions among *A. petiolata* rosettes and other plants. The situation for *I. capensis* and *A. negundo* plants growing with mature *A. petiolata* plants would have been substantially different since *A. petiolata* can reach up to 1.5 m in height during its second year (Cavers et al. 1979). Therefore, although rosettes may not be competing with these native plants, mature *A. petiolata* plants might be capable of competing successfully with a larger variety of native understory plant species.

The intensity and outcome of competition between individuals may also be affected by other seasonal or spatial factors such as time of year and soil productivity. Fowler (1982) found that both of these variables significantly altered the outcome of competition between six pairs of competing grassland species. In addition, competition between neighbor roots and neighbor shoots can lead to different competitive outcomes. In one study, plants grown in the presence of neighbor roots and shoots had significantly lower plant biomass than plants grown with just neighbor roots, but only at high nitrogen availability (Wilson and Tilman 1991).

Although competition for light, nutrients, or other factors may be important in determining the effect of *A. petiolata* on its neighbors, competition among understory plants and *A. petiolata* for physical space in a habitat may be just as significant. Seedlings of *A. petiolata*, *A. negundo*, *I. capensis*, and *Q. prinus* are all present together in the spring, but *A. petiolata* seeds germinate several weeks before *I. capensis* (Leck 1979) and rosette plants are already present when *I. capensis* germinates. If *A. petiolata* germinates earlier than other species, or if *A. petiolata* rosettes are present in an area already, then other plants may be unable to grow there. In southern Ohio, *A. petiolata* typically germinates in the early spring, February or March, overwinters as a basal rosette, bolts in the following March, and begins flowering in April (Trimbur 1973). There are few other understory plants germinating or actively growing during this early spring period, potentially allowing *A. petiolata* to usurp more space and/or resources for seedlings or mature plants.

An additional consideration when interpreting the results of competition experiments is the density at which the plants were grown. Experimental plant densities in this study ranged from 44 (one plant per pot) to 711 plants per m² (16 plants per pot). These densities reflect the range of densities found in nature for *A. petiolata*. *Alliaria petiolata* densities have been reported as high as 500 flowering plants per m², with up to 95% cover. Since *A. petiolata* seedlings may have survival rates to reproductive age under 2% in some habitats (Byers and Quinn 1998), this indicates that a very high number of seedlings or rosettes would have been present in these areas originally. *Impatiens capensis* also has high spring germination rates that can lead to seedling stands with densities up to 1848 plants per m² (Lively et al. 1995). Again, mortality is high and only 20% may survive to the end of the growing season (Leck 1979). These high seedling densities indicate that *A. petiolata* and *I. capensis* could potentially encounter each other in fairly dense populations in natural settings.

Quercus species seedlings, in contrast, usually occur at lower densities. Rhoades (1992) found densities of about two seedlings per m² growing in an upland oak forest in southwestern Virginia, but seedling densities could be higher in a good mast year. Therefore, individual *Quercus* seedlings would be more likely to encounter dense stands of *A. petiolata* plants than vice versa. The results from this experiment indicated that, even at low densities, *Quercus* seedlings were negatively affected by competition with *A. petiolata*, so in forested habitats it is likely that *Quercus* seedlings could be seriously affected by the presence of *A. petiolata*.

Although *A. negundo* seedlings can often be found at high densities in riparian habitats, it may be more realistic to expect lower densities than those represented in this experiment. *Acer negundo* was not negatively affected by the presence of *A. petiolata* at any density, while *A. petiolata* was only affected by competition with *A. negundo* in the higher density situations. In natural settings, *A. petiolata* may be unlikely to encounter *A. negundo* seedling densities at high enough levels to be affected by interspecific competition.

An interesting aspect of the results from this study deals with the negative effect that *A. petiolata* had on the growth of *Q. prinus* seedlings. An important problem in many North American mixed oak forests is the failure of *Quercus* spp. (oaks) to regenerate. Originally, oaks dominated large tracts of these hardwood forests, but oaks are systematically being replaced by other hardwood species, such as *Acer rubrum*, *A. saccharum*, *P. serotina*, *Liriodendron tulipifera*, and *Carya* spp. (Abrams and Nowacki 1992). Many possible causes have been suggested to explain this problem, including acorn predation by rodents, deer, and insects (Marquis et al. 1976); seedling browsing by deer and insects; environmental change to cooler and moister conditions; decreasing fire frequency; forest fragmentation; and competition from other vegetation (Lorimer 1992).

