Responses of the biennial forest herb *Alliaria petiolata* to variation in population density, nutrient addition and light availability

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Summary

1 *Alliaria petiolata*, a European biennial herb, is an important pest in temperate North American deciduous forests. Habitat resource structure has probably been important for invasion and proliferation of this species.

2 *Alliaria* was grown in an experimental garden at two densities (equivalent to 17 and 170 plants m^{-2}), three nutrient levels (no, low, or high nutrient addition) and three light levels (ambient sunlight and two shading treatments) to determine the effects of environmental heterogeneity on growth, reproduction and resource allocation in both mature and rosette plants.

3 Overall, rosette growth and allocation patterns were significantly affected by all three variables tested. Low plant density, nutrient addition and high light availability resulted in plants with more leaves and greater dry weight biomass. Biomass allocation to shoots was greatest for plants in high-density and low-light treatments. Leaf chlorophyll content was significantly greater for plants in the two shaded treatments.

4 Mature plants also responded to environmental manipulation with significantly greater total dry weight biomass at low plant density, high light availability and with nutrient addition. Low density and high light availability resulted in significantly higher seed production. Plants in the lowest light treatment allocated significantly more biomass to shoot production and less to root production. Leaf chlorophyll content was lowest for plants in the highest light treatment and increased with nutrient addition at the two highest light treatments.

5 Plants growing at high density responded to nutrient addition and light attenuation in the same direction but with greatly reduced magnitude compared with plants growing at low density. The effect of irradiance was the most important determinant of all facets of growth and allocation patterns in both rosettes and mature plants.

6 Our results indicate that although density and site fertility may play important roles in *Alliaria* invasion and establishment, light availability may be the most important factor affecting subsequent growth and proliferation.

Key-words: biomass allocation, fertilization, garlic mustard, non-indigenous plants, shading

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Introduction

The responses of annuals and perennials in terms of plant growth and biomass allocation patterns to environmental heterogeneity is well known (e.g. Dale & Causton 1992; Burslem *et al.* 1995; Grubb *et al.* 1996; Casper & Cahill 1998), but few studies have addressed the implications of resource variation for obligate biennials, for which both rosette and mature individuals must be considered (Harper 1977). In addition, many of the ecophysiological investigations have been short-term studies, despite the fact that for biennials and perennials the effects

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– particularly on reproduction – must be evaluated over the entire life of the individual or over many growing seasons (Pons 1977).

Environmental heterogeneity includes variations in soil nutrient availability, solar radiation and density of plants within a population. The two soil resources assumed to limit growth most often are nitrogen and phosphorus (Bieleski 1973; Grace & Tilman 1990) and in deciduous forests these resources are typically distributed in a spatially and temporally heterogeneous manner (Hammer *et al.* 1987). Light distribution within a forest can also be heterogeneous in nature, with frequent disturbances leading to the formation of canopy gaps of various sizes (Runkle 1985; Pearcy 1990). Plant density within a population can be highly variable and depends in part on reproduction within the population, competition, herbivory and various abiotic factors (Crawley 1997). All these variations can have profound effects on plant growth, reproduction and distribution (Harper & White 1974; Griffith 1996, 1998).

Plants are assumed to respond to environmental heterogeneity by altering growth and/or adjusting biomass partitioning to various organs (Mooney & Winner 1991; Dale & Causton 1992; Reynolds & D'Antonio 1996) and various models have been proposed to explain and predict plant responses. Optimal partitioning models state that changes in the partitioning of plant biomass should allow plants to maximize their relative growth rates and optimize resource capture in variable environments (e.g. Reynolds & Thornley 1982; Bloom *et al.* 1985; Hilbert 1990; Gleeson 1993). According to these models, the nature of the limiting resource can have a substantial influence on how plant biomass is allocated to the vegetative and reproductive tissues; availability of soil resources and light may, for instance, alter the root : shoot ratio (Wilson 1988; Olff *et al.* 1990). Plants in a nutrient-limited environment may allocate a greater proportion of their total biomass to roots rather than to leaves and stems (Chapin 1980; Smart & Barko 1980), whereas light-limited plants increase plant height in an effort to avoid shading by neighbours (more stem biomass), or may increase the amount of photosynthetic material available for light interception (greater leaf biomass, Abrahamson & Gadgil 1973). Allocation to reproductive organs is also affected by resource availability: in more disturbed habitats, which presumably have greater light availability, such allocation tends to be higher than in less disturbed or more mature habitats (Abrahamson & Gadgil 1973; Abrahamson 1975; Pitelka & Curtis 1986).

Plant life history can also influence plant growth and biomass allocation patterns (Abrahamson 1979). Perennials, annuals, clonal herbs and aclonal herbs may exhibit differing growth strategies (Barrett & Wilson 1981; Delph 1990; Figiel *et al.* 1995) and strategies may also change over the life of the individual. In particular, perennials tend to allocate more resources to root production than annuals (Tilman 1988) and fewer resources to reproduction (Gadgil & Solbrig 1972). Furthermore, species vary in their invasive ability or 'weediness', typified by having no special germination prerequisites, fast seedling growth, a high degree of phenotypic plasticity, rapid attainment of reproductive maturity, quick flowering, high seed yield and high competitive ability (Baker 1965). Botanical invaders, especially in disturbed habitats, also often show high population growth rates and short generation times (Bazzaz 1986). Although no one plant possess all of these characteristics, it is still useful to consider the impact they can have on plant growth and biomass allocation, especially under variable environmental conditions. For example, an invasive plant with high fecundity may allocate a greater proportion of its total biomass to reproduction (flowers, fruits and seeds) under a wide variety of conditions, whereas species with high phenotypic plasticity may show greater flexibility in growth and allocation strategies over a range of habitats.

We examined the effects of density, nutrient level and light attenuation on the survival, growth, reproduction, biomass allocation and leaf chlorophyll content of rosette and mature plants of *Alliaria petiolata* (M. Bieb.) Cavara and Grande, an aggressive, non-indigenous biennial herb that invades upland forested habitats primarily in the mid-western and north-eastern United States and adjacent Canada (Nuzzo 1993). In particular, we wanted to (i) see how manipulation of these three environmental parameters affects *Alliaria* growth and biomass allocation patterns, and (ii) determine if rosette and mature plants show different responses.

Materials and methods

STUDY ORGANISM

Alliaria petiolata is a member of the Brassicaceae (Gleason & Cronquist 1993) commonly called garlic mustard because of the odour produced when above-ground parts of the plant are crushed (Grieve 1985). Native over much of Europe (Italy to Sweden and England to western Russia, Grime *et al.* 1988), it is thought to have been introduced to North America in the 1800s by early European colonists (Cavers *et al.* 1979; Nuzzo 1993) in Canada and the United States. It is now commonly considered to be an invasive threat to a variety of deciduous forest communities. In its native habitat, *Alliaria* is classified as a biennial, winter annual (Cavers *et al.* 1979), or monocarpic perennial (Grime *et al.* 1988). In the United States, however, *Alliaria* appears to be an obligate biennial (Baskin & Baskin 1992), always

producing a basal rosette of leaves during the first year's growth, which before senescence overwinters and produces flowers and fruits (siliques) in the spring of the second year. In the north-eastern United States, *Alliaria* seeds typically germinate from late February through March, depending on the year and habitat (Baskin & Baskin 1992). Rosettes grow throughout the spring and summer months, before growth slows in late autumn. Rosettes typically remain green over winter and then grow rapidly in March and April, producing tall inflorescences. Flowers open from April to May and mature fruits form by June (Cavers *et al.* 1979; Anderson *et al.* 1996; Byers & Quinn 1998). Seeds, which are released from July to October (Anderson *et al.* 1996), exhibit innate physiological dormancy at maturity and require cold stratification before initiation of germination (Lhotská 1975). Both rosette and mature plants possess a taproot system.

In its native environment, *Alliaria* is commonly found growing in mesic shaded areas (Grime *et al.* 1988), but it can also survive in well-drained sunny sites and forested areas with varying levels of canopy closure (Cavers *et al.* 1979). *Alliaria* possesses many of the characteristics of a 'classic' weed, including self-compatibility (Cruden *et al.* 1996), pollination by insect generalists (Cruden *et al.* 1996), production of numerous, dormant seeds (Trimbur 1973; Baskin & Baskin 1992), a high degree of phenotypic plasticity (Byers & Quinn 1998) and the ability to thrive in disturbed or waste areas (Cavers *et al.* 1979). These characteristics may explain its ability to threaten native communities in North America, although *Alliaria* does not appear to be invasive in its native habitat.

EXPERIMENTAL DESIGN

Mature seeds of *Alliaria* were collected from a population in Athens, Ohio in July 1996 and stored dry at 4 °C. On 15 November 1996, seeds were placed on filter paper moistened with 5 mL distilled water in sterilized glass Petri dishes and then sealed with parafilm. The Petri dishes were placed in a seed germinator at 4 °C. After approximately 4 months of cold stratification, seeds germinated. Germinated seedlings were transplanted to round, black plastic pots that were 25 cm diameter by 25 cm deep. Pots contained one part Sunshine Mix™ (Sun Gro Horticulture Canada Ltd, Bellevue, WA, USA) peat potting soil (70–80% sphagnum peat moss with perlite and trace quantities of dolomitic limestone and gypsum) and two parts field soil mixture (50% sand : 50% field soil). Field soil was used to inoculate pots with appropriate microflora and microfauna. Pots were randomly assigned to one of 18 treatment combinations and placed in the ground at a depth of approximately 23 cm in a grid pattern 1.5 m apart from one another in an experimental garden in an open field in Athens, Ohio on 15 March 1997. There were 10 replicates per treatment ($n = 180$ pots). Pots were weeded for the first month; after that point no further weeding was necessary.

Two density levels, three nutrient levels and three light levels were applied in a completely randomized factorial design. Light attenuation levels simulate conditions in open habitats, forest edges or large forest gaps and closed secondary forest, nutrient treatments represent the range of soil heterogeneity from ambient levels to nutrient-enriched and density was typical of individuals growing in a dense, established population or those involved in a colonizing event or newly established population.

One seedling was placed in each pot for the low-density treatment and 10 seedlings were placed in each pot for the high-density treatment. Equivalent densities (17 and 170 plants m^{-2}, respectively) are frequently observed in naturalized populations of *Alliaria* in forested areas (Trimbur 1973; Nuzzo 1991) where scattered individuals that are initially present often develop into a dense, virtually mono-specific stand.

Osmocote™ (Scotts-Sierra Horticultural Products Company, Marysville, OH, USA) controlled-release fertilizer (14–14–14) was applied to the nutrient addition treatments when seedlings were transplanted. The nutrients in Osmocote™ pellets are typically released evenly over a 4-month period. High nutrient treatment plants received 12 g of fertilizer per pot (from the recommended dose for herbaceous plants growing in a comparable area, equivalent to 2445.4 kg ha^{-1}). Low nutrient treatment plants received half this dose and control plants received no fertilizer. At the beginning of the following season (10 March 1998), treatments were repeated before the plants initiated bolting. Fertilizer was added to the top layer of soil in treatment pots and mixed in gently, but thoroughly, to ensure equal fertilizer distribution within the pot without disturbing plant roots. Since most of the significant differences among fertilizer treatments were either between the high- and the no-fertilizer treatment or between the low- and the no-fertilizer treatments, but not between the high and low treatments, data for the two fertilizer treatments are often grouped in the results section in order for comparisons to be made between fertilized and non-fertilized treatments.

Pots in the low- and medium-light treatments were shaded with one layer of 90% or 50% black plastic Sudden Shade (DeWitt Inc., Sikeston, MO, USA) shade cloth, respectively. Plants in the high light treatment were uncovered and received full ambient sunlight. A tube-shaped wire frame 1.2 m high by 30 cm diameter was placed over each shaded pot and the shade cloth was fastened to the top and sides of the frame. Light quantity attenuation was measured for 10 pots in each light treatment on a

sunny day using a Quantum Photometer Model Li-189 (Li-Cor, Lincoln, NE, USA) and averaged. Light levels were somewhat lower than expected from the designation of the shade cloth, with high light receiving 100%, medium light 42% and low light 5% of ambient light.

HARVESTING

Plants were watered occasionally throughout the growing season as necessary. On 12 September 1997, rosette plants from half of the pots ($n = 90$) were harvested. Roots were rinsed to remove soil particles and length of the largest primary root and the number of leaves was determined for each rosette. Plants were then separated into above- and below-ground parts, dried to a constant weight at 80 °C and weighed on a Mettler Toledo PB3002 balance (Hightstown, NJ). Dry weight was used to determine the percentage of total biomass allocated to roots and leaves.

From 6 to 8 June 1998, mature plants were harvested, dried and weighed as above. Dry weight was used to calculate the percentage of total biomass allocated to roots, stems and leaves and reproductive structures for each plant. In addition, height, the number of fruits produced and fruit weight were determined for each plant. The mean number of seeds produced per plant was determined by multiplying the mean number of seeds produced by 10 random fruits on that plant by the number of fruits on the plant. Mean seed mass was determined by weighing 10 randomly chosen seeds from each pot of plants on a Mettler AE 200 analytical balance (Hightstown, NJ).

CHLOROPHYLL ANALYSIS

To analyse leaf chlorophyll content, four $0.63 \, cm^2$ discs were removed from plants in each of the treatments on 10 October 1997 (rosette plants) and 25 May 1998 (mature plants). Leaf discs were placed in 1.5 mL Eppendorf tubes and stored on ice in a dark storage container while in the field. In the laboratory, leaf discs were weighed, placed in glass test tubes and 4 mL N, N-dimethylformamide (DMF) was added to each tube. Tubes were stored in a dark refrigerator for 12 h at 4 °C. Leaf samples were then shaken on a Fisher Scientific orbital shaker Model 361 (Naperville, IL) in a dark cold room for 24 h, then analysed using the methods of Moran (1982) and Inskeep & Bloom (1985). Samples were read using a Milton Roy Spectronic 20D spectrophotometer (Rochester, NY) set to $\lambda = 665.0$ and 647.0 nm for chlorophyll a and b determination, respectively.

DATA ANALYSIS

A suite of variables were measured or derived for rosette and/or mature plants. Vegetative characteristics measured included dry weight biomass (root, shoot, fruit and total), root:shoot ratio, plant height, number of leaves, number of stems and root length. Biomass allocation variables included percentage of total biomass allocated to roots, shoots (stems and leaves) and fruits including seeds. Reproductive parameters included number of fruits and seeds produced per plant, number of seeds per fruit and seed mass. Leaf variables included specific leaf mass, amount of leaf chlorophyll a, b and total, and chlorophyll a:b ratio.

The data were analysed separately for rosette and mature plants using a three-factor multivariate analysis of variance (MANOVA) to test for the effects of density, nutrient addition and light level. Each main effect was considered fixed. We utilized a multivariate analysis because we measured numerous dependent variables and were interested in looking at both the overall response across this suite of variables and the individual responses for each variable (Scheiner & Gurevitch 1993). Wilk's Lambda was used to test for the significance of each MANOVA. The standardized canonical coefficients were also examined in order to determine the response variable or variable combinations that led to the differences detected among groups (Scheiner & Gurevitch 1993). Before multivariate analysis, all dependent variables were tested for intercorrelation and those that were significantly intercorrelated ($P < 0.05$) were removed (Hintze 1997). Root biomass, root allocation and leaf chlorophyll a content were therefore removed from the rosette MANOVA and root biomass from the mature plant MANOVA.

Three-factor protected GLM analysis of variance (ANOVA) employing type III sums of squares, to correct for missing data, was used to assess which individual factors significantly influenced the measured variables (Scheiner & Gurevitch 1993). Only those variables that were analysed in the MANOVA were also analysed by subsequent ANOVA. Significance levels were adjusted for experiment-wise error using a Bonferroni correction. Significant results were explored *post hoc* using Bonferroni tests corrected for pair-wise experimental error. All variables were $\log_{10}$-transformed to meet assumptions of normality and homogeneity of variances implicit in the parametric statistical procedures employed. The MANOVA and ANOVAs were performed using SAS version 6.12 (SAS 1990). Untransformed means and standard errors are reported throughout the text. Survival data for rosettes and mature plants were examined separately using a non-parametric Kruskal–Wallis test (Hintze 1997).

Table 1 Multivariate analysis of variance results for the effects of density, nutrient addition, and light level on the growth, allocation, and leaf variables measured for rosette plants of *Alliaria petiolata* (see text). The parameters d.f. (H) and d.f. (E) denote the degrees of freedom for the hypothesis and error sum of squares cross product matrices, respectively

Source	d.f. (H)	d.f. (E)	Wilks' Lambda	*P*
Density	10	56	104.87	< 0.001
Nutrient	20	112	5.02	< 0.001
Density × Nutrient	20	112	3.38	< 0.001
Light	20	112	33.99	< 0.001
Density × Light	20	112	13.46	< 0.001
Nutrient × Light	40	214	2.69	< 0.001
Density × Nutrient × Light	40	214	2.48	< 0.001

Results

ROSETTE PLANTS

Results from the MANOVA indicated that density, nutrient addition and light level all significantly affected the variables measured for rosettes. In addition, all two-way interactions and the three-way interaction were significant (Table 1). Examination of standardized canonical coefficients indicated that most of the significant differences among treatment groups were due to variation in total rosette biomass (Table 2). Separate three-way ANOVAs indicated that all rosette variables measured, except specific leaf mass and leaf chlorophyll content, were significantly affected by density (Table 3). Nutrient addition affected only the number of leaves produced per plant, shoot biomass and total rosette biomass. Light significantly affected all variables except root length and chlorophyll $a:b$. All three two-way inter-

actions significantly affected the number of leaves produced per plant and total biomass, and all except density × nutrient affected shoot biomass. Four variables, number of leaves per plant, root:shoot ratio, shoot allocation and leaf chlorophyll b content, were significantly affected by a density × nutrient × light interaction.

Density and light level had the largest influence on the vegetative and allocation parameters measured, followed by nutrient addition (Table 2). For instance, basal rosettes grown at a low density (1 plant per pot) had significantly greater total dry weight biomass (10.6 ± 1.6 g) than plants grown at a high density (10 plants per pot; 1.3 ± 0.1 g; Fig. 1) and produced significantly more leaves (27.2 ± 3.4 at low density vs. 7.0 ± 0.2 at high density). Generally, plants grown in the high- and medium-light treatments had significantly greater dry weight total biomass (10.0 ± 2.7 g and 6.2 ± 1.08 g, respec-

Table 2 Standardized canonical coefficients for variables measured when *Alliaria petiolata* rosettes were grown under varying density, nutrient addition, and light levels

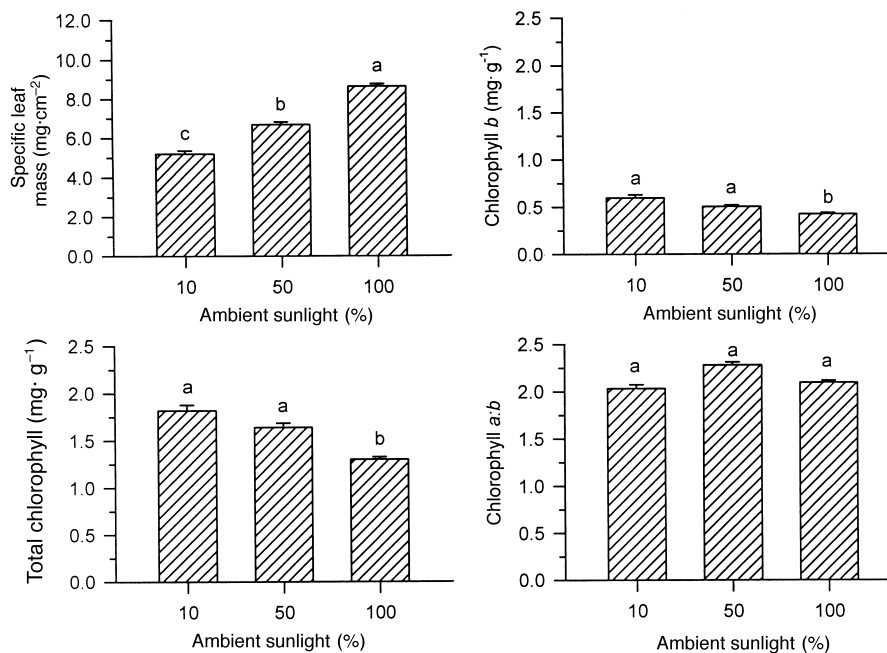|	SLM	Chlorophyll *b*	Total chlorophyll	Chlorophyll *a:b*	Root length	Number of leaves	Shoot biomass	Total biomass	Root: Shoot biomass	% Shoot
Density	0.03	2.30	− 2.28	2.26	0.01	1.95	− 4.15	7.87	− 2.39	− 1.95
Nutrient	− 0.54	− 0.11	− 0.05	0.13	0.22	2.60	− 5.41	7.64	− 0.48	0.55
	0.21	− 0.72	0.88	− 1.20	0.28	− 1.10	4.77	− 3.86	1.35	1.22
D × N	0.05	1.64	− 1.38	1.62	0.30	3.76	− 6.35	5.85	2.52	3.15
	− 1.45	3.28	− 2.98	3.41	0.08	− 1.88	− 1.56	4.45	1.86	2.93
Light	1.10	1.32	− 1.50	1.31	− 0.44	0.63	0.53	3.71	− 3.35	− 3.73
	− 0.46	− 2.28	2.77	− 2.22	0.17	− 0.46	2.49	− 0.48	− 0.26	0.18
D × L	− 0.29	0.98	− 1.16	1.09	0.19	1.81	− 7.52	10.59	− 1.98	− 0.52
	0.12	− 4.86	4.32	− 4.72	− 0.08	− 4.37	1.29	3.57	− 2.87	− 2.51
N × L	− 0.21	3.29	− 3.36	3.41	0.09	2.62	− 7.64	9.21	0.25	1.62
	0.27	− 1.61	1.86	− 2.13	− 0.41	1.41	4.35	− 3.47	2.59	1.27
	0.76	− 0.74	0.75	− 0.70	− 0.47	− 2.99	1.60	2.28	− 0.79	0.17
	1.16	− 0.14	− 0.11	− 0.38	0.75	− 0.88	− 1.63	2.71	− 1.71	− 1.46
D × N × L	− 0.06	− 2.21	2.37	− 2.46	0.21	1.76	1.64	− 5.71	3.72	2.23
	− 1.04	− 0.86	0.23	− 0.34	0.38	2.87	− 6.50	6.79	1.79	2.67
	0.23	− 1.74	2.24	− 2.29	0.78	− 0.01	− 3.16	2.81	− 0.42	0.94
	− 0.37	4.51	− 3.43	3.52	− 0.31	− 1.16	0.96	3.63	− 0.69	− 1.26

Table 3 Three-factor GLM analysis of variance of growth and allocation and leaf variables measured for rosette plants of *Alliaria petiolata* grown under varying densities, nutrient conditions, and light levels. Numbers in the table are *F*-ratios. Degrees of freedom (d.f.) are also listed. A Bonferroni correction was used to adjust for experiment-wise error by dividing by 10. * $P < 0.005$, ** $P < 0.001$

Source	Density	Nutrient	D × N	Light	D × L	N × L	D × N × L
d.f.	1	2	2	2	2	4	4
No. of leaves per plant	477.68**	43.23**	14.49**	159.52**	82.17**	9.54**	4.19*
Root length	27.75**	2.33	0.92	2.01	0.21	0.58	1.02
Shoot biomass	234.16**	20.18**	1.56	197.83**	19.30**	4.12*	3.60
Root : shoot	9.67*	3.18	1.76	19.14**	4.68	2.19	7.22**
Total biomass	682.41**	33.57**	8.40**	391.87**	84.89**	7.79**	4.00
Shoot allocation	10.02*	4.51	1.00	20.56**	4.06	2.56	6.46**
Specific leaf mass	3.63	2.51	1.82	147.54**	0.26	0.97	0.92
Chlorophyll *b*	1.12	0.24	0.40	17.61**	0.64	1.90	4.22*
Chlorophyll *a* : *b*	0.00	0.80	0.72	0.46	0.78	1.85	2.46
Total chlorophyll	2.62	0.55	0.27	33.84**	0.00	0.40	0.32

tively) than plants growing in the low-light treatment (0.7 ± 0.1 g). Rosettes that received added nutrients produced more leaves (19.4 ± 3.6, mean of low- and high-nutrient treatments) and greater biomass (6.9 ± 1.7 g) than plants that did not receive additional nutrients (8.2 ± 1.0 leaves per plant; 2.2 ± 0.6 g total biomass). Shoot dry weight biomass data followed a similar pattern to total rosette dry weight biomass data. Root length was significantly affected by only density: being greater at low density (22.6 ± 1.3 cm) than at high density (15.4 ± 0.6 cm).

The rosette growth parameters measured were also influenced by combinations of the three main treatments. Fertilized plants grew significantly larger (18.4 ± 1.9 g) than unfertilized plants (6.6 ± 1.8 g) under medium- and high-light conditions in the low-density treatment, but there was no significant difference in total biomass between fertilized (1.5 ± 0.1 g) and unfertilized (1.0 ± 0.1 g) plants in the high-density treatment. At low density, nutrient addition significantly increased the number of leaves produced by rosettes in the high- and medium-light
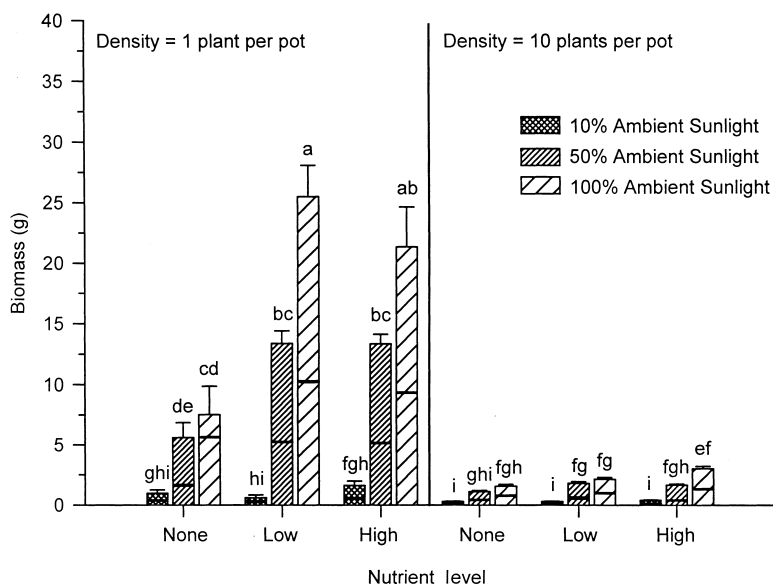
Fig. 1 Effect of density, nutrient addition, and light on mean (+ SE) dry weight shoot, root and total biomass measured for rosette plants of *Alliaria petiolata* grown under two densities, three nutrient conditions and three light treatments. Each bar represents total rosette biomass with the lower portion of each bar representing root biomass and the upper portion representing shoot biomass. Standard error bars refer to total rosette biomass data. Letters above the bars indicate significant differences ($P < 0.005$) in total biomass among treatments.

Fig. 2 Effect of light on mean (+ SE) leaf specific mass and leaf chlorophyll content measured for rosette plants of *Alliaria petiolata* grown under two densities, three nutrient treatments and three light treatments. Letters above the bars indicate significant ($P < 0.005$) differences in total biomass among treatments.

treatments (43.8 ± 4.9) compared with plants in low light (13.9 ± 3.0), but there were no significant differences in the number of leaves produced by high-density treatment plants due to nutrient level. There were few rosette plant deaths and no differences in survival among rosette plants in the 18 treatment combinations ($P = 0.483$).

Biomass partitioning varied among treatment groups. Plants grown at low density allocated significantly less biomass to shoot growth ($60.6 \pm 2.0\%$) than plants grown at high density ($66.2 \pm 1.8\%$; Fig. 1). Shade had the greatest influence on biomass allocation. Rosette plants in the full-sunlight treatment allocated significantly less biomass ($55.4 \pm 2.5\%$) to shoot production than plants in the medium- and low-light treatments ($67.1 \pm 1.9\%$).

Leaf chlorophyll content and specific leaf mass, in contrast with the vegetative variables, were not significantly affected by density or nutrient addition (Table 3). Specific leaf mass, chlorophyll b content and total leaf chlorophyll content were all significantly affected by light level. Specific leaf mass increased as light level increased (0.0168 ± 0.0007 mg cm^{-2}, high light; 0.0102 ± 0.0004 mg cm^{-2}, low light; Fig. 2). Total leaf chlorophyll content was significantly greater in the low- (1.9464 ± 0.0797 mg g^{-1}) and medium-light treatment plants (1.4933 ± 0.1173 mg g^{-1}) than in the high-light treatment plants (1.1449 ± 0.0927 mg g^{-1}). The ratio of chlorophyll $a:b$ was not significantly affected by any of the treatments.

Table 4 Multivariate analysis of variance results for the effects of density, nutrient addition, and light level on the growth, allocation, and leaf variables measured for mature plants of *Alliaria petiolata* (see text and legend of Table 1 for details)

Source	d.f. (H)	d.f. (E)	Wilks' Lambda	P
Density	17	48	13.87	< 0.001
Nutrient	34	96	7.63	< 0.001
Density × Nutrient	34	96	1.60	0.038
Light	34	96	23.88	< 0.001
Density × Light	34	96	3.41	< 0.001
Nutrient × Light	68	191	2.90	< 0.001
Density × Nutrient × Light	68	191	1.81	< 0.001

MATURE PLANTS

As with rosette plants, all of the main effects and interactions of the three-way MANOVA were significant for the parameters measured for mature *Alliaria* plants (Table 4). The standardized canonical coefficients indicated that many of the significant differences among treatment groups were again the result of variation in total biomass, although shoot biomass was often found to be important as well. Nutrient level responses, however, were principally influenced by leaf chlorophyll content (Table 5). Light level had the largest overall effect on the variables with only root : shoot ratio not significantly affected by light level (Table 6). Density significantly affected the number of stems per plant, shoot biomass, fruit biomass, total biomass, number of fruits per plant and number of seeds per plant. Of the growth and reproductive variables measured, only shoot biomass, total biomass and number of fruits per plant were affected by nutrient addition. A density × light interaction affected all vegetative and reproductive parameters except plant height, root : shoot ratio and seed mass. A nutrient × light interaction significantly affected number of stems per plant and total biomass. A three- way interaction affected shoot biomass, fruit biomass and number of seeds per fruit.

Plants in the medium- and high-light treatments were taller (77.5 ± 3.3 cm) than plants in the low-light treatment (46.0 ± 2.3 cm), produced more stems (5.1 ± 0.9 vs. 1.34 ± 0.13), had greater total dry weight biomass (10.1 ± 2.0 g vs. 0.8 ± 0.1 g), produced more fruits (137.8 ± 24.0 vs. 8.2 ± 1.2) and had greater seed production (1868.8 ± 340.5 vs. 63.0 ± 10.9). Plants grown at low density produced more stems (6.7 ± 1.0) than plants grown at high density (2.1 ± 0.2), had greater dry weight biomass (13.5 ± 2.3 g vs. 3.3 ± 0.5 g), produced more fruits (177.1 ± 29.1 vs. 46.6 ± 5.7) and had greater seed production (2427.1 ± 434.9 vs. 614.4 ± 86.7). Plants with added nutrients were larger overall (10.0 ± 2.4 g) and produced more fruits (131.9 ± 31.5) than plants that had no nutrients added (4.8 ± 1.4 g total dry weight biomass; 63.2 fruits per plant ± 17.4). Percentage survival was significantly lower for plants in the high-density, low-light, high-fertilizer treatment ($12.0 \pm 4.0\%$) than for plants in the low-density, medium-light treatments, the low-density, low-fertilizer, low-light treatment, and the high-density, high-fertilizer, high-light treatment ($100.0 \pm 0.0\%$; $P = < 0.001$).

Biomass and seed production varied within density according to light level. There were significant differences in shoot biomass among the low- (0.7 ± 0.2 g), medium- (18.7 ± 2.7 g) and high- (7.1 ± 1.7 g) light treatments at low density, but at high density both the medium- (2.5 ± 0.3 g) and high- (3.5 ± 0.6 g) light treatment plants were significantly larger

than the low-light treatment plants (0.4 ± 0.04 g), but were not significantly different from each other (Fig. 4). The same pattern was evident for fruit biomass. Total biomass and number of seeds per plant followed a slightly different pattern. Within a density treatment, plants in the medium- and high-light treatments produced significantly more seeds and had greater total dry weight biomass than plants in the low-light treatment, but were not significantly different from each other.

Total biomass allocation to root, shoot and fruit tissue and to seed production were significantly affected by light level (Table 6). Root allocation was also affected by a density × light level interaction. At low density, plants in the medium-light treatment allocated a significantly smaller proportion of their total biomass to root production than plants at low light. Mature plants allocated more biomass to shoot production in the lowest light treatment ($59.9 \pm 2.1\%$) than in the medium- and high-light treatments ($46.6 \pm 1.3\%$) and less biomass to reproductive organs ($13.8 \pm 1.7\%$) than plants in the higher light treatments ($34.0 \pm 1.9\%$).

Leaf chlorophyll content was significantly affected by nutrient addition, light level and a nutrient × light interaction (Table 6). Specific leaf mass was only affected by light treatment. Plants in the high-light treatment had significantly greater specific leaf mass (0.0168 ± 0.0007 mg cm^{-2}) and lower total chlorophyll content (1.1449 ± 0.0927 mg g^{-1}) than plants in the medium- (0.01135 ± 0.0004 mg cm^{-2}) or low- (1.7199 ± 0.0985 mg g^{-1}) light treatments (Fig. 4). In general, under the two highest light levels, plants in the high-nutrient treatment group had higher chlorophyll *a, b, a : b* ratio and total chlorophyll content than plants in the group with no nutrients added.

Discussion

The effect of light availability, density and nutrient addition on the invasive biennial *Alliaria petiolata* were examined in an experimental garden. The impact of these effects on *Alliaria* growth, reproduction, leaf chlorophyll content and biomass allocation patterns is discussed along with references to other herbaceous and invasive species. We compare and contrast the responses of rosette and mature plants and discuss the developmental and ecological implications. We also discuss the implications of variation in the experimental parameters on *Alliaria* colonization of new habitats, population proliferation and possible management strategies.

Availability of resources such as water, nutrients and light varies within ecosystems. Disturbance is often associated with changes in resource availability (Fetcher *et al.* 1996) and can increase both nutrient and light levels (Marino *et al.* 1997). *Alliaria* often invades disturbed habitats (Cavers *et al.* 1979;

Table 5 Standardized canonical coefficients for variables measured when *Alliaria petiolata* mature plants were grown under varying density, nutrient addition, and light levels

	SLM	Chloro. *a*	Chloro. *b*	Total chloro.	Chloro. *a:b*	Height	No. of stems	Shoot biomass	Total biomass	R:S biomass	Fruit biomass	% Shoot	% Fruit	No. of Fruits	Seeds per fruit	Seeds per plant	Seed mass
Density	−0.03	1.51	1.28	−1.22	0.74	−1.26	0.40	−1.72	6.30	0.53	0.01	0.70	−0.43	−0.42	0.20	−0.28	−0.41
Nutrient	1.13	5.43	6.55	−6.94	2.04	−0.44	0.63	4.35	−2.83	0.17	0.05	−0.15	0.41	0.08	−0.64	−0.28	−0.22
	−0.26	2.80	1.17	−3.79	0.33	2.34	0.43	13.49	−16.61	0.14	−0.06	−2.63	0.92	0.78	−2.46	0.46	0.28
D × N	0.65	2.35	3.37	−4.10	1.88	2.19	0.89	6.18	−7.31	0.01	0.01	−1.41	0.86	0.23	−1.29	1.02	1.17
	0.20	2.01	−0.91	−1.84	−0.86	0.97	0.81	20.33	−20.59	1.08	−0.46	−2.74	0.49	0.20	−1.57	−0.46	−0.41
Light	0.94	0.60	−0.08	−0.26	0.34	0.50	0.49	6.62	−4.15	0.22	−0.02	−1.38	0.13	−0.04	−0.06	−0.68	−0.48
	−0.58	3.34	4.47	−4.48	1.66	1.19	0.71	4.76	−3.53	0.02	0.04	−0.73	0.55	0.34	−1.56	0.04	−0.23
D × L	0.85	−0.97	−0.10	1.75	−0.01	−0.74	1.62	−10.42	12.34	−0.81	0.36	1.60	−0.18	−0.12	0.67	−0.41	−0.30
	0.99	−1.82	−3.44	4.63	−1.34	0.58	−0.99	−1.95	5.22	1.13	−0.01	0.62	−0.66	−0.58	−0.15	−0.20	−0.47
N × L	0.92	4.01	5.26	−4.32	1.89	−0.08	0.59	7.06	−4.21	0.51	−0.03	−0.62	0.40	0.00	−0.82	−0.39	−0.41
	−0.31	5.18	4.15	−8.77	0.63	0.57	0.75	4.18	−6.59	0.16	−0.22	−0.78	0.30	0.10	0.09	−0.30	−0.14
	−0.06	−2.98	−2.08	3.63	−0.85	−0.23	0.32	−3.33	6.03	0.63	0.33	0.54	−0.71	−0.83	0.17	−0.21	−0.14
	0.67	−0.06	−2.68	1.58	−1.60	0.76	1.60	−11.75	11.85	−0.67	0.11	1.93	0.38	0.48	−0.76	0.10	0.13
D × N × L	0.42	2.98	6.55	−5.65	2.95	0.19	0.19	7.80	−7.09	−0.44	0.20	−0.94	0.88	0.61	−0.66	0.65	0.79
	0.10	−4.55	−2.55	7.22	−0.84	0.20	−0.57	−15.07	19.05	0.95	0.47	3.16	−0.53	−0.63	0.46	0.04	0.01
	1.32	3.51	0.88	−3.60	−0.07	1.97	0.95	15.02	−15.66	0.30	0.12	−2.31	0.63	0.57	−2.27	−0.77	−0.97
	−0.18	−0.06	0.10	1.24	0.41	1.18	0.53	8.10	−7.99	0.13	−0.54	−2.00	−0.08	−0.32	−1.78	0.93	0.82

Table 6 Three-factor GLM analysis of variance of growth, allocation, and leaf variables measured for mature plants of *Alliaria petiolata* grown under varying densities, nutrient conditions, and light levels. Numbers in the table are *F*-ratios. Degrees of freedom (d.f.) are also listed

| Source	Density	Nutrient	D × N	Light	D × L	N × L	D × N × L
d.f.	1	2	2	2	2	4	4
Height	0.00	2.57	6.26	92.36**	4.23	0.90	3.26
No. of stems per plant	109.58**	2.65	1.43	84.25**	26.57**	4.56*	0.81
Shoot biomass	91.91**	7.29*	1.85	226.22**	19.81**	3.89	4.56*
Root:shoot	1.53	2.48	1.64	6.36	4.89	2.54	3.51
Fruit biomass	72.14**	4.69	5.63	174.41**	42.94**	3.07	6.59**
Total biomass	113.57**	6.80*	2.66	321.49**	22.03**	4.68*	4.46
Seed mass	0.00	0.69	0.03	6.67*	1.16	0.33	0.28
No. of fruits per plant	64.34**	7.07*	3.31	213.88**	22.46**	1.01	1.88
No. of seeds per fruit	0.02	2.66	1.01	63.81**	9.21**	0.95	5.63*
No. of seeds per plant	30.19**	5.47	2.77	188.66**	13.45**	1.41	2.84
Root allocation	1.44	2.97	3.16	11.73**	6.66*	2.87	4.36
Shoot allocation	0.25	3.12	0.34	33.78**	0.54	0.85	0.65
Fruit allocation	8.32	5.48	4.04	80.64**	4.45	1.25	3.09
Specific leaf mass	5.32	3.89	2.13	107.23**	2.02	0.87	1.51
Chlorophyll *a*	2.28	14.01**	1.26	70.55**	0.32	14.32**	0.49
Chlorophyll *b*	6.12	55.02**	0.79	94.07**	0.50	18.38**	0.83
Chlorophyll *a*:*b*	5.03	13.86**	2.42	11.04**	1.53	6.73**	1.18
Total chlorophyll	0.20	19.50**	1.63	97.93**	0.28	18.18**	0.62

Nuzzo 1993), so it is probable that plants growing under field conditions will encounter levels of nutrient and light heterogeneity similar to the range represented in this experiment. It is also likely that *Alliaria* plants will encounter changes in population density as new populations are established and spread throughout an area.

RESPONSES TO LIGHT

Abiotic resources can limit growth, reproduction and allocation in a variety of forest understorey plants (Griffith 1998) with light, in particular, often being important (Canham *et al.* 1996). Experimental shading can lead to reductions in stolon mass (Griffith 1998), root biomass (Eickmeier & Schussler 1993; Robison & McCarthy 1999), specific leaf mass (Robison & McCarthy 1999), biomass allocation to roots and relative growth rates (Dale & Causton 1992; Robison & McCarthy 1999). As previously reported by Anderson *et al.* (1996), light level had a large influence on growth of both rosette and mature plants of *Alliaria* with all measured variables, except root length and root:shoot ratio, positively affected by increased light availability.

Although *Alliaria* rosettes and mature plants allocated more biomass to above-ground vegetative organs when irradiance was low, shading significantly reduced allocation to fruits and seeds. Allocation patterns were similar to those reported by Anderson *et al.* (1996) for *Alliaria* plants growing in a forest in central Illinois. In nutrient-limited environments, plant success may depend on increased biomass allocation to roots, whereas, in light-limited habitats, plants that allocate proportionately more resources to stem tissue may benefit from enhanced competitive ability (Tilman 1988). Shade often increases carbon allocation to stem and leaf tissue and decreased allocation to roots (Grubb *et al.* 1996) and may also reduce allocation to sexual reproductive tissues (Pitelka & Curtis 1986; Iason & Hester 1993). *Alliaria* also responded to light availability at another level by altering specific leaf mass and leaf chlorophyll content. Both plant fitness and competitive ability are affected by the efficiency with which a plant captures and utilizes available light resources (Chazdon *et al.* 1996). Non-indigenous plants often have greater phenotypic plasticity, enabling them to respond to changes in their light environment by shifting biomass allocation strategies or adjusting photosynthetic activities (Pattison *et al.* 1998). It has been often noted that specific leaf mass and leaf thickness increase as irradiance increases (Chabot *et al.* 1979; Nobel 1991; Eickmeier & Schussler 1993), while specific leaf area decreases (Grubb *et al.* 1996). Data from other experiments indicate that low light levels commonly lead to higher leaf chlorophyll content and a reduced chlorophyll *a*:*b* ratio (Björkman 1981). This combination of thinner leaves with larger area and higher chlorophyll content is characteristic of leaves grown in low light conditions (shade leaves), while thicker, smaller leaves with lower chlorophyll content are associated with higher light conditions (sun leaves; Björkman 1981). Both rosettes and mature *Alliaria* plants responded to shade by decreasing specific leaf mass while chlorophyll content increased (i.e. they possess typical shade leaves).
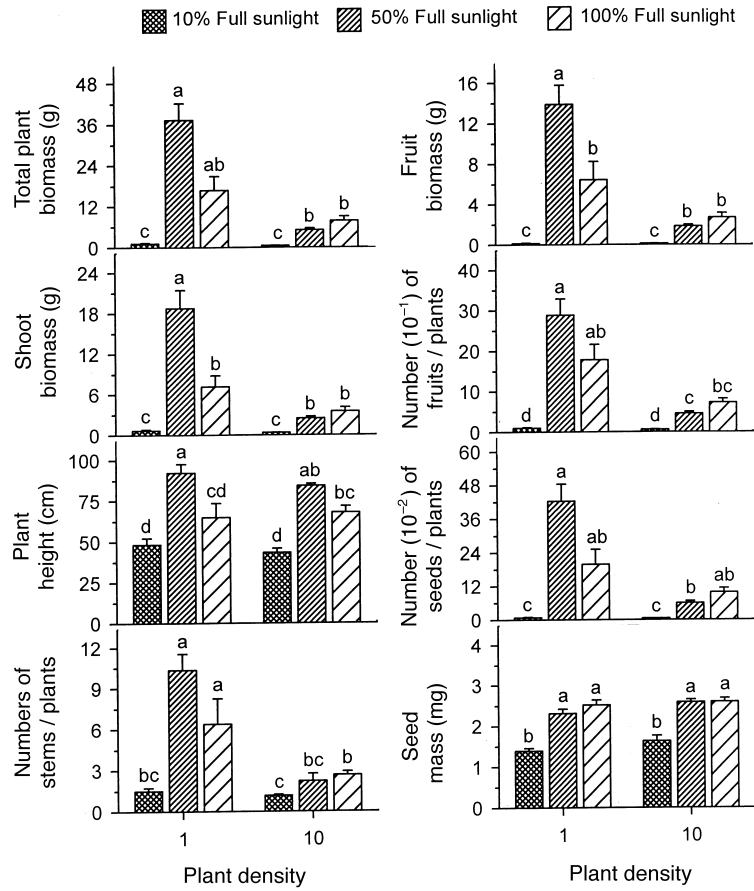
Fig. 3 Effect of plant density and light on mean (+ SE) growth, reproduction and allocation variables measured for mature plants of *Alliaria petiolata* grown under two densities, three nutrient treatments and three light treatments. Letters above the bars indicate significant (*P* < 0.0028) differences in total biomass among treatments.
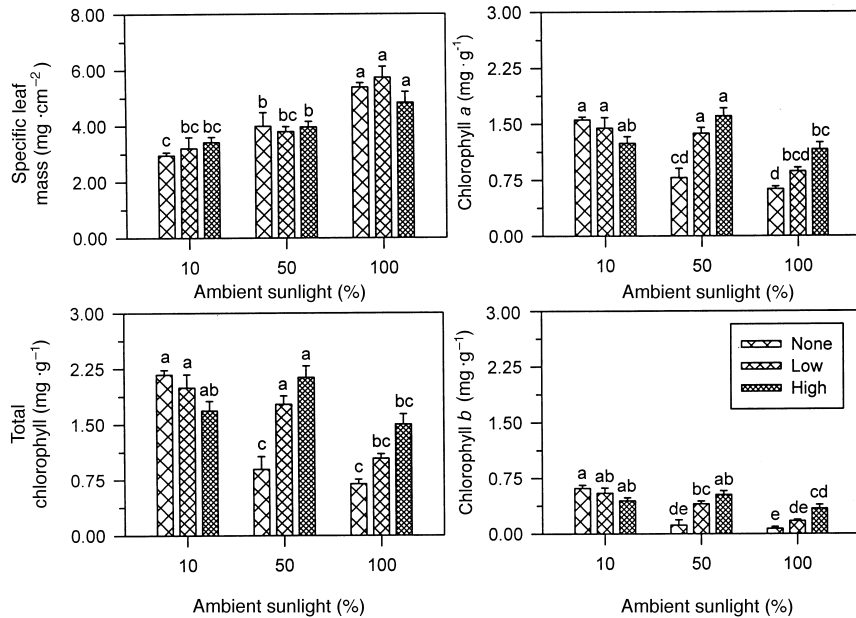
Fig. 4 Effect of light and nutrient addition on mean (+ SE) specific leaf mass and leaf chlorophyll content measured for mature plants of *Alliaria petiolata* grown under two densities, three light treatments and three nutrient conditions. Letters above the bars indicate significant (*P* < 0.0028) differences in total biomass among treatments.

This greater investment in leaf chlorophyll content can be advantageous in low-light habitats because it allows plants to maximize their photosynthetic capacity (Crawford 1989).

As an invasive species associated with disturbance, *Alliaria* may be capable of capturing and using light resources for biomass production better than native forest understorey species. *Alliaria* has been shown to respond plastically to changes in light environment and habitat (Byers & Quinn 1998; Morrison 1998; Dhillion & Anderson 1999). When grown under experimental conditions of high irradiance, stomatal conduction and maximum photosynthetic rates of *Alliaria* rosettes increased, as did shoot biomass (Dhillion & Anderson 1999). In general, however, photosynthetic behaviour was more similar to that of shade-adapted species than to sun-adapted ruderals, which may help to explain the more common occurrence of *Alliaria* in shaded habitats. *Alliaria* rosettes remain green over the winter season and this may give them a further benefit of being able to take advantage of the higher irradiance under a forest canopy in the winter and spring months. Under conditions of greater light availability within a forest, *Alliaria* may therefore have a competitive advantage over other understorey plants.

In this experiment, only light quantity was manipulated so it is possible that some responses of *Alliaria* to light availability may differ from those in the field. Light that reaches plants on the forest floor is often both quantitatively and qualitatively changed by passing through the canopy overhead (Stoutjesdijk 1972; Goodfellow & Barkham 1974). Previous studies of shade-tolerant and shade-intolerant species suggest that responses to neutral shade and green shade (which has a high far-red : red ratio, Mitchell & Woodward 1988; Kitajima 1994) are similar overall, although some shade-intolerant species may react more strongly to green shade (Morgan & Smith 1979; Kwesiga & Grace 1986).

RESPONSE TO DENSITY

Plant density can be another important determinant of plant growth and reproduction. In a densely occupied habitat, there may be a decrease in individual plant biomass due to competition for factors such as nutrients, water, light and physical space (see Grace & Tilman 1990). Casper & Cahill (1998) found that overall (i.e. not necessarily individual) *Abutilon theophrasti* biomass was lower when plants were grown in monospecific stands under higher density conditions. Within stands, there were large differences in plant size, possibly due to competition with neighbours. Even if overall above-ground biomass decreases, allocation to above-ground vegetative biomass might still be favoured at high density (Willson 1983). Reproductive allocation may also

change in response to increasing plant density, either increasing (Hickman 1977) or decreasing (Snell & Burch 1975).

Alliaria rosettes and mature plants grown at higher densities produced less shoot and root biomass, probably as a result of intraspecific competition. Mature plants produced significantly more seeds per plant in the low-density treatment, although on a per pot basis, the 10 *Alliaria* plants at high density still produced more seeds than the one low-density plant. Therefore, although increasing plant density had an overall detrimental affect on individual plant performance, a dense population could produce more biomass and seeds on a per area basis, enhancing the species' competitive ability and colonization potential. Oddly, biomass allocation patterns for mature *Alliaria* plants were unaffected by density, but rosettes allocated a higher proportion of resources to above-ground growth in the high-density treatment. Since North American populations of *Alliaria* are strict biennials and always flower in their second year, mature plants may have a more fixed pattern of biomass allocation which is unaffected by population density.

SOIL RESOURCES

The response of a plant to soil nutrient availability depends on the nature of the nutrient and its distribution in the soil (Burslem *et al*. 1995). Increased nutrient availability leads to greater biomass allocation to leaves in relation to roots for many plant species (Chapin 1980; Smart & Barko 1980) and can also affect reproduction. *Mertensia paniculata* responded positively to fertilizer addition in a boreal forest over a 5-year period by producing more leaves, vegetative and flowering stems (John & Turkington 1997). Addition of phosphorus fertilizer to *Viola blanda* plants had no affect on vegetative growth, but significantly increased reproductive biomass and cleistogamous seed mass (Griffith 1998). Shoot biomass, leaf production, total biomass and fruit production of *Alliaria* were positively affected by nutrient addition, but to a lesser extent than by density or light availability.

The smaller effect of increased nutrient availability on *Alliaria* growth could be due to several factors. Overall, the soil mixture used for this experiment was richer than field soil from an *Alliaria* population in a local forest (8 vs. 3 g^{-1} nitrate-nitrogen, 30 vs. 10 $\mu g\,g^{-1}$ phosphorus, but 71 vs. 120 $\mu g\,g^{-1}$ potassium). Unfertilized soil may therefore have been sufficiently resource rich for both fertilized and unfertilized rosettes to have stored enough resources for reproduction the following year. Mature plants would not then be as dependent on additional soil nutrients for growth promotion in the second year as were rosettes in the first year.

Even if growing conditions are not optimal, there was no detected minimum size requirement for flower and seed production in *Alliaria*, merely an age requirement: every plant that survived to the second year produced flowers and seeds. Therefore, as long as one rosette can become established in a habitat and survive until the second year, some seed will be produced and a population may become established. Mature plant growth was most strongly influenced by light manipulation, suggesting that the response to nutrients may be overshadowed by a response to light, as shown by Eickmeier & Schussler (1993). Light level and nutrient addition can act synergistically to affect plant performance (Iason & Hester 1993; Marino *et al*. 1997). The effect of nutrients was greater when added to *Alliaria* rosettes growing in the high-light condition: total biomass was significantly greater and plants produced more leaves. The most influential interaction however, especially for mature plants, was between irradiance and plant density: both rosette and mature *Alliaria* plants were able to take better advantage of increased light levels when growing at low density and thus to produce more leaves, vegetative tissues and reproductive biomass.

Although photosynthetic rate was not measured in this experiment, it has recently been shown that *Alliaria* rosettes respond to increased light levels by increasing maximum photosynthetic rates and stomatal conductance (Dhillion & Anderson 1999). In many species, light-saturated photosynthetic rates are positively correlated with leaf nitrogen content (Field & Mooney 1986) as well as with phosphorus and potassium availability (Chapin 1980). Photosynthesis may also be affected by nutrient availability. Nitrogen is particularly important because it is a component of chlorophyll and photosynthetic proteins; therefore, there is a positive relationship between photosynthetic rate and leaf nitrogen content and leaf area and nitrogen availability (Field & Mooney 1986; Evans 1989). In *Oenothera biennis*, the photosynthetic rate of reproductive plants was lower under conditions of low nutrient availability than high nutrient availability (Saulnier & Reekie 1995). Further, photosynthetic rates can be influenced by the interaction of light and nutrient availability (Gulmon & Chu 1981). Mature *Alliaria* plants receiving added soil nutrients had greater chlorophyll content. It is therefore possible that this enhanced photosynthetic rate of *Alliaria* at increased irradiance and nutrient level led to an increase in rosette and mature plant growth.

The results of this experiment also provide partial support for the optimal partitioning theory (Reynolds & Thornley 1982; Bloom *et al*. 1985; Hilbert 1990; Gleeson 1993). Biomass allocation patterns of rosette and mature plants differed among treatment groups due to light level, but only rosette shoot allocation patterns were significantly affected by density and neither rosettes nor mature plants were affected by nutrient addition. Root : shoot allocation was significantly affected by density and light level only for rosette plants. Overall, however, *Alliaria* showed a greater response to variable environmental conditions via growth than via biomass partitioning. Those differences in allocation that were observed may have been the result either of adjustments by the plant to its environment or of differences in ontogeny among treatment groups. At one point in time, plants of the same chronological age may be at different developmental stages due to differing growth rates in different environments (Evans 1972) and, especially for reproductive plants, constraints may prevent them from investing in certain types of tissues at particular developmental stages (Geber 1989). For example, early in growth, some herbaceous plants invest more biomass in roots relative to shoots in order to promote establishment in the soil and only then does shoot investment increase (Ledig *et al*. 1970; Bazzaz *et al*. 1989). These ontogenetic dissimilarities may translate into different allocation strategies. McConnaughay & Coleman (1998) found that when three species of annual plants were switched from one nutrient regime to another (e.g. high to low nutrient levels) early in ontogeny, plants adjusted their shoot growth and leaf biomass allocation patterns. However, in two of the species the ratio of root to shoot biomass allocation did not change and was apparently developmentally fixed. These results do not support optimal partitioning theory and indicate that plant growth in response to environmental variation may not be dependent on concordant changes in biomass allocation patterns between shoot and root tissue, although it is possible that adjustments are made within the shoot and root systems (Reynolds & D'Antonio 1996). Such changes have been reported in root length per gram root mass (Berntson *et al*. 1995), root densities (Berntson *et al*. 1993), branching patterns of roots (Taub & Goldberg 1996) and fine and coarse root mass (Berntson *et al*. 1993).

The differences in growth and allocation patterns observed for *Alliaria* basal rosettes and mature plants underscore the potential importance of density and habitat fertility for initial invasion and rosette plant growth and the importance of light availability throughout the life cycle. They also indicate that interactions among biotic and abiotic environmental components can be extremely important in affecting plant performance in a particular habitat. These differences also stress the importance of examining the effects of resource heterogeneity over the entire life span of a species, whenever possible. Rosette plants were more responsive overall to environmental heterogeneity than mature plants.

The rosette stage is the most vulnerable phase of the life cycle, especially over the summer months, with mortality as high as 92–98% (Anderson *et al*. 1996; Byers & Quinn 1998). Higher light and nutrient availability and lower plant density may therefore be important factors in determining rosette survival and growth, suggesting that higher quality habitats with some degree of canopy disturbance might be more vulnerable to invasion by *Alliaria*. Although *Alliaria* rosettes and mature plants showed similar positive responses to increased light availability and low plant density, rosettes responded to increased nutrient availability with greater increases in plant biomass than did mature plants. Mature plants may depend more on stored resources and light availability during flower and seed production, so overall habitat quality may be less important.

When considering the possible effects that density, light and nutrients might have on *Alliaria* growth in a non-experimental setting, the aggressive, invasive character of *Alliaria* in forested habitats in North America must be taken into account. Non-indigenous, invasive plants can outcompete natives and *Alliaria* is capable of outcompeting and displacing native plants in both field (McCarthy 1997) and glasshouse settings (Meekins & McCarthy 1999). If reproductive abilities and herbivore pressures are the same for non-indigenous plants and natives, displacement may be due to more efficient usage of limiting abiotic resources or by taking advantage of resources at times when they are not available to native plants (Vitousek 1986). *Alliaria* seedlings emerge early in the spring and may thus be able to capture important light and soil resources before other (native) plants emerge, enabling the resulting rosettes to use these resources to promote growth.

The results of this experiment provide an indication of how *Alliaria* might respond to variations in irradiance, nutrient availability and plant density in the field. Extrapolation must, however, be done with caution since other factors such as soil moisture, pH, disease and herbivory are likely to interact with these experimental variables (Dale & Causton 1992; Jurena & Van Auken 1996; John & Turkington 1997). The success of an invasive, non-indigenous organism in a new habitat is often due to its release from native predators (Vitousek 1986). In particular, herbivory, or the lack thereof, may be an important contributing factor to the success of *Alliaria* in North America. In Europe, *Alliaria* is a food source for the butterflies *Pieris napi* (the green-veined white; Lees & Archer 1974) and *Pieris brassicae* (the large white; Fernando 1971), but little herbivore damage has been reported in North America (Cavers *et al*. 1979; B. C. McCarthy, personal observation).

Some possible management strategies for North American forests not yet invaded by *Alliaria* can be proposed. For example, it is advisable to prevent anthropogenic disturbance in a natural area by keeping the number of trails, roads and other light-intensifying disturbances to a minimum as *Alliaria* growth and reproduction are enhanced under conditions of higher light availability. It should also be noted that even environments that have moderate levels of light intensity may be more prone to *Alliaria* invasion and proliferation if they are nutrient rich.

Acknowledgements

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