Influence of shading on the growth and leaf photosynthesis of the invasive non-indigenous plant garlic mustard [*Alliaria petiolata* (M. Bieb) Cavara and Grande] grown under simulated late-winter to mid-spring conditions

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MYERS, C. V., R. C. ANDERSON, AND D. L. BYERS (Behavior, Ecology, Evolution, and Systematics Section, 4120 Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120). Influence of shading on the growth and leaf photosynthesis of the invasive non-indigenous plant garlic mustard [*Alliaria petiolata* (M. Bieb) Cavara and Grande] grown under simulated late-winter to mid-spring conditions. J. Torrey Bot. Soc. 132: 1–10. 2005.—Plasticity in photosynthetic response to varied light conditions likely contributes to the successful spread and domination of eastern deciduous forest ground layers by the invasive, non-indigenous plant species *Alliaria petiolata*. We examined the effects of growing plants with no shading, or under 30% or 60% black shade cloth on leaf photosynthetic rates, maximum rates of leaf photosynthesis (A_{max}) and stomatal conductance (g_{Smax}), light compensation point, above and below ground biomass, chlorophyll content and specific leaf mass of *A. petiolata* grown under simulated late-winter to mid-spring conditions of temperature, photoperiod, and irradiance in a growth chamber. The 0% shade treatment plants exhibited a significantly greater leaf photosynthetic rate than the 60% shade treatment plants between 800 and 1600 μmol·m^{-2}·s^{-1} photosynthetically active photon flux density (PPFD). Leaf A_{max} was significantly greater for plants grown under no shade than for plants grown under either the 30 or 60% shade treatments and g_{Smax} was higher for plants grown under no shade than plants in the 60% shade treatment. Plants grown under 0 and 30% shade produced significantly more biomass and had greater specific leaf mass than plants grown under 60% shade. Leaves of the 60% shade treatment had significantly greater chlorophyll *a* and *b* content than leaves of the 0 and 30% shade treatments. Our results indicate that *A. petiolata* displays a plastic response to varied light levels in a way that would likely increase its success in invading eastern deciduous forest ground layers.

Key words: *Alliaria petiolata*, invasive plant, light compensation point, non-indigenous, plasticity, photosynthesis, stomatal conductance, chlorophyll, biomass, specific leaf mass, A_{max}, g_{Smax}, sun leaves, shade leaves.

Non-indigenous plants can successfully dominate areas they invade, eliminate indigenous native plants, and reduce biodiversity (Randall 1996, Vitousek et al. 1996, Mack et al. 2000). *Alliaria petiolata* (M. Bieb), Cavara and Grande, a native of Eurasia, is an invasive biennial plant introduced to the United States in 1868 (Clapman et al. 1952). It has colonized most of the northeastern United States and southeastern parts of Canada (Haber 2001). In the USA, *A. petiolata* occurs south to northern Georgia, and as far west as Kansas, Nebraska, and Oklahoma with isolated occurrences of the plant reported in Oregon, Utah, and Washington (Nuzzo 1991, Blossey et al. 2001). It appears to be more competitive than native species and often dominates eastern deciduous forest ground layers in North America (Cavers et al. 1979, McCarthy 1997,

Meekins and McCarthy 1999, Blossey et al. 2001). For these reasons, resource managers consider it a nuisance plant (Nuzzo 1991).

In novel environments, non-indigenous species frequently are exposed to environmental conditions that differ from those of their native range (Mack et al. 2000). To develop strategies to control invasive species it is important to understand ecophysiological attributes and other characteristics of invasives that allow them to persist in variable environments and displace indigenous species (Mulligan 1965, Mack et al. 2000). The ability of *Alliaria petiolata* to successfully occur under a wide range of irradiances (Dhillion and Anderson 1999, Meekins and McCarthy 2002, Myers and Anderson 2003) suggests that it has a plastic response to varied light conditions, a trait that would contribute to its successful spread.

Alliaria petiolata grows in areas with irradiance levels varying from deep shade, such as forest ground layers, to areas of full sunlight near forest edges, adjacent to trails, forest openings, and old fields (Cavers et al. 1979, Nuzzo 1991, Byers and Quinn 1998, Dhillion and An-

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derson 1999, Myers and Anderson 2003). Additionally, *A. petiolata* plants remain green and potentially photosynthetically active year round (Cavers et al. 1979, Anderson et al. 1996). For this reason, *A. petiolata* plants experience seasonal variation in irradiance due to tree canopy closure. In central Illinois, USA, Myers and Anderson (2003) reported that in early spring before canopy closure, high photosynthetically active photon flux density (PPFD, mean ± SE, 822 ± 30 μmol·m^{-2}·s^{-1}) reached the ground layer. Under these early spring conditions, *A. petiolata* leaves achieve high maximum rates of photosynthesis (A_{max}) (13.26 ± 0.63 to 17.77 ± 0.55 μmol CO_2 m^{-2}·s^{-1}). However, following canopy closure in late May, mean PPFD in the ground layer declined to 189 ± 93 μmol·m^{-2}·s^{-1} and A_{max} declined to 4.73 ± 0.41 μmol CO_2 m^{-2}·s^{-1} (Myers and Anderson 2003).

