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**Phenological niche separation from native species increases
reproductive success of an invasive species: *Alliaria petiolata*
(Brassicaceae) – garlic mustard¹**

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Phenological niche separation from native species increases reproductive success of an invasive species: *Alliaria petiolata* (Brassicaceae) – garlic mustard¹

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ENGELHARDT, M. J. AND R. C. ANDERSON (School of Biological Sciences, Behavior, Ecology, Evolution, and Systematics Section, Illinois State University, Normal, IL 61790-4120 USA). Phenological niche separation from native species increases reproductive success of an invasive species: *Alliaria petiolata* (Brassicaceae) – garlic mustard. J. Torrey Bot. Soc. 138: 418–433. 2011.—Successful biological invasion requires correspondence between invader functional traits and their utility in novel environments. We focused on specific phenological and ecophysiological characteristics of an herbaceous biennial, *Alliaria petiolata*, related to its successful invasion of deciduous forest groundlayers in eastern North America. We tested for phenological separation between *A. petiolata* and native groundlayer species during spring of its second year, when the plant accumulates 91% of its total biomass, and assessed importance of availability of high irradiance before tree canopy closure on growth and reproductive output. We experimentally shaded plants *in situ* during three intervals: Early: before native groundlayer was well developed (3 March–20 April), Mid: 21 April to tree canopy closure (18 May), and Late: after canopy closure to 29 May. We measured maximum photosynthetic rates (A_{max}) in early (13–14 April) and late (22–26 May) spring. *Alliaria petiolata* began rapid growth and reached maximum cover earlier than most native groundlayer species. Shading effect on plant growth and resource allocation to vegetative growth and reproduction varied depending upon timing and duration of shading. Comparison of treatments differing by being shaded or unshaded in only one of three intervals showed that unshaded plants consistently had significantly higher production than shaded plants only during the Early interval. Greatest A_{max} occurred in early spring (13–14 April), when ground layer irradiance was high. Success of *A. petiolata* in invading this community is likely related to phenological niche separation and temporal availability of resources not available to most native species in early spring.

Key words: *Alliaria petiolata*, deciduous forest, invasive species, phenological niche separation, shading.

Biological invasion studies often focus solely on either traits of the invader or the community that it invades (Parker and Gilbert 2007). Nevertheless, successful invasion requires correspondence between functional traits of the invader and their utility in the novel environment (Mack 2003, Facon et al. 2006). In this study, we focused on how specific phenological and ecophysiological characteristics of *Alliaria petiolata* (M. Bieb) Cavara & Grande relate to the invaded community, eastern North American deciduous forest, and the success of the invader. Phenological differences between invasive and native species have been shown to be an important factor in invasive species success in novel environments (Harrington et al. 1989a, 1989b, Woods 1993, Gould and

Gorchov 2000, Zotz et al. 2000, Xu et al. 2007, Godoy et al. 2009, Willis et al. 2010, Wolkovich and Cleland 2011); however, we believe our study may be the first to use experimental manipulation under field conditions to test this assumption.

The Eurasian biennial herb *Alliaria petiolata* is one of the most widespread and troublesome herbaceous invaders in eastern North American deciduous forest groundlayers (McCarthy 1997, Nuzzo 1999, Meekins and McCarthy 2002, Carlson and Gorchov 2004, Hochstedler et al. 2007, Slaughter et al. 2007, Rodgers et al. 2008). Since its introduction in New York in the 19th century (Nuzzo 1993), *A. petiolata* has spread to 37 USA states and 5 Canadian provinces (USDA 2010) where it often dominates the herbaceous spring groundlayer (Anderson et al. 1996, Nuzzo 1999). Multiple introductions into North America (Meekins et al. 2001, Durka et al. 2005) have contributed to relatively high genetic diversity of the species in its introduced range.

Several mechanisms have been proposed to explain the success of this highly invasive species as summarized in Rodgers et al. (2008).

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Alliaria petiolata has high seed production, (Nuzzo 1993, Pardini et al. 2008), abundant seedling establishment (Anderson et al. 1996, Byers and Quinn 1998), a persistent seed bank (Baskin and Baskin 1992, Davis et al. 2006), flowers adapted for generalist pollinators, and successful cross- and self-pollination (Anderson et al. 1996, Cruden et al. 1996). It has high photosynthetic phenotypic plasticity with high plasticity to varied light regimes (Myers and Anderson 2003). The plant is chemically well defended by secondary compounds that cause low levels of herbivory in novel environments (Blossey et al. 2001, Knight et al. 2009), reduce seed germination or plant growth of other plant species (allelopathic compounds) (Vaughn and Berhow 1999, Roberts and Anderson 2001, Prati and Bossdorf 2004, Pisula and Meiners 2010), kill arbuscular mycorrhizal fungi (AMF), which form mutualistic associations with 70–90% of herbaceous native groundlayer species (Roberts and Anderson 2001, Stinson et al. 2006, 2007, Callaway et al. 2008, Anderson et al. 2010), and suppress ectomycorrhizae (Wolfe et al. 2008).

In North America, *Alliaria petiolata* is an obligate biennial with a three-stage life cycle: seeds, rosettes, and adults (Anderson et al. 1996, Pardini et al. 2009). The details of the life cycle of *A. petiolata* in central Illinois, including germination time, seasonal changes in leaf area, root, shoot, and reproductive biomass, flowering times, and seed release are provided by Anderson et al. (1996). Like wintergreen species, *A. petiolata* can remain photosynthetically active during late fall and early winter of its first year (Cavers et al. 1979, Anderson et al. 1996). In early spring, before the tree canopy is well developed, its second-year rosette of leaves efficiently captures high levels of early spring irradiance reaching the groundlayer (Dhillon and Anderson 1999, Myers and Anderson 2003) a pattern also displayed by native spring ephemerals (Taylor and Percy 1976, Graves 1990, Rothstein and Zak 2001, Hull 2002). Later in its second spring, *A. petiolata* exhibits rapid stem elongation, a characteristic of later growing summer dominant species (Givnish 1982, Hicks and Chabot 1985), with stem elongation of 1.9 cm per day between 18 April and 13 May leading to leaf elevation (Anderson et al. 1996), thereby increasing its competitiveness for light (Meekins and McCarthy 2000, Myers and Anderson 2003, Myers et al. 2005). In response

to declining irradiance in the groundlayer, *A. petiolata* produces shade-adapted leaves with low A_{max} (Myers and Anderson 2003).