The presence of understory vegetation can be particularly detrimental to young oaks. Many oak seedlings divert much of their initial reserves into root growth, and if the neighboring vegetation overtops the oaks, intercepting most of the sunlight, seedling reserves may be depleted and the plants may die (Crow 1988). In one study, oak survival was found to be greater on sites where the understory layer had been removed than on sites where the vegetation was left intact (Pubanz and Lorimer 1992). This study indicates that a dense understory composed primarily of shade-tolerant species can lead to a drastic decline

in oak survival (Lorimer 1992). In another study, Kolb and Steiner (1990) found that *Q. rubra* seedling biomass was significantly reduced by both shading and competition with grass roots. *Alliaria petiolata* rosettes did overtop some of the oak seedlings in this study, and mature *A. petiolata* plants, which can grow up to 1.5 m in height, would certainly overtop oak seedlings. Since *A. petiolata* often forms dense stands and can grow in upland oak forests (Nuzzo 1991), rosettes and mature plants could possibly contribute to oak regeneration failure by competition with oak seedlings for light. This competition would probably have the greatest effect on low densities of oak seedlings germinating in dense understory populations of *A. petiolata*.

It seems likely that there are several factors that allow *A. petiolata* to displace herbaceous and woody plants from hab-itats that it has invaded. *Alliaria petiolata* may outcompete the extant vegetation for nutrients, water, or physical space. This plant's biennial nature, ability to self-fertilize, copious production of easily dispersed seed, and ability to survive in various types of habitats ranging from river flood plains to upland forests may all contribute to its success.

Acknowledgments

Literature Cited

Aarssen LW 1992 Causes and consequences of variation in competitive ability in plant communities. J Veg Sci 3:165–174.

Aarssen LW, GA Epp 1990 Neighbor manipulations in natural vegetation: a review. J Veg Sci 1:13–30.

Abrams MD, GJ Nowacki 1992 Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bull Torrey Bot Club 119:19–28.

Anderson RC, SS Dhillion 1991 Acclimatization of garlic mustard (*Alliaria petiolata*) (Brassicaceae) to varied levels of irradiance. Am J Bot 78:129–130 (abstract).

Anderson RC, SS Dhillion, TM Kelley 1996 Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in Central Illinois. Restor Ecol 2:181–191.

Baker HG 1965 Characteristics and modes of origin of weeds. Pages 147–168 *in* HG Baker, GL Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

Baskin JM, CC Baskin 1992 Seed germination biology of the weedy biennial *Alliaria petiolata*. Nat Areas J 12:191–197.

Begon M, JL Harper, CR Townsend 1986 Ecology, individuals, populations, and communities. Blackwell, Oxford. 876 pp.

Binggeli P 1996 A taxonomic, biogeographical and ecological overview of invasive woody plants. J Veg Sci 7:121–124.

Blossey B, R Nötzold 1995 Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889.

Braithwaite RW, WM Lonsdale, JA Estbergs 1989 Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. Biol Conserv 48:189–210.

Byers DL 1988 Life history variation of *Alliaria petiolata* in a range of habitats in New Jersey. MS thesis. Rutgers University, New Brunswick, N.J.

Byers DL, JA Quinn 1998 Demographic variation in *Alliaria petiolata* (Brassicaceae) in four contrasting habitats. Bull Torrey Bot Club 125:138–149.

Cavers PB, MI Heagy, RF Kokron 1979 The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb.) Cavara and Grande. Can J Plant Sci 59:217–229.

Crawley MJ 1987 What makes a community invasible? Pages 429–453 *in* AJ Gray, MJ Crawley, PJ Edwards, eds. Colonization, succession and stability. Blackwell Scientific, Boston.

Cronk QC, JL Fuller 1995 Plant invaders. Chapman & Hall, New York. 241 pp.

Crow TR 1988 Reproductive mode and mechanism for self-replacement of northern red oak (*Quercus rubra*): a review. For Sci 34:19–40.

deWit CT 1960 On competition. Versl Landbouwkd Onderz 66:1–82.

DiTommaso A, LW Aarssen 1991 Effect of nutrient level on competition intensity in the field for three coexisting grass species. J Veg Sci 2:513–522.