Alliaria petiolata responds to varied light conditions by producing sun and shade leaves (Dhillion and Anderson 1999, Meekins and McCarthy 2000). In general, sun leaves differ from shade leaves by having higher maximum rates of photosynthesis (A_{max}) and greater specific leaf mass and amounts of Rubisco per leaf area (Koizumi and Oshima 1985, Givnish 1988, Hamerlynck and Knapp 1994, Skillman et al. 1996, Muraoka et al. 1997, Rothstein and Zak 2001, Piel et al. 2002), greater stomatal densities (Nobel et al. 1975, Gauhl 1976, Patterson et al. 1978, Muraoka et al. 1997) and conductances (Hamerlynck and Knapp 1994, Piel et al. 2002), higher chlorophyll *a:b* (Patterson et al. 1978, Reginer et al. 1988, Lei and Koike 1998), lower specific leaf area (Larcher 1995, Muraoka et al. 1997, Lei and Koike 1998, Rothstein and Zak 2001, Turnball et al. 2002) and lower chlorophyll concentrations (Lei and Koike 1998, Rothstein and Zak 2001).

We hypothesize that *A. petiolata* is adapted to a varied light regime and would display a plastic photosynthetic response to experimentally induced variation in irradiance. To test this hypothesis we evaluated the effects of growing plants in a growth chamber at 0, 30, or 60% shade under a light regime similar to field conditions during late winter and early spring. We compared leaf photosynthetic rates, A_{max}, specific leaf mass, chlorophyll content (*a, b, a:b,* and total), stomatal conductance, g_{Smax}, and biomass production and allocation, of *A. petiolata* plants grown under the various shade treatments. We predicted that *Alliaria petiolata* would display physiological plasticity, with plants grown under higher levels of light having characteristics typical of sun plants with higher A_{max}, g_{Smax}, specific leaf mass, biomass production, and chlorophyll *a:b,* but lower total chlorophyll than plants grown under lower light.

Materials and Methods. ENVIRONMENTAL TREATMENTS. Seeds used in the experiments were collected on July 31, 1998 from a population of *A. petiolata* located on the 284 ha ParkLands Foundation Merwin Nature Preserve, located 25 km north of Normal, IL USA. On October 15, 1998, seeds were scattered on the surface of potting soil in a greenhouse flat, watered, and placed outside to receive cold stratification. On February 1, 1999 the flat was transferred to a greenhouse that was maintained at 27 °C. Following seedling emergence, each plant was grown in a separate 10 × 10 cm (100 cm²) square plastic pot filled with 600 ml of Sun Gro Horticulture Professional Mix 1 containing a mixture of peat moss, perlite, gypsum, dolomitic lime and a wetting agent (Sun Gro Horticulture Canada LTD, Seba Beach, Alberta, Canada). *Alliaria petiolata* plants were grown in two environmental chambers (Model GCW 15, Environmental Growth Chambers, Chagrin Falls, OH 44022) for 90 days under conditions that simulated those experienced by populations in the field during late winter to early spring at Normal, IL (40° 30′ N, 89° 29′ W).

The 90-day growth period was divided into three 30-day intervals. Day length, temperature, and irradiance for the first, second, and third 30-day intervals simulated average daily conditions between February 15 and March 15, March 16 and April 15, and April 16 and May 15, respectively (NOAA 1997, Famighetti 1998). The light period of each day was divided into seven equal time intervals. Irradiance levels and temperatures were changed to simulate average irradiance and temperature variations during a day for each of the seven time intervals (NOAA 1997). During the dark period, temperatures in the growth chambers were set to gradually decrease 2 °C from the end of interval 7 to the beginning of interval 1 to simulate nighttime temperature changes for each 30-day period. For the first, second, and third 30-day intervals maximum and minimum temperatures were 2 and 8, 12 and 16, and 12 and 18 °C and mean temperature for the same intervals were 5.4, 14.1, and 14.7 °C, respectively. The set ranges in PPFD were 260–869, 250–885, and 303–890 μmol·m^{-2}·s^{-1} and means were 513, 543, and 572 μmol·m^{-2}·s^{-1}, for

the first, second and third intervals, respectively. To determine actual irradiance levels in the growth chambers, irradiance measurements were made on February 24, 1999 and April 28, 1999 at 5 separate locations in both growth chambers during each of the seven intervals receiving irradiance (Myers 2000). Relative humidity of the growth chambers was maintained at approximately 60 percent throughout the experiment.