A relatively small percentage (2–8%) of *Alliaria petiolata* seedlings survive to sexual maturity (Baskin and Baskin 1992, Anderson et al. 1996, Byers and Quinn 1998, Meekins and McCarthy 2002, Pardini et al. 2009). Seedling development to sexual maturity involves transitions from seedling to rosette and rosette to flowering plant. Davis et al. (2006) concluded that reductions of seed output and rosette mortality are the most important life cycle stages in determining *A. petiolata* demography. Rosette demography was examined by Meekins and McCarthy (2002) in three stages: summer rosettes, fall rosettes, and second year rosettes in populations of low, medium, and high densities. Transitions between summer and fall rosettes were lower (0.67–0.57) than between fall rosettes and second year rosettes (0.82–0.66), likely due to droughty summer conditions, which can result in summer mortality (Byers and Quinn 1998). However, high proportions (0.93–0.96) of second-year rosettes survived to the flowering stage (Meekins and McCarthy 2002). The high survival of second-year rosettes to the flowering stage and fecundity of second-year plants (Davis et al. 2006) are important determinants of plant success and may be strongly influenced by favorable spring conditions. In addition, *A. petiolata* accumulates about 91% of its total biomass during its second year between March 1 and May 31 with a majority (66%) of this biomass accumulated in April (Anderson et al. 1996).

In temperate deciduous forests, irradiance availability fluctuates seasonally as tree canopy cover changes, resulting in selection for native groundlayer species adapted to different irradiance conditions (Givnish 1982, Kudo et al. 2008). Givnish (1982) categorized North American deciduous forest groundlayer species into three generalized groups with different phenological and ecophysiological strategies to avoid shading (wintergreen and spring ephemerals) or compete for low irradiance following canopy closure (summer dominants) (Curtis 1971, Taylor and Percy 1976, Mahall and Bormann 1978, Givnish 1982, Harrington et al. 1989a, 1989b, Hull 2002). Generally, the species of herbaceous plants increase in maximum height to be more competitive for irradiance as the tree canopy closes (Givnish 1982).

As previously described, *Alliaria petiolata* has phenological traits consistent with all three native phenological groups. However, because native herbaceous species in eastern deciduous forest understories are well defined by phenological niches (Givnish 1982), the successful invasion of *A. petiolata* in this community could be due to temporal differences in vegetative growth and flowering between *A. petiolata* and later growing summer dominant native species, which grow taller and produce more cover than spring ephemerals (Wolkovich and Cleland 2011). We hypothesized that this partial phenological niche separation would allow *A. petiolata* to utilize resources not accessible to most later-growing native species, in early spring of its second year. We make the following predictions:

- (1) *A. petiolata* will exhibit phenological niche separation by initiating active growth earlier than most native species.
- (2) *A. petiolata* will have decreased vegetative growth and reproductive output without access to high intensity ambient irradiance in early spring, which is not utilized by most later growing native species.
- (3) *A. petiolata* will not have decreased vegetative growth and reproductive output, if ambient irradiance is reduced from when the native groundlayer is well developed to the time of canopy closure.
- (4) A reduction in ambient irradiance after canopy closure will have no effect on the vegetative growth or reproductive output of *A. petiolata*.

Materials and Methods. CHARACTERIZING PHENOLOGICAL NICHE SEPARATION. We tested for phenological separation between *Alliaria petiolata* and native ground layer species by sampling percent ground cover of herbaceous species from early April through May 1999 in two second-growth hardwood forest sites: the 284 ha ParkLands Foundation Merwin Nature Preserve (PL), 25 km north of Normal, Illinois, USA and the 60 ha Sears-Davis Tract (SD) located 1 km northeast of the PL site. Herbaceous ground layer cover was sampled by species in 1999 on 6 April, and 2 and 27 May at SD and on 13 April, and 11 May at PL. Visual cover estimates were made using 50 × 50 cm quadrats located 1 m north and 1 m south of stratified random sampling points every 5 m along a 50 m transect at PL ($n = 20$) and a 75 m transect at SD ($n = 30$).

CHARACTERIZING GROUND LAYER LIGHT CONDITIONS. We measured irradiance in the center of each quadrat used to estimate plant cover ($n = 30$) at SD on clear days between 11 AM and 1 PM on 24 March, 6 April, and 2 and 26 May 1999. Measurements were made 10 cm above ground level using the hemispherical external sensor on the LI-COR 6400.

EXPERIMENTAL PROCEDURE. *Experimental Design.* Experimental plants were located in a randomized block design at two similar sites within the PL that were 1 km apart. Site 1 occurs on a nearly level terrace 4–5 m above an intermittent stream flood plain at the base of a south-facing slope. Site 2 is located on a broad ridge with a slight slope to the north and is above a narrow stream valley to the west that allowed afternoon irradiance to reach the site below the tree canopy. Both sites were dominated by second-growth oak-hickory forest that had a history of selective cutting and grazing but had been protected for 20 years.

Ambient irradiance available to second-year plants was reduced by experimentally shading *in situ*. A truncated cone-shaped wire tomato cage (70 cm tall, upper and lower diameters of 28 cm and 12 cm, respectively) was placed over each plant and shaded treatment plants were covered with 60% shade cloth leaving a 2.5 cm gap at the bottom for air flow. Sixty percent shade cloth was used because plants of *Alliaria petiolata* grown under 60% shade cloth displayed characteristics more typical of shade plants (chlorophyll A:B, photosynthetic rates, specific leaf mass, and biomass production) than plants grown under 30% shade cloth (Myers et al. 2005).

A previous shading experiment showed that the cover, and, therefore, the competition from native plants, within exclosures (100 cm × 70 cm × 70 cm, H × L × W) decreased with increasing shading with native cover of 63.7%, 49.6%, and 30.9% on 29 July, for 0%, 30%, and 70% shade (R. C. Anderson, unpublished). Because we were interested in determining the influence of seasonal variation in the amount of irradiance reaching the groundlayer on *Alliaria petiolata* growth, having varied amount of cover of native species in the tomato cages, due to treatment conditions, would have been a confounding effect in our experiment. Consequently, all other plants growing inside the cage were removed to create uniform competition across

treatments from nearby groundlayer plants. Also, other than the second-year *A. petiolata*, there were few other plants initially growing inside most of the 12 cm diameter (113 cm²) tomato cages.