Equihua M, MB Usher 1993 Impact of carpets of the invasive moss *Campylopus interflexus* on *Calluna vulgaris* regeneration. J Ecol 81:359–365.

Firbank LG, AR Watkinson 1985 On the analysis of competition within two-species mixtures of plants. J Appl Ecol 22:503–517.

Fowler N 1982 Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. J Ecol 70:77–92.

Gleason HA, A Cronquist 1991 Manual of vascular plants of Northeastern United States and adjacent Canada. 2d ed. New York Botanical Garden, New York. 910 pp.

Goldberg DE, AM Barton 1992 Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am Nat 139:771–801.

Goldberg DE, A Novoplansky 1997 On the relative importance of competition in unproductive environments. J Ecol 85:409–418.

Goldberg DE, PA Werner 1983 Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. Am J Bot 70:1098–1104.

Gould AM 1996 Effects of the exotic invasive shrub *Lonicera maackii*, amur honeysuckle, on native forest annual herbs. MS thesis. Miami University, Oxford, Ohio.

Grace JB, D Tilman 1990 Perspectives on plant competition. Academic Press, San Diego, Calif. 484 pp.

Grieve M 1959 A modern herbal. Vol 2. Hafner, New York. 912 pp.

Grime JP 1979 Plant strategies and vegetation processes. Wiley, New York. 222 pp.

Grubb PJ 1977 The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145.

Gurevitch J, LL Morrow, A Wallace, JS Walsh 1992 A meta-analysis of competition in field experiments. Am Nat 140:539–572.

Gurevitch J, P Wilson, JL Stone, P Teese, RJ Stoutenburgh 1990 Competition among old-field perennials at different levels of soil fertility and available space. J Ecol 78:727–744.

Hamilton NRS 1994 Replacement and additive designs for plant competition studies. J Appl Ecol 31:599–603.

Harper JL 1977 Population biology of plants. Academic Press, London. 892 pp.

Herbold B, PB Moyle 1986 Introduced species and vacant niches. Am Nat 128:751–760.

Heywood VH 1989 Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 *in* JA Drake, HA Mooney, F di Castri,

RH Groves, FJ Kruger, M Rejmanek, M Williamson, eds. Biological invasions: a global perspective. Wiley, New York.

Hintze JL 1995 User's guide 6.0. Number Cruncher Statistical Systems, Kaysville, Utah. 777 pp.

Huenneke LF 1988 SCOPE program on biological invasions: a status report. Conserv Biol 2:8–10.

Huenneke LF, JK Thomson 1995 Potential interference between a threatened endemic thistle and an invasive nonnative plant. Conserv Biol 9:416–425.

Kadmon R 1995 Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. J Ecol 83: 253–262.

Keddy PA 1989 Competition. Chapman & Hall, London. 202 pp.

Keddy PA, L Twolan-Strutt, IC Wisheu 1994 Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? J Ecol 82:635–643.

Kelley T, RC Anderson 1990 Examination of the allelopathic properties of garlic mustard (*Alliaria petiolata*). Trans Ill State Acad Sci 83:31–32.

Kolb TE, KC Steiner 1990 Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. For Sci 36:34–44.

Law R, AR Watkinson 1987 Response-surface analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. J Ecol 75:871–886.

Leck MA 1979 Germination behavior of *Impatiens capensis* Meerb. (Balsaminaceae). Bartonia 46:1–14.

Lively CM, SG Johnson, LF Delph, K Clay 1995 Thinning reduces the effect of rust infection on jewelweed (*Impatiens capensis*). Ecology 76:1859–1862.

Lorimer CG 1992 Causes of the oak regeneration problem. Pages 14–39 *in* DL Loftis, CE McGee, eds. Oak regeneration: serious problems, practical recommendations. USDA, Forest Service, General Technical Report SE-84, Asheville, N.C.

Maier CT 1976 An annotated list of the vascular plants of Sand Ridge State Forest, Mason County, Illinois. Trans Ill State Acad Sci 69: 153–175.

Marquis DA, PL Eckert, BA Roach 1976 Acorn weevils, rodents, and deer all contribute to oak regeneration difficulties in Pennsylvania. USDA, Forest Service, Research Paper NE-356. Upper Darby, Pa.

Marshall DR, SK Jain 1969 Interference in pure and mixed populations of *Avena fatua* and *A. barbata*. J Ecol 57:251–270.

McCarthy BC 1997 Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). Pages 117–130 *in* JO Luken, JW Thieret, eds. Assessment and management of plant invasions. Springer, New York.

McCarthy BC, SL Hanson 1998 An assessment of the allelopathic potential of the invasive weed *Alliaria petiolata* (Brassicaceae). Castanea 63:68–73.

McGilchrist CA, BR Trenbath 1971 A revised analysis of plant competition experiments. Biometrics 27:659–671.

McKnight BN 1993 Biological pollution: the control and impact of invasive exotic species. Indiana Academy of Science, Indianapolis. 261 pp.

McLellan AJ, R Law, AH Fitter 1997 Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. J Ecol 85:479–490.

Mooney HA, JA Drake eds 1986 Ecology of biological invasions of North America and Hawaii. Vol 58. Springer, New York. 321 pp.

Nuzzo VA 1991 Experimental control of garlic mustard [*Alliaria petiolata* (Bieb.) Cavara & Grande] in Northern Illinois using fire, herbicide, and cutting. Nat Areas J 11:158–167.

—— 1993 Distribution and spread of the invasive biennial *Alliaria petiolata* (garlic mustard) in North America. Pages 137–145 *in* BN McKnight, ed. Biological pollution: the control and impact of invasive exotic species. Indiana Academy of Science, Indianapolis.

Pubanz DM, CG Lorimer 1992 Oak regeneration experiments in southwestern Wisconsin: two-year results. Research Report R3552. School of Natural Resources, College of Agricultural and Life Sciences, University of Wisconsin—Madison.

Pyle LL 1995 Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. Am Midl Nat 134: 244–253.

Radosevich SR 1988 Methods to study crop and weed interactions. Pages 121–142 *in* MA Altieri, M Lieberman, eds. Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla.

Rhoades RW 1992 Compositional changes in an oak forest in southwestern Virginia after twenty years. Castanea 57:252–263.

Roush ML, SR Radosevich 1985 Relationships between growth and competitiveness of four annual weeds. J Appl Ecol 22:895–905.

SAS Institute 1990 SAS/STAT user's guide, release 6.12. 4th ed. SAS Institute, Cary, N.C.

Schoener TW 1983 Field experiments on interspecific competition. Am Nat 122:240–285.

Shaw RG, T Mitchell-Olds 1993 ANOVA for unbalanced data: an overview. Ecology 74:1638–1645.

Snyder KM, JM Baskin, CC Baskin 1994 Comparative ecology of the narrow endemic *Echinacea tennesseensis* and two geographically widespread congeners: relative competitive ability and growth characteristics. Int J Plant Sci 155:57–65.

Tilman D 1987 On the meaning of competition and the mechanism of competitive superiority. Func Ecol 1:304–315.

—— 1988 Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J. 360 pp.

Trimbur TJ 1973 An ecological life history of *Alliaria officinalis*, a deciduous forest "weed." MS thesis. Ohio State University, Columbus, Ohio.

Tripathi RS, JL Harper 1973 The comparative biology of *Agropyron repens* (L.) Beauv. and *A. caninum* (L.) Beauv. I. The growth of mixed populations established from tillers and from seed. J Ecol 61: 353–368.

Trisel DE 1997 The invasive strub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae): factors contributing to its success and its effect on native species. PhD diss. Miami University, Oxford, Ohio.

Vitousek PM, CM D'Antonio, LL Loope, R Westbrooks 1996 Biological invasions as global environmental change. Am Sci 84:468–478.

Walker LR, PM Vitousek 1991 An invader alters germination and growth of a native dominant tree in Hawaii. Ecology 72:1449–1455.

Webb SL, CK Kaunzinger 1993 Biological invasion of the Drew University (New Jersey) Forest Preserve by Norway maple (*Acer platanoides* L.). Bull Torrey Bot Club 120:343–349.

Whitney GG 1994 From coastal wilderness to fruited plain—a history of environmental change in temperate North America. Cambridge University Press, Cambridge. 451 pp.

Williamson M 1996 Biological invasions. Chapman & Hall, New York. 244 pp.

Wilson SD, D Tilman 1991 Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72: 1050–1065.

Woods KD 1993 Effects on invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. Am Midl Nat 130: 62–74.