SHADE TREATMENTS. The pots of all shade treatment plants were fitted with a wire frame consisting of two 46 cm pieces of metal wire that were bent into a U-shape. The ends of each piece were placed in the soil at diagonal corners of the pot, thus creating a frame to support shade cloth. Thirty or 60 percent light reducing black propylene mesh shade cloth (PAK Unlimited, Inc.) was used; however, measured shading for the two grades of shade cloth using a range of irradiances from 37 to 1,059 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were (mean $\pm$ SE) 34.2% $\pm$ 1.51 and 67.8% $\pm$ 1.49, respectively. We refer to these two shade cloths as providing 30 and 60 percent shade throughout this paper. Shade cloth was folded over the frames and attached along their vertical sides with strips of adhesive Velcro to produce the 30 and 60% shade treatments, respectively. There was approximately a 1-cm gap between the top of the pot and the bottom of the shade cloth to permit air flow around the plant. Plants assigned to the 0% shade treatment received a wire frame but no shade cloth.

Soil moisture was maintained so plants were well watered with deionized water. Plants were fertilized six times, once every 15 days starting at the beginning of the experiment using Peter's Peat Light Special ™ with N, P, K ratio of 20:10:20. Plants retained a healthy green appearance throughout the experiment and did not appear to be nutrient stressed.

Twelve plants were randomly assigned to each of the shade treatments (0, 30, 60% shade) and growth chambers on February 26, 1999. To determine if there were differences in the size of plants assigned to the shade treatments and growth chambers, leaf area was estimated by converting length and width measurements of each leaf to leaf areas using the regression equation (Leaf Area = 0.0273 + 0.787X (leaf length $\times$ width), r^2 = 0.979, df = 98, P < 0.0001) (Anderson et al. 1996) after assigning plants to treatments and growth chamber but before they were exposed to experimental conditions.

PHOTOSYNTHETIC AND CONDUCTANCE MEASUREMENTS. Light response curves for leaves were measured using the auto light curve program of the LI-COR 6400 with a LED red/blue light source and the following settings: flow rate at 500 μmol s^{-1} and CO_2 concentration at 400 $\mu mol \cdot mol^{-1}$. The CO_2 concentration (mean $\pm$ SE, 391 $\pm$ 0.4 $\mu mol \cdot mol^{-1}$) in the measurement chamber was near current ambient CO_2 conditions. Light response curves were measured on the most recently developed leaves that would fill the 2 $\times$ 3 cm measurement chamber from 18 (six per shade treatment) randomly chosen plants per growth chamber on May 18–21 and 24, 1999 between the hours of 9:00 and 15:00 central standard time (CST). A single leaf was measured on each plant. Light response curves were created by measuring leaf photosynthesis at 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD. Leaf photosynthetic rate, temperature and stomatal conductance were recorded at each programmed irradiance level. We determined A_{max} and g_{Smax} at 1600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD for each shade treatment. Light compensation points were estimated from the linear portion of the light response curve for each plant. The LI-COR 6400 was calibrated once a week during the time measurements were made following the instructions provided in the LI-COR 6400 technical manual (LI-COR 1995).

PLANT BIOMASS. At the end of the 90 d, all plants were harvested by treatment and growth chamber and separated into aboveground (stems and leaves) and belowground components (roots). The roots were washed and all tissue was dried in an oven for 48 h at 70 °C and weighed.

CHLOROPHYLL MEASUREMENTS AND SPECIFIC LEAF MASS. After 90 d, a leaf from each plant was removed and two 1 cm diameter discs were cut from the harvested leaf using an electric cork borer. One disc was used to extract chlorophyll and the second disc was used to determine specific leaf mass. Each disc used for chlorophyll extraction was placed in a separate labeled test tube and 5 ml of N, N-Dimethylformamide was added. The test tubes were covered with aluminum foil and shaken on a Thermolyne slow speed Rotomix (model No. M1735) in a refrigerator for 24 hours to allow the chlorophyll to be fully extracted (Inskeep and Bloom 1985). The absorbency (A) of each sample was then measured at 664.5 and 647.0 nm using a double

beam Beckman Coulter DU 640B spectrophotometer. The equations used to calculate chlorophyll a, chlorophyll b, and total chlorophyll ($g \cdot m^{-2}$) were those developed by Inskeep and Bloom (1985): Chlorophyll $a = 12.70\ A_{664} - 2.79\ A_{647}$, chlorophyll $b = 20.70\ A_{647} - 4.62\ A_{664.5}$, and total chlorophyll $= 17.90\ A_{647} + 8.08\ A_{664.5}$, where A equals the absorbance in 1.00 centimeter cuvettes and chlorophyll is in $mg \cdot l^{-1}$.

The second 1 cm diameter disc cut from each leaf was weighed immediately on an electronic microbalance to the nearest 0.1 mg. The sample was then dried in a drying oven at 65 °C for 48 h and weighed. Specific leaf mass was expressed as $mg \cdot cm^{-2}$ on a dry weight basis. The percent moisture content of the disc was calculated and used to compute the dry matter contained in the disc used for chlorophyll extraction. The dry mass of both discs was then added to the aboveground weight of each plant.

DATA ANALYSIS. To test for differences among plants assigned to the two growth chambers and treatments within chambers, ANOVA with multiple comparisons were performed on the total leaf area at the beginning of the experiment.

Analysis of variance with multiple comparisons were used to determine if there were significant effects of shade treatment and growth chamber for photosynthesis, A_{max}, total biomass, chlorophyll concentration mg g^{-1} (fresh weight) for chlorophyll a, b, total, $a{:}b$ ratio, and specific leaf mass. Differences in light compensation points and g_{Smax} among treatments were tested using log transformed data and one-way ANOVA with multiple comparisons.

Data for total leaf area, chlorophyll a, b, total chlorophyll, g_{Smax}, and light compensation points were log$_{10}$ transformed to meet assumptions for normality.

The light response curves generated from the LI-COR 6400 were analyzed using a repeated measures analysis with a Helmert transformation that compares mean photosynthetic rate at given irradiance to the mean of subsequent irradiances to test for differences among treatments at selected irradiances (SAS Institute 1989a). The photosynthetic measurements at 100 and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD were not normally distributed for the two growth chambers and transformations did not achieve normality based on Shapiro-Wilk's test for normality. However, the F-values were non-significant for both irradiances ($P = 0.2429$; $P = 0.1981$) so it was unlikely

that a normal distribution would have affected the significance of the F-test (Sokol and Rohlf 1995). A repeated measures analysis was performed on the stomatal conductance data of each light regime to test for effects due to shade treatment. Across a range in stomatal conductance common to all treatments (0.045 to 0.182 mol H_2O m$^{-2} \cdot s^{-1}$) photosynthesis was regressed against conductance separately for each of the three treatments. Slopes and intercepts for all regressions were tested for significant differences from zero using t-tests. Differences in regression slopes and intercepts among treatments were tested using ANOVA (Draper and Smith 1981). A Spearman correlation analysis was performed on the photosynthesis and stomatal conductance data.

The above and below ground mass for all treatments were significantly correlated ($r = 0.8455$; $P < 0.05$), so a two-way MANOVA and separate protected ANOVAs were used to determine if there was a significant effect of shade treatment on above and below ground mass (Scheiner 1993).

Treatment effects were considered significant for all statistical analyses if $P < 0.05$. Ryan-Einot-Gabriel-Welsch multiple range tests were used when appropriate. All multiple comparisons were corrected for experimentwise error using a Bonferroni correction. All statistical analyses were performed using SAS version 6.12 (SAS 1989b).

Results. PRETREATMENT CONDITIONS. There were no significant ($F_{1,70} = 0.38$; $P < 0.5393$) differences in leaf areas between plants assigned to the growth chambers or among treatments ($F_{2,69} = 0.55$; $P < 0.5805$).

PHOTOSYNTHETIC AND CONDUCTANCE MEASUREMENTS. The mean ($\pm$ SE) irradiance level for the two growth chambers for all seven time intervals were 513 ± 36 and 511 ± 34 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on February 24, 1999 and 598 ± 37 and 585 ± 38 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on April 28, 1999.

There were significant effects on leaf photosynthesis due to irradiance (Wilk's $\lambda_{9,22} = 0.0054$; $P < 0.0001$) and no significant effect due to shade treatment ($F_{2,30} = 2.05$; $P = 0.1460$). However there was a significant shade treatment and irradiance interaction (Wilk's $\lambda_{18,44} = 0.1856$; $P = 0.0008$). Shade treatment significantly affected leaf photosynthesis of plants measured at 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD and greater

Table 1. Results of repeated measures analysis for treatment effects on photosynthesis at 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50 irradiances (μmol·m^{-2}·s^{-1} PPFD), df = 5, 30.

Source	MS		F	$P > F$
	Treatment	Error		
1600	18.24	3.832	4.76	0.003
1400	16.85	3.728	4.52	0.003
1200	15.22	3.534	4.31	0.005
1000	13.32	3.391	3.93	0.007
800	9.862	3.088	3.19	0.019
600	6.414	2.845	2.25	0.075
400	2.308	2.395	0.96	0.455
200	2.919	2.698	1.08	0.390
100	4.912	3.440	1.43	0.243
50	6.222	3.958	1.57	0.198

(Table 1). Leaves of the 0% shade treatment plants had a significantly ($P < 0.05$) greater photosynthetic rate than those of the 60% shade treatment plants when measured at 800 μmol·m^{-2}·s^{-1} PPFD and above (Fig. 1A). Leaf photosynthesis at 50 μmol·m^{-2}·s^{-1} PPFD is not shown in the figure for clarity but rates were: $-3.77 \pm 0.52, -2.36 \pm 0.63$, and -1.86 ± 0.52 μmol·m^{-2}·s^{-1}, for the 0, 30, and 60% shade treatments, respectively. There was a significant effect of irradiance (Wilk's $\lambda_{9, 22} = 0.07902$; $P < 0.0001$) on stomatal conductance and a significant correlation ($r_s = 0.7417$; $P < 0.0001$) between photosynthesis and stomatal conductance for plants grown across all shade treatments. However, there was no significant effect of shade treatment ($F_{2,30} = 0.32$; $P = 0.7311$) or a significant interaction between shade treatment and irradiance (Wilk's $\lambda_{18, 44} = 0.4677$; $P = 0.3578$). Across shade treatments, stomatal conductance ranged from 0.0336 to 0.2360 mol H$_2$O

m^{-2}·s^{-1} (Fig. 1B). Regressing photosynthesis against conduction across a range of conductance common to all three treatments produced similar linear equations [Y (photosynthesis) $= -2.679 + 70.727X$ (conductance), $r^2 = 0.277$, df = 87, $P < 0.001; -0.463 + 58.647X$, $r^2 = 0.258$, df = 92, $P < 0.001$; and $-0.433 + 61.937X$, $r^2 = 0.345$, df = 107, $P < 0.001$ for the 0, 30, and 60% shade treatments, respectively]. All of the slopes were significant ($P < 0.001$, in all cases) but none of the intercepts were significantly different from zero ($P = 0.064$, $P = 0.689$, and $P = 0.627$, for the 0, 30, and 60% shade treatments, respectively). There were no significant differences in slopes ($F_{2,283} = 0.370$; $P > 0.75$) or intercepts ($F_{2,285} = 3.320$; $P > 0.25$) among the treatments. Shade treatment significantly affected g_{Smax} ($F_{2,13} = 3.35$; $P = 0.490$) and the 0% shade treatment had significantly higher g_{Smax} than the 60% shade treatment. For the 0, 30 and 60% shade treatment plants, g_{Smax} was 0.164 ± 0.011, 0.135 ± 0.011, and 0.123 ± 0.014 mol H$_2$O m^{-2}·s^{-1}, respectively.

There was a significant ($F_{2,29} = 9.50$; $P < 0.0006$) effect of shade treatment on A_{max} but there was no significant effect of growth chamber ($F_{1,29} = 12.80$; $P = 0.076$) or two-way interactions ($F_{2,29} = 1.912$; $P = 0.6089$). Leaves grown under 0% shade had a significantly ($P < 0.0001$) higher A_{max} (12.26 $\pm$ 0.57 μmol C0$_2$ m^{-2}·s^{-1}) than leaves grown under the 60% shade treatment (8.81 $\pm$ 0.52 μmol C0$_2$ m^{-2}·s^{-1}). There was no significant ($P > 0.05$) difference in A_{max} between the 30 % (10.29 $\pm$ 0.61 μmol C0$_2$ m^{-2}·s^{-1}) and 60 % shade treatments or between the 0% and 30% shade treatment plants.
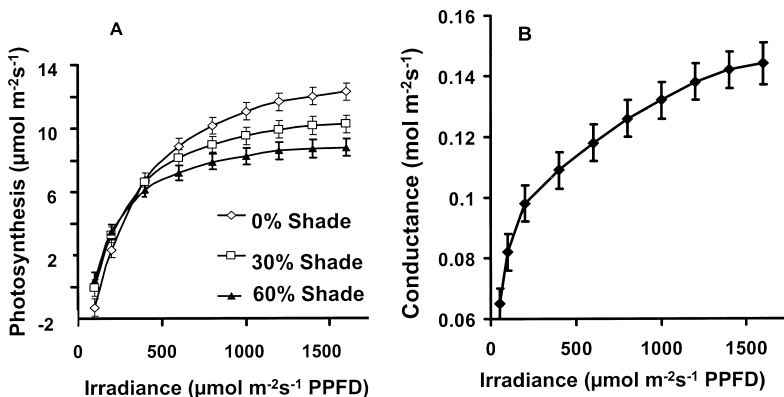

FIG. 1. Mean ($\pm$ 1 SE) leaf photosynthetic rates (A) for the 0, 30 and 60% shade treatments and stomatal conductance (B) for the shade treatments combined across selected irradiances.

Table 2. ANOVA results for total, aboveground and belowground biomass with main effects of shade treatment (Treat) and growth chamber (GC). Error df = 66 for all ANOVAs.

Source	df	MS	F	P > F
Total Mass				
Treat	2	65.60	33.92	0.0001
GC	1	161.03	83.26	0.0001
Treat × GC	2	5.046	2.61	0.0812
Aboveground Mass				
Treat	2	9.25	44.58	0.0001
GC	1	14.13	64.66	0.0001
Treat × GC	2	0.3806	1.74	0.1834
Belowground Mass				
Treat	2	23.55	20.98	0.0001
GC	1	77.69	69.19	0.0001
Treat × GC	2	0.0051	0.50	0.6087

Table 3. Results of MANOVA for shade treatment (Treat) and growth chamber (GC) effects on aboveground and belowground biomass.

Source	Wilk's λ	F	df	P > F
Treat	0.3999	18.89	4, 130	0.0001
GC	0.4404	41.29	2, 130	0.0001
Treat × GC	0.9180	1.419	4, 130	0.2310

	Can 1	Can 2
Eigenvector	1.2940	0.0898
Proportion	0.9351	0.0649
Likelihood ratio	0.3999	0.9176
F	18.89	5.930
df	4, 130	1, 66
P	<0.0001	0.0176
Standardized canonical coefficient		
Above ground	1.639	−1.493
Below ground	0.1983	2.015

There were significant differences in light (PPFD) compensation points among treatment plants ($F_{2,12}$ = 5.12; P = 0.02). The 60% shade treatment plants had a significantly lower light compensation point (75.90 ± 18.08 μmol m^{-2}s^{-1}) than did plants in the 30% (150.97 ± 25.99 μmol·m^{-2}·s^{-1}) or 0% (135.48 ± 18.87 μmol·m^{-2}·s^{-1}) shade treatments.

BIOMASS. Mean biomass (± SE) per plant was significantly different among the three shade treatments and was 7.19 ± 0.53, 5.75 ± 0.40, and 3.89 ± 0.30 g for the 0, 30, and 60% treatment plants, respectively. There were significant effects owing to shade treatment and growth chamber for aboveground and belowground biomass (Table 2, Table 3). The first eigenvector of the MANOVA accounted for 93% of the variance and standard canonical coefficients for this eigenvector indicated that aboveground biomass (1.639) was more important than belowground biomass (0.198) in determining differences due to shade treatment (Table 3). There were significant differences among the three shade treatments for aboveground and belowground plant biomass. For the 0, 30, and 60% shade treatments, respectively, mean (± SE) belowground biomass was 4.5 ± 0.40, 3.46 ± 0.29, and 2.53 ± 0.20 g and mean aboveground biomass was 2.61 ± 0.17, 2.29 ± 0.13 and, 1.40 ± 0.09 g.

CHLOROPHYLL AND SPECIFIC LEAF MASS. The 60% shade treatment had significantly greater chlorophyll *a, b,* and total than the 0 and 30% shade treatments (Table 4). For the 0, 30, and 60% shade treatments, respectively, mean (± SE) for chlorophyll *a* were 1.178 ± 0.016, 1.20 ± 0.015, and 1.981 ± 0.015 mg·g^{-1} and for chlorophyll *b* the same values were 0.282 ± 0.003, 0.336 ± 0.011, and 0.489 ± 0.004 mg·g^{-1}. There was no significant effect on the chlorophyll *a*:*b* ratio.

For specific dry leaf mass, there was a significant effect of shade treatment ($F_{2,66}$ = 33.24; P < 0.001), but not growth chamber ($F_{1,66}$ =0.17; P = 0.6788) or two-way interactions ($F_{2,66}$ = 0.41; P = 0.6702). Plants grown under 0% (5.95 ± 0.31 mg·cm^{-2}) and 30% (5.55 ± 0.41 mg·cm^{-2}) shade had significantly greater dry specific leaf mass than plants grown under 60% shade (3.39 ± 0.26 mg·cm^{-2}).

Table 4. Results of ANOVAs for treatment (Treat) and growth chamber (GC) effects on chlorophyll *a, b, a:b,* and total. Error df = 66 for all ANOVAs.

	df	MS	F	P > F
Chlorophyll *a*				
Treat	2	0.1805	17.90	0.0001
GC	1	0.0024	0.240	0.6291
Treat × GC	2	0.0051	0.500	0.6087
Chlorophyll *b*				
Treat	2	0.1814	9.710	0.0006
GC	1	0.0047	0.250	0.6186
Treat × GC	2	0.0162	0.860	0.4317
Chlorophyll *a:b*				
Treat	2	0.1061	0.210	0.8158
GC	1	0.0053	0.010	0.9203
Treat × GC	2	0.9520	1.840	0.1765
Total Chlorophyll				
Treat	2	0.1805	17.90	0.0001
GC	1	0.0024	0.240	0.6291
Treat × GC	2	0.0051	0.500	0.6087

Discussion. *Alliaria petiolata* displays plasticity to varied habitat conditions including levels of shading (Byers and Quinn 1998, Dhillion and Anderson 1999, Susko and Lovett-Doust 2000, Meekings and McCarthy 2000, Myers and Anderson 2003). We found a significant increase in total biomass with decreasing shade as reported in other studies of *A. petiolata* (Dhillion and Anderson 1999, Meekins and McCarthy 2000). Several researchers (e.g., Patterson et al. 1978, Reginer et al. 1988, Lei and Koike 1998) reported that sun leaves have higher chlorophyll *a:b* ratios than shade leaves. We found that the 60% shade treatment had significantly greater chlorophyll *a, b* and total chlorophyll than did the 0 and 30% shade treatments, but there was no significant effect of shade treatment on *a:b* ratio, similar to the results reported by Meekins and McCarthy (2000) for *A. petiolata*. The lack of significant changes in *a:b* ratios in both studies may be the result of experimentally using shade cloth to change light intensity but not quality (i.e., decreasing the red:far-red ratio), which alters the chlorophyll *a:b* ratio in some species (Anderson 1986, Chow et al. 1990). As reported by Meekins and McCarthy (2000), we found that *A. petiolata* leaves grown under less shade had greater specific leaf masses than plants grown under more shaded conditions.

The ability to efficiently capture and utilize light directly impacts a plant's fitness and its ability to compete (Chazdon et al. 1996). Therefore, the ability to carry on photosynthesis over a wide range of irradiances is of benefit to a plant's overall success when invading an area. As reported for other plant species (Farnsworth and Ellison 1996, Muraoka et al. 1997), our study and Dhillion and Anderson (1999) found that A_{max} of *A. petiolata* leaves were significantly inversely related to the amount of shading to which the plants were exposed. These results indicate that plants grown at the lowest level of shading effectively utilized the higher amounts of irradiance available to them. Additionally, there was a direct relationship between irradiance plants received and the amount of biomass they produced. However, there appeared to be less plasticity displayed by *Alliaria* when photosynthesis was measured at low levels of irradiance. There were no significant differences among the shade treatments for photosynthetic rates measured between 50 and 800 $\mu mols \cdot m^{-2} \cdot s^{-1}$. Nevertheless, there was a direct relationship between the level of shading plants received and leaf photosynthetic rates at 200,

100 and 50 $\mu mols \cdot m^{-2} \cdot s^{-1}$. Moreover, only the 60% shade treatment plants leaves had positive net photosynthesis at 100 $\mu mols \cdot m^{-2} \cdot s^{-1}$ and these leaves had significantly lower light compensation points than leaves of plants grown under less shading.

Shade treatment did not significantly affect g_S but it was strongly affected by PPFD as reported by Lei and Lechowicz (1998). Linear regression indicated that across a range of stomatal conductance common to all three treatments rates of photosynthesis were not significantly different among treatments. These results, as well as the reduced photosynthetic plasticity at low irradiances, could be due to the relatively low levels of irradiance under which all treatment plants were grown, maximum PPFD for unshaded plants was 890 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Nevertheless, there were significant effects of shading on g_{Smax} as reported by other investigators (e.g., Lei and Lechowicz 1998, Piel et al. 2002) with unshaded plants having significantly higher g_{Smax} rates than the most shaded plants (60% shade treatment).

We found significant growth chamber effects for A_{max}, total biomass, and above and below ground biomass. However, there were no significant two-way interactions between growth chamber and shade treatments so the response of plants to shade treatments in the two growth chambers was not different, although the absolute differences in measured variables were different between growth chambers. For example, mean total biomass for the two growth chambers was 7.19 ± 0.38 and 4.11 ± 0.23 g. These results suggest that comparison of absolute differences in treatment responses between studies using different growth chambers may not be valid.

Our light response curves for *Alliaria* differ from those of Dhillion and Anderson (1999) who reported that plants grown at low irradiance of 124, 243, or 469 $\mu mols \cdot m^{-2} \cdot s^{-1}$ experienced markedly reduced leaf photosynthesis and g_S at 1,104 or 1,780 $\mu mols \cdot m^{-2} \cdot s^{-1}$. In contrast, we found no suppression of leaf photosynthesis or g_S at 1,600 $\mu mols \cdot m^{-2} \cdot s^{-1}$ for 30 or 60% shade treatment plants that received maximum levels of irradiance of 305 and 603 $\mu mols \cdot m^{-2} \cdot s^{-1}$, respectively. Differences in results between the studies appear to be related to stomatal control of photosynthesis, which may be due to differences in experimental conditions. Dhillion and Anderson (1999) reported that stomatal conductance was significantly affected by shade treatment, irradiance, and their interaction, whereas in our study conductance was only significantly

affected by irradiance. Dhillion and Anderson (1999) grouped plants for each treatment under a wooden frame, which was covered by one, two, or three layers of shade cloth to expose plants to different levels of irradiance, plants were watered daily, and would have experienced little air movement. Plants grown at low levels of irradiance that had reduced g_S at high levels of irradiance (1,104 and 1,780 mols·m^{-2}·s^{-1}) were likely less tolerant of conditions associated with high irradiance than those in our study resulting in a decline in photosynthesis. Additionally, our experimental results are consistent with those reported by Myers and Anderson (2003) for plants grown under reduced levels of radiation under a forest canopy that did not experience a decline in photosynthesis measured in the field at high levels of irradiance (1,000 to 1,600 μmols·m^{-2}·s^{-1}).

Successful invasive plants use a variety of strategies to compete with native species for irradiance. Invasive, non-indigenous plants such as the vine *Lonicera japonica* and the grass *Microstegium vimineum* persist in variable light conditions (Evans 1984, Barden 1996), which appears to contribute to their success in new ranges. Other invasive species display phenological niche separation by taking advantage of seasonally available high levels of radiation on forest ground layers when native species are not actively growing. For example, the non-indigenous invasive shrubs *Rhamnus cathartica* and *Lonicera × bella* developed leaves sooner and retained them longer than indigenous shrubs. Before the indigenous shrub *Cornus racemosa* began leaf emergence *R. cathartica* and *L. × bella* acquired 29% and 35% of their annual carbon gains, respectively (Harrington et al. 1989a, 1989b).

Alliaria utilizes both of the strategies found among indigenous deciduous forest herbs to maximize photosynthesis (Givnish 1982). Wintergreen species gain a photosynthetic advantage over more rapidly growing species that are less active in fall, winter, and early spring when light intensities can be 35–50% of full sunlight. At these times of the year, wintergreen species are limited by temperature and maximize photosynthesis by producing leaves close to the ground, which is the warmest part of the forest understory in the spring before the tree canopy closes (Curtis 1971). As temperatures warm and the canopy begins to close, irradiance limits growth and later growing species gain an advantage by having their leaves higher where they can com-

pete more effectively for light. The invasive biennial garlic mustard utilizes both of these strategies by maintaining a basal rosette during fall, winter, and early spring. In April of its second growing season, basal rosette leaves of *A. petiolata* achieve their maximum leaf photosynthetic rates before the tree canopy is closed, when irradiance levels on the forest floor are high, and there is little competition from native ground layer species. As temperatures warm and the canopy closes, between late-April and mid-May, the plant bolts and produces new shade-adapted leaves on rapidly elongating shoots that compete more effectively with native ground layer species (Anderson et al. 1996, Myers and Anderson 2003). Thus, phenological niche separation and photosynthetic plasticity in response to changing irradiances play an important role in the success of *A. petiolata* in invading native deciduous forest communities. Under controlled conditions, our study has shown that *A. petiolata* produces sun and shade leaves and responds plastically to its light environment. These characteristics contribute to the success of *A. petiolata* when it invades forested habitats with irradiance levels that vary in time and space.

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