To ensure that variability within populations and environmental conditions at each site were included in the study, treatment blocks were located using stratified random sampling along a transect running through the approximate middle of the study population of *Alliaria petiolata* parallel to its longest dimension at both sites. Data were collected in 2005 and 2006; however, in 2005 there were four treatment conditions and in 2006 the number of treatments was increased to six. At 5 m intervals, one block of four second-year plants in 2005 and six second-year plants in 2006, was randomly located either to the right or left of the transect and marked. Selected plants were at least one meter apart and each plant was randomly assigned to one of four (2005) or six treatments (2006).

Phenology and Experimental Manipulation.

To determine when to manipulate the experimental shade treatments (adding or removing shade cloth) we used two phenological events on our study sites. The first phenological event occurred when the native groundlayer was well developed, defined as having greater than 30% cover. Prior to this time, *Alliaria petiolata* received high levels of ambient irradiance, but potential competition from later growing native species was relatively low. The second phenological event occurred when the tree canopy was fully expanded. For both years of the study, the second phenological event was used to manipulate shade treatments. However, the first phenological event was used to manipulate shade treatments only in 2006 to evaluate growth of experimentally shaded and unshaded plants before the native groundlayer was well developed.

We estimated percent canopy cover using a spherical densiometer (Forest Densiometers, Model-A) periodically from March through May at both sites in 2005 and 2006. Measurements were taken facing each of the four cardinal directions at all blocks and were averaged by site. Overall, site 1 had a slightly denser tree canopy than site 2. The canopy was considered to be fully expanded at both sites on 17 and 18 May in 2005 and 2006, respectively, (canopy cover, mean \pm SE = 93.3 \pm 0.5%).

To determine when the native herbaceous ground cover reached 30% for the 2006 study, cover of native species was visually estimated in a 50 \times 50 cm quadrat in each block at both sites ($n = 20$ or 21). Cover of native species increased from 1.0 \pm 0.1% to 12.8 \pm 1.4%, between 24 February and 9 April and reached 30.3 \pm 3.8% on 18 April 2006. Based on this information the first manipulation of treatment conditions occurred on 20 April 2006. By this date, *Podophyllum peltatum* L. had nearly fully expanded leaves, but it was not taller than *Alliaria petiolata*. Other native summer dominant species, e.g., *Laportea canadensis* (L.) Wedell and *Verbena alternifolia* (L.) Britton ex Kearney, were not taller than *A. petiolata* until after full tree canopy development. To compare the rate of native groundlayer cover development between years, we used data from the 1999 sample of groundlayer species, which was collected in this study, to characterize phenological niche separation. A linear relationship was found between cover of native herbaceous groundlayer species and Julian Day, [Y (% Cover) = 1.4292 X (Julian Day) - 129.49, $r^2 = 0.9722$, $P < 0.013$, $df = 3$]. Using the equation above, the estimated cover for 18 April (Julian Day 108) 1999 was 25%, indicating that the rate of native cover development was similar between the two years (1999 and 2006), at least up to 18 April. Tree canopy cover (tree trunks and leafless branches) increased from about 12% on 3 March at the beginning of the experiment to 44% on 18 April 2006.

Experimental Treatments. In 2006, plants were experimentally shaded during three intervals: **Early**, from 3 March to 20 April, before the native groundlayer was well established; **Mid**, 21 April to canopy closure on 18 May; **Late**, from 19 May to the end of the experiment 29 May (Fig. 1). Positive and negative controls were either experimentally shaded (Shaded-Control) or received ambient irradiance (Unshaded-Control), respectively, for the duration of the experiment. Early- & Mid-shaded treatment plants were experimentally shaded from 3 March until the overstory canopy was fully closed, 17 and 18 May in 2005 and 2006, respectively, and then they received ambient irradiance for the remainder of the experiment. A reciprocal treatment group (Late-Shaded) received ambient irradiance until canopy closure and then the treat-

Date	3-Mar ↓	20-Apr ↓	18-May ↓	29-May ↓
Shade Treatments	Early	Mid	Late	
UnShaded-Control				
Shaded-Control				
Early-Shaded				
Early- & Mid-Shaded				
Mid- & Late-Shaded				
Late-Shaded				
Length of Shade Period	48 Days	28 Days	11 Days	
Phenological Events		↑ 30% Native Ground Cover	↑ Canopy Closure	

FIG. 1. Shading regime assigned to six treatments during the length of the experiment from 3 March to 29 May 2006. There were three times during the experiment when plants were shaded: **Early** – from the beginning of the experiment (3 March) until after the time native ground layer cover reached 30 percent cover (20 April); **Mid** – April 21 until the time of tree canopy closure (18 May); and **Late** – from 19 May until the end of the experiment 29 May. Control plants were either experimentally shaded (Shaded Control) or received ambient irradiance (Unshaded-Control) for the duration of the experiment. For the remaining treatments, Early-Shaded, Late-Shaded, Early- & Mid-Shaded, Mid- & Late-Shaded, the names indicate when the treatment received experimental shading. In 2005, only the Unshaded-Control, Shaded-Control, Early- & Mid-Shaded, and Late-Shaded treatments were used. Canopy closure occurred on 17 May and the experiment ended on 26 May.

ment plants received experimental shading to the end of the experiment, 26 and 29 May for 2005 and 2006, respectively.

In 2006, we tested the importance of irradiance received before substantial native ground-layer cover (>30%) had developed by using two treatment conditions: Early-Shaded treatment plants were experimentally shaded from 3 March 2006 until 20 April, shortly after the native groundlayer reached 30% cover, and then they received ambient irradiance to the end of the experiment, 29 May (Fig. 1). A reciprocal treatment group (Mid- & Late-Shaded) received ambient irradiance until 20 April and then experimental shading until the experiment ended (21 April to 29 May).

Plant Harvest. The effect of receiving 100% or 40% of ambient irradiance during specific times in the early spring on *Alliaria petiolata* growth and reproductive success was assessed by comparing vegetative and reproductive biomass among the treatments. Plants were harvested on May 26 and 29 in 2005 and 2006, respectively, when plants showed little vegetative senescence and green fruits typically reach their maximum size (Anderson et al. 1996). Each plant was placed in a separate plastic bag, and stored in a refrigerator at 4° C prior to processing. Tissue was oven dried at 65° C for 48 h before weighing.

We tested for temperature differences among treatments due to shading in 2006, using Thermocron iButton data loggers (Imbedded

Data Systems, catalogue number DS19121G-F5) attached inside paired shaded and unshaded tomato cages in all blocks at both sites. Sensors were shielded from direct sunlight and placed near the top of the tomato cage. Temperature was recorded every three hours beginning at 3 AM central standard time (CST) throughout the experiment. We tested for temperature difference due to shading using repeated measures ANOVA on three consecutive days in March, April, and May. We assumed that shade cloth would have the greatest effect on temperature on sunny days. Because cloud cover data were not available, dates were chosen which had no reported precipitation throughout the county. Data on precipitation was collected by the National Oceanic & Atmospheric Administration's National Climatic Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>, accessed 1 July 2007) from six stations throughout McLean County, Illinois (Timpe 2007). There was no significant effect of shade treatment on temperature in March (between subject treatment: $F_{1,37} = 0.34$, $P = 0.5506$), April ($F_{1,37} = 1.14$, $P = 0.2922$) or May ($F_{1,37} = 0.03$, $P = 0.8715$). The mean \pm SE temperatures (°C) showed little difference between treatments for the shaded and unshaded treatments, respectively, in March (2.10 ± 0.79 , 2.29 ± 0.8), April (14.62 ± 0.07 , 14.73 ± 0.07) or May (15.65 ± 0.20 , 15.55 ± 0.20).

We observed little or no herbivory on shaded or unshaded *Alliaria petiolata*, and

in North America little herbivory has been detected on *A. petiolata* (Blossey et al. 2001, Pardini et al. 2008). No fungal parasites were observed on any *A. petiolata* plants used in this study.

Photosynthesis measurements. Maximum photosynthesis (A_{max}) was measured on May 14 and 17 in 2005 prior to manipulation of experimental conditions for Late-Shaded and Early- & Mid-Shaded treatments. In 2006, A_{max} was measured twice: first on 13–14 April before the initial experimental conditions were changed and on 22–26 May after early (20 April) and late (18 May) changes in experimental shade manipulation had occurred. In both years, light saturation for *Alliaria petiolata* was determined using the auto light curve program of the LI-COR 6400 infrared gas analysis system with a LED red/blue light source: flow rate of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$, CO_2 concentration of $400 \mu\text{mol l}^{-1}$ and 1200, 1000, 800, 600, 400, and $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD of irradiance. Based on the light saturation point derived from the light response curve, we measured A_{max} for each plant at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD on the most recently formed leaf large enough to fill the leaf chamber ($2 \times 3 \text{ cm}$).

STATISTICAL ANALYSES. *Photosynthesis.* For the A_{max} data, we used mixed model ANOVA to analyze the 2005 data and mixed model MANOVA to analyze April and May A_{max} data collected in 2006. In both models, site and block nested within site were considered to be random effects and treatment was a fixed effect.

Biomass Production. We analyzed root, shoot, and fruit biomass using mixed model MANOVA. For data from the four treatments (Unshaded-Control, Shaded-Control, Early- & Mid-Shaded, and Late-Shaded) that were applied in both 2005 and 2006, site, block nested within site, and year were considered random effects while treatment was a fixed effect. For analysis of the 2006 data, site and block nested within site were considered to be random effects and treatment was considered to be a fixed effect. In addition, planned multivariate linear contrasts were used as a follow-up analysis to determine the importance of plants receiving ambient irradiance or 40% of ambient radiation (60% shade) during the three shade intervals (Early, Mid, and Late).

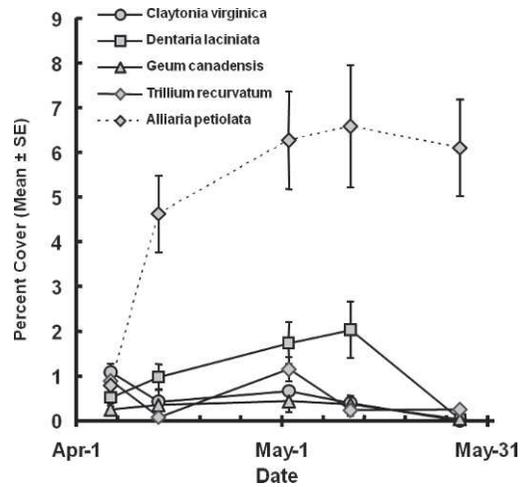


FIG. 2. Mean \pm SE percent ground cover of *Alliaria petiolata* and selected early spring native species plotted by sample date. *A. petiolata* cover was higher than native spring dominant groundlayer species during April.

For each of the three intervals, treatments were compared that differed only by being shaded or unshaded in that interval.

All analyses were done using SAS version 9.1. For ANOVA and MANOVA, PROC GLM was used (SAS Institute 2002–2003). A Ryan-Einot-Gabriel-Welsh multiple range test was used as follow-up tests when appropriate. Response variables, except A_{max} in 2005, were natural log transformed for all analyses to meet assumptions of normality and homogeneity of variances implicit to ANOVA/MANOVA, which were tested using normality plots, box plots, and scatterplots of residuals over predicted values. Except for A_{max} measured in 2005, means \pm SE presented in text, figures and tables are back-transformed from a natural log transformation.

Results. **CHARACTERIZING PHENOLOGICAL NICHE SEPARATION.** As spring progressed, total cover of herbaceous species exclusive of *Alliaria petiolata* increased from $11.8 \pm 1.4\%$ on 6 April to $81.3 \pm 6.3\%$ on 27 May 1999. *Alliaria petiolata* cover increased from $0.8 \pm 0.2\%$ on 6 April to its maximum cover of $6.6 \pm 1.4\%$ on 11 May 1999. The dominant ground layer species during April, *Claytonia virginica* L., *Dentaria laciniata* (Michx.) Sw., *Geum canadense* Jacq., and *Trillium recurvatum* Beck, had low cover compared to *A. petiolata* (Fig. 2). On 27 May, *Podophyllum*

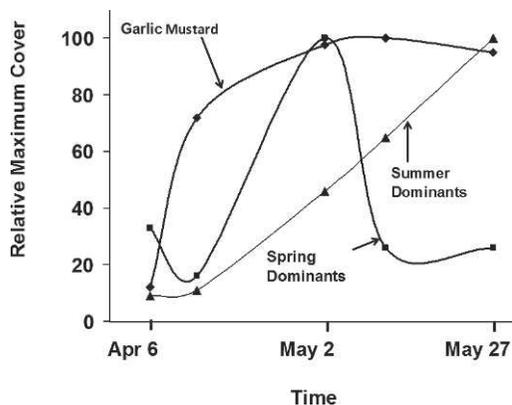


FIG. 3. Relative Maximum Cover (RMC) of *Alliaria petiolata*, spring ephemerals, and summer dominant species as a percentage of their respective maximum cover.

peltatum and *L. canadensis* reached their maximum cover during the sampling period, $36.6 \pm 5.6\%$ and $11.0 \pm 2.7\%$, respectively, and were the only species to accumulate greater cover than *A. petiolata*.

To compare the relative rates of development of *Alliaria petiolata* and native spring ephemerals and summer dominant species, the percent cover measured at each sampling date was expressed as a percentage of the maximum cover that each respective group reached during the study, which was 6.6%, 14.7%, and 77.5%, for *A. petiolata*, spring ephemerals, and summer dominants, respectively (Fig. 3). Initially, the relative maximum cover (RMC) of *A. petiolata* increased more rapidly than the RMC of ephemerals and summer dominants. On 6 April, *A. petiolata* reached 11.9% of its RMC. However, by 13 April *A. petiolata* had attained 70.3% of its RMC, whereas the RMC of ephemerals was 16.0%, and summer dominants reached 11.4% of their RMC on the same date. After April 16, ephemerals increased their RMC more rapidly than *A. petiolata* and summer dominant species reached their maximum cover on May 2, and then cover sharply declined for these species. *A. petiolata* reached its relative maximum cover on May 11, and then had a slight decline in RMC from mid- to late-May. The summer dominants had a significant linear increase in RMC [$Y(\text{RMC}) = 1.492X(\text{Julian Day}) - 129.49$, $r^2 = 0.9772$, $P < 0.0001$, $df = 3$] and after April 13 they had increases in RMC similar to or greater than those of *A. petiolata*.

CHANGES IN IRRADIANCE IN THE GROUND LAYER. Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) in the groundlayer increased from $793 \pm 14 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD on 24 March to 980 ± 114 on 6 April. As the tree canopy continued to close, irradiance declined from 289 ± 65 on 2 May to 78 ± 59 on 26 May after the canopy reached maximum closure.

LIMITING SPRING IRRADIANCE-MAXIMUM PHOTOSYNTHESIS (A_{max}). In 2005, treatment plants were either shaded or unshaded prior to measurement of leaf A_{max} on 14 and 17 May. The ANOVA indicated significant effects owing to treatment ($F_{3,72} = 41.04$, $P < 0.0001$), site ($F_{1,72} = 8.97$, $P = 0.0043$), and block nested within site ($F_{17,72} = 4.81$, $P < 0.001$), but not treatment by site interaction ($F_{3,72} = 1.63$, $P = 0.1958$). The A_{max} values of the Shaded-Control ($3.14 \pm 0.45 \mu\text{mol CO}_2 \text{m}^{-1} \text{s}^{-1}$) and Early- & Mid-Shaded (2.88 ± 0.38) treatments were significantly lower than those of the Late-Shaded (6.30 ± 0.40) and Unshaded-Control (6.09 ± 6.20) treatments and site 1 (5.17 ± 0.36) had a slightly higher A_{max} than site 2 (4.14 ± 0.40).

Shading had a significant affect on leaf A_{max} on 13–14 April and 22–26 May 2006. MANOVA indicated significant treatment effects (Wilks's Lambda = 0.2173, $F_{1,108} = 388.6$, $P < 0.0001$) and treatment by time interaction (Wilks' Lambda = 0.7969, $F_{5,108} = 5.50$, $P < 0.001$), but no significant effects for time by site interaction (Wilks' Lambda = 0.9892, $F_{1,108} = 1.17$, $P > 0.2816$) or time by treatment by site interaction (Wilks' Lambda = 0.9456, $F_{5,108} = 1.24$, $P > 0.2954$). Prior to measurement of A_{max} in April, all plants were under the same treatment shading regime as they were since the start of the experiment. Shaded plants had lower A_{max} than plants receiving ambient radiation; however, not all of these differences were significant. Late-Shaded, Mid- & Late-Shaded, and Unshaded-Control treatments had significantly higher A_{max} than the Early- & Mid-Shaded treatment, which was not significantly different from Early-Shaded and Shaded-Control treatments (Table 1a).

As canopy cover increased between April and May, the concomitant reduction in irradiance levels reaching the forest floor resulted in lower A_{max} in new leaves for all treatments for May as compared to April (Table 1a and 1b). Mid- & Late-Shaded and Early-Shaded treatment

Table 1. Mean \pm SE maximum photosynthesis (A_{max}) measured on 13–14 April, 2006 (a) and 22–26 May, 2006 (b). Within April or May measurements, means with the same letter are not significantly different using Ryan-Einot-Gabriel-Welsh multiple range test.

Treatment	Shade manipulation at time of measurement	N	Mean \pm SE ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
a. April			
Late-Shaded	Unshaded	20	13.29 \pm 1.07 ^b
Mid- & Late-Shaded	Unshaded	20	13.25 \pm 1.06 ^b
Unshaded-Control	Unshaded	20	13.19 \pm 1.09 ^b
Early-Shaded	Shaded	20	10.21 \pm 1.08 ^{ab}
Shaded-Control	Shaded	20	9.91 \pm 1.07 ^{ab}
Early- & Mid-Shaded	Shaded	20	8.85 \pm 1.12 ^a
b. May			
Unshaded-Control	Unshaded	20	5.99 \pm 1.06 ^y
Late-Shaded	Shaded*	20	4.49 \pm 1.11 ^{yz}
Early-Shaded	Unshaded**	20	4.27 \pm 1.18 ^z
Early- & Mid-Shaded	Unshaded*	20	3.44 \pm 1.10 ^{yz}
Mid- & Late-Shaded	Shaded**	20	2.63 \pm 1.12 ^x
Shaded-Control	Shaded	20	2.59 \pm 1.16 ^x

* For previous 4–8 days, **For previous 32–36 days.

plants were shaded or received ambient irradiance, respectively, for at least 26 days prior to May measurements and had A_{max} measurements that were not significantly different than Shaded-Control or Unshaded-Control plants, respectively (Table 1b). However, results of the late A_{max} measurements were complicated because irradiance conditions of two treatments were changed 4–8 days before A_{max} measurements were made and there was insufficient time for new leaves to be produced with an A_{max} corresponding to their changed irradiance regime. The Early- & Mid-Shaded treatment was changed from being experimentally shaded to receiving ambient irradiance and the Late-Shaded treatment was changed from receiving ambient irradiance to being experimentally shaded. Consequently, these treatments had A_{max} measurements that reflected irradiance conditions prior to the change in experimental conditions (Table 1b). The Late-Shaded was not significantly different from Unshaded-Control and Early-Shaded treatments and the Early- & Mid-Shaded and Shaded-Control were not significantly different.

BIOMASS RESPONSE TO TREATMENTS. Spring 2005 & 2006. The MANOVA results indicated significant effects of treatment (Wilks' $\lambda = 0.3625$, $F_{9,299.5} = 17.21$, $P < 0.0001$), year (Wilks' $\lambda = 0.5870$, $F_{3,123} = 28.84$, $P < 0.0001$), and site (Wilks' $\lambda = 0.9190$, $F_{3,123} = 3.59$, $P = 0.0157$) but not block nested within site (Wilks' $\lambda = 0.6857$, $F_{57,367.57} = 0.87$, $P =$

0.7357), year by treatment interaction (Wilks' $\lambda = 0.9769$, $F_{9,299.5} = 0.32$, $P < 0.9679$), or site by treatment interaction (Wilks' $\lambda = 0.9234$, $F_{9,299.5} = 1.11$, $P = 0.3574$) on fruit, shoot, and root mass.

For treatment, only the first eigenvector was significant ($F_{9,299.5} = 17.21$, $P < 0.0001$) and it accounted for 95% of the variation (Table 2). Treatment most strongly influenced fruit mass followed by root and shoot masses. Standard canonical coefficients for fruit, root, and shoot mass were 1.2599, 0.9579, and -0.8337 , respectively, with shoot mass being negatively correlated with the other two variables across treatment. Fruit, shoot, and root masses were not significantly different between Shaded-Control and Early- & Mid-Shaded treatments, but both treatments had significantly smaller mean masses for all variables than the Late-Shaded and Unshaded-Control, which were not significantly different from each other (Table 2).

Fruit mass was more strongly influenced by variation between years than root or shoot mass, and was negatively correlated with these two variables across years with standard canonical coefficient values of -2.4668 , 1.900, and 0.1957 for the three variables, respectively. Mean fruit mass was significantly greater in 2006 than in 2005; however, in 2005 root mass was significantly greater than in 2006. Differences in shoot mass between the two years were not significantly different (Table 2). For fruit, shoot, and root mass, site 2 had significantly greater mean mass than site 1.

Table 2. Mean \pm SE fruit, shoot and root mass (mg) for the four treatments used in both of the two study years. Results for the two study sites and the two years of the study are combined across treatments. For treatments within a column, means with the same superscript letter are not significantly different using Ryan-Einot-Gabriel-Welsh multiple range test. Site 2 had significantly greater mass than site 1 for all variables.

Treatment	Fruit	Shoot	Root	N
Shaded-Control	58.2 \pm 1.2 ^a	474.6 \pm 1.1 ^a	124.9 \pm 1.1 ^a	39
Early- & Mid-Shaded	69.1 \pm 1.2 ^a	500.5 \pm 1.2 ^a	124.8 \pm 1.2 ^a	38
Late Shaded	258.8 \pm 1.1 ^b	1086.8 \pm 1.2 ^b	325.8 \pm 1.1 ^b	39
Unshaded-Control	410.7 \pm 1.1 ^b	1219.9 \pm 1.2 ^b	330.2 \pm 1.1 ^b	40
Site				
Site 1	119.0 \pm 1.2 ^c	615.4 \pm 1.1 ^c	181.1 \pm 1.1 ^c	83
Site 2	182.7 \pm 1.2 ^d	948.3 \pm 1.1 ^d	232.9 \pm 1.1 ^d	73
Year				
Year 2005	111.2 \pm 1.2 ^e	785.6 \pm 1.1 ^f	233.9 \pm 1.1 ^e	75
Year 2006	186.4 \pm 1.2 ^f	724.8 \pm 1.1 ^f	179.2 \pm 1.1 ^f	81

Spring 2006. There was a significant effect of treatment in a multivariate analysis of fruit, shoot, and root mass (Wilks' $\lambda = 0.5141$, $F_{15,243} = 4.42$, $P < 0.0001$); however, there was no significant effect of site (Wilks' $\lambda = 0.8491$, $F_{3,17} = 1.01$, $P = 0.41$), block nested within site (Wilks' $\lambda = 0.7611$, $F_{3,17} = 1.78$, $P = 0.1894$), or site by treatment interactions (Wilks' $\lambda = 0.825$, $F_{15,240} = 1.12$, $P = 0.3356$). For treatment, only the first eigenvector was significant ($F_{15,240} = 5.72$, $P < 0.0001$) and it accounted for 87.4% of the variance. Standardized canonical coefficients indicated treatment most strongly affected fruit mass (2.2935), followed by shoot mass (-1.3043)

and root mass (0.0375). The standardized canonical coefficient for shoot mass was negatively correlated with those of fruit and root masses across treatments indicating that the pattern of resource allocation changed across treatments. Unshaded-Control, Late-Shaded, and Early-Shaded treatments did not differ significantly in fruit mass produced or the proportion of total biomass allocated to fruits; however, they produced significantly more fruit mass and allocated a significantly larger proportion of total biomass to fruits than the other treatments, which did not differ from one another with respect to reproductive biomass (Fig. 4). For the Unshaded-Control,

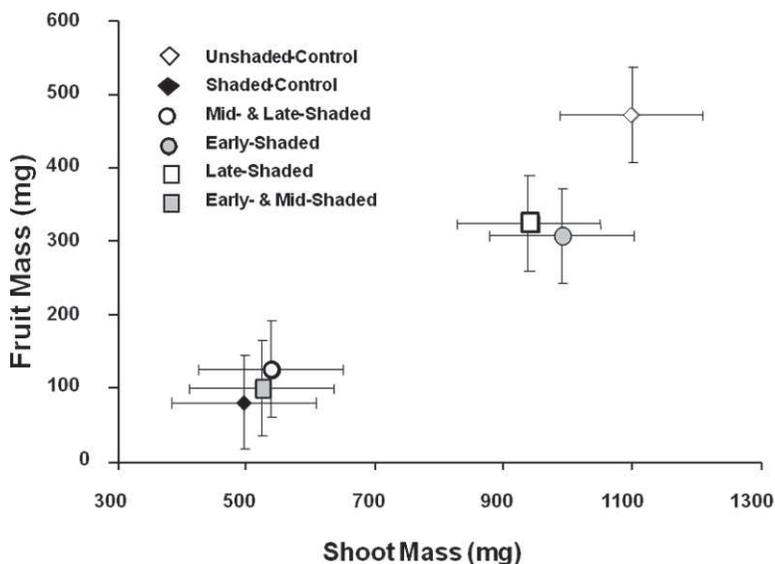


FIG. 4. Treatment means \pm SE of harvested biomass comparing dried shoot and fruit biomass allocation. Data shown are back-transformed means and standard errors from a natural log transformation.

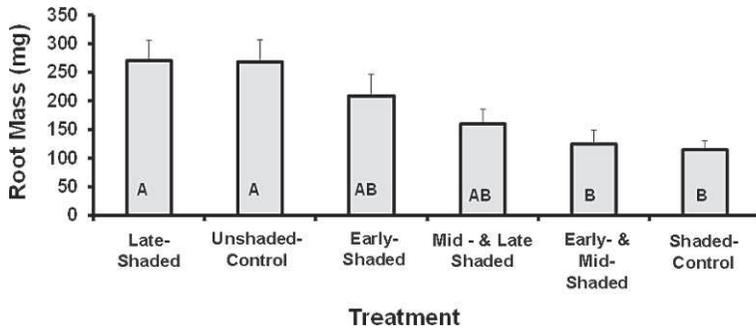


FIG. 5. Mean \pm SE root mass for treatments at the end of the experiment. Means with same letter are not significantly ($P < 0.05$) different. The Late-Shaded and Unshaded-Control treatments have significantly greater root mass than the Early- & Mid-Shaded and Shaded-Control.

Early-Shaded, and Late-Shaded treatments, fruit:total biomass ratios were 0.254 ± 0.008 , 0.209 ± 0.014 , and 0.194 ± 0.011 , respectively, and for the Mid- & Late-Shaded, Early- & Mid-Shaded, and Shaded-Control the ratios were 0.141 ± 0.009 , 0.128 ± 0.014 , and 0.111 ± 0.015 , respectively. There were no significant differences in shoot mass among treatments. For root mass, Late-Shaded and Unshaded-Control treatments had significantly higher mean root masses than the Early- & Mid-Shaded and Shaded-Control treatments (Fig. 5). However, there were no significant ($F_{5,111} = 1.04$, $P = 0.3985$) treatment effects on root:shoot ratios, which ranged from 0.211 ± 1.070 for the Early-Shade Treatment to 0.311 ± 1.206 for the Mid- & Late-Shaded treatment.

TESTING IMPORTANCE OF SHADING IN VARIOUS SHADE INTERVALS. Results of planned multivariate linear contrasts between treatments that differed only by being shaded or unshaded for a single shade interval were consistent for Early and Mid intervals (Table 3). For the Early interval unshaded plants had significantly higher biomass production than experimentally shaded plants for both pairs of treatments. Standard Canonical Coefficients for both comparisons indicated treatment most strongly influenced fruit mass. For the Mid interval there were no overall significant differences between treatments for either comparison (i.e., Early- & Mid-Shaded vs. Early-Shaded or Mid- & Late-Shaded vs. Late-Shaded). Contrasts for the Late interval yielded mixed results. Late-Shaded and Unshaded-Control treatments were not significantly different. However, overall there were significant differences between the Shaded-Control and Early- & Mid-Shaded. For this comparison, treatment

most strongly influenced shoot mass followed by fruit mass and root mass (Table 3).

Discussion. Our study indicates *Alliaria petiolata* is phenologically out of phase with most native species that might be effective competitors with this invasive species in early spring. Native early spring dominant species have A_{max} and light response curves (Hull 2002, Anderson and Nanayakkara 2007) similar to *A. petiolata*, but on our study site, these species had a maximum ground cover of 14.7% and their short stature is not effective for shading potential competitors. Summer dominant species accumulate most of their biomass after the canopy has developed, but many begin growth before canopy closure when irradiance levels are still high (Taylor and Pearcy 1976, Graves 1990, Rothstein and Zak 2001). However, *A. petiolata* approaches maximum height and photosynthetic rates in early- to mid-April (Myers and Anderson 2003) when summer dominant species, which will eventually grow taller than *A. petiolata* and be competitive for light, are of short stature and have low cover. For example, on 13 April 2006, *A. petiolata* had reached 70.3% of its RMC, whereas the summer dominant species had attained only 11.4% of their RMC, respectively. These results support our first prediction that *A. petiolata* will exhibit phenological niche separation by initiating active growth earlier than most native species.

Comparison of treatment effects in 2005 and 2006 on biomass indicated that treatment effects were consistent across sites and years. Plants continually shaded (Shaded-Control) or receiving ambient light only after canopy closure (Early- & Mid-Shaded) had signifi-

Table 3. Multivariate linear contrasts between treatments that differ for only one interval of the shade treatments. Degrees of freedom for all *F*-values are 3,17 (numerator, denominator).

Interval	Treat. Shaded	Treat. Unshaded	Wilks' Lambda	<i>F</i>	<i>P</i>	Std. Canonical Coeffs.		
						Fruit	Shoot	Root
Early								
3 Mar.-20 Ap.	Early-Shaded	Unshaded-Control	0.6963	12.64	<0.0001	2.235	-1.416	0.130
3 Mar.-20 Ap.	Shaded Control	Mid- & Late-Shaded	0.8405	5.50	0.0017	-2.118	0.109	1.438
Mid								
20 Ap.-18 My.	Early- & Mid-Shaded	Early-Shaded	0.9727	0.81	0.4902	-2.643	1.033	0.973
20 Ap.-18 My.	Mid- & Late-Shaded	Late-Shaded	0.9293	2.21	0.0931	-0.850	-1.412	2.352
Late								
18 My.-29 My.	Shaded-Control	Early- & Mid-Shaded	0.8988	3.26	0.0252	1.690	-2.114	1.116
18 My.-29 My.	Late-Shaded	Unshaded-Control	0.9243	2.37	0.0758	-2.421	0.2681	1.665

cantly less fruit, root and shoot mass than plants receiving ambient light (Unshaded-Control) or those shaded only after canopy closure (Late-Shaded). However, there were differences in the amount of total biomass allocated to fruit production and root mass between the two years, which may be due to differences in precipitation between the two years.

In 2006, plants allocated a higher percentage (17.0%) of total biomass to fruit production than in 2005 (9.8%), and the amount of biomass allocated to fruit production in 2005 (111.2 mg) was 59.6 percent of that allocated in 2006 (186.4 mg). For root mass, there was a reversal of the patterns seen between years for fruit mass, with greater biomass, and a higher percentage of total biomass, being allocated to root mass in 2005 than in 2006, 233.9 mg (20.7%) and 179.2 mg (16.4%) for 2005 and 2006, respectively. Drier conditions in 2005 than 2006 may have been a factor contributing to greater root mass production in 2005, with plants allocating a greater amount of resources to enhance water uptake (Grace 1997, Quezada and Gianoli 2010), and a smaller allocation of resources to fruit production than in 2006.

In 2005, precipitation at Chenoa, Illinois located 17 km northeast of our study site for March, April, and May (Weather Warehouse 2011), were 47%, 66% and 17% below the long term (1970–2000) averages for these months (Angel 2007), which are 77 mm, 84 mm, and 98 mm, respectively (Angel 2007). However, in 2006 precipitation exceeded the long-term averages in March (179%) and April (198%), but it was only 64% of the long-term average in May (Weather Warehouse 2011).

Mean total biomass for the Unshaded-Control treatment was not significantly different between the two years ($F_{1,38} = 0.29$, $P = 0.5935$) and was 3.0 ± 0.5 g and 2.5 ± 0.2 g in 2005 and 2006, respectively. This yearly variation in total biomass is similar to that reported by Anderson et al. (1996) for plants growing under ambient light conditions in a forested portion of Ewing Park in Bloomington, Illinois, 27 km to the south of our study site, with total mean biomass of 2.3 ± 0.4 g and 3.2 ± 0.8 g ($n = 30$) in 1990 and 1991, respectively.

Effect of shading on plant growth in spring varied depending upon the shade interval being considered and, in the Late interval,

irradiance conditions to which plants were exposed prior to this interval. Shading in the Early interval before native groundlayer vegetation was well developed (3 March–20 April), reduced plant growth compared to plants receiving ambient irradiance (Early-Shaded vs. Unshaded-Control and Shaded-Control vs. Mid- & Late-Shaded), with reproductive mass being most strongly influenced by treatment. These results support prediction 2—shading before the native groundlayer is well developed will reduce vegetative growth and reproductive output of *Alliaria petiolata*.

For the Mid interval (20 April–18 May), there were no significant differences between shaded or unshaded treatments, thus supporting prediction 3, which posited that shading from the time native groundlayer is well developed to tree canopy closure would not reduce vegetative growth and reproductive output. The length of the Early interval was 48 days compared to 28 for the Mid interval, and the shorter length of the Mid interval might have been a factor contributing to not detecting differences between shaded and unshaded treatment in the Mid interval. However, temperature is often a limiting factor in spring, and degree-days, the accumulated daily mean temperatures above a threshold temperature, are often used to predict the occurrence of spring phenological events (Anderson 1994, Martin 1996, Lechowicz 2002). Using a threshold temperature of 5° C, 233 and 245 degree-days were accumulated during the Early and Mid intervals, respectively. Between 3 March and 20 April (Early Interval) there were 18 days with mean temperatures below 5° C, including 4 days with mean temperatures 0° C or lower. In contrast, after 9 April there were no days with temperatures lower than 5° C. However, during the Early interval at least 18 days had temperatures which were sufficiently low so that it is likely that little or no growth occurred. Thus, the potential functional time for growth may have been similar between the two intervals.

Results from the Late interval (18 May–29 May) were equivocal and were related to the prior light condition to which plants were exposed. Late-Shaded plants were exposed to shaded conditions for only 11 days late in the growth period and were relatively unaffected by shading, resulting in a lack of significant

difference between Late-Shaded and Unshaded-Control treatments. These results support prediction 4; shading *Alliaria petiolata* after canopy closure will not affect vegetative growth and reproductive output. In contrast, Early- & Mid-Shaded plants were continuously shaded prior to receiving ambient irradiance and benefited from relatively modest increases in irradiance and had greater overall growth than Shaded-Control plants largely attributed to shoot growth over fruit and root production, which does not support prediction 4. However, the critical factor for plant success would be fruit production, which was not significantly different between the two treatments, as predicted (Fig. 4). In addition, the combined results for the two years of the study showed that the Early- & Mid-Shaded treatment was not significantly different from the Shaded-Control treatment, supporting prediction 4. The weak response of *A. petiolata* to late shade or ambient irradiance is likely due to the plant being in a late stage in its life cycle (approaching senescence), low levels of irradiance in the groundlayer, and, perhaps, the short length of the Late interval (11 days).

In 2006, early spring ambient irradiance regimes were sufficiently high for shaded plants to achieve moderately high rates of photosynthesis, resulting in some mitigation of treatment effects early (Myers and Anderson 2003), but not later, as ambient irradiance in the groundlayer declined correspondingly with tree canopy development. For example, in April the A_{max} of the Shaded-Control was 75% of the Unshaded-Control; however, in May, the A_{max} of the Shaded-Control was reduced to 43% of the Unshaded-Control A_{max} . Similar results were obtained about 8 days earlier in 2005 when A_{max} of the Shaded Control was 52% of the Unshaded-Control. The significantly greater fruit production of Early-Shaded plants than Mid- & Late-Shaded plants is congruent with these results. When Mid- & Late-Shaded plants received experimental shading, the proportion of net photosynthesis of unshaded plants achieved by shaded plants was substantially smaller than it was in the first shade treatment interval when the Early-Shaded treatment received experimental shading. Thus, even though the Early-Shaded treatment plants produced less biomass than the Unshaded Control, the early shading received by the Early-Shaded treatment plants was not as

detrimental as shading for the Mid- & Late-Shaded treatment as the tree canopy closed, because of high levels of irradiance reaching the forest floor in early spring.

Our results emphasize the importance of the early spring period with high irradiance, and apparently with relatively little competition from native species, to the reproductive output and growth of garlic mustard. Other successful invasive species exhibit phenological niche separation from native plants in their invasive range. For example, the exotic herb *Bunias orientalis* L. achieves half of its annual carbon gain during a time when competition from native species is low (Zotz et al. 2000). Exotic invasive shrubs, such as *Lonicera maackii* (Rupr.) Herder, *L. morrowii* A. Gray, *L. tatarica* L., and *L. ×bella* Zabel and *Rhamnus cathartica* L., leaf out earlier in the spring than most native understory species, taking advantage of high irradiance and effectively shading natives (Harrington et al. 1989a, 1989b, Woods 1993, Gould and Gorchoff 2000, McEwan et al. 2009). Xu et al. (2007) determined that in spring the invasive shrub *Berberis thunbergii* DC. had greater C gain capacity per unit of leaf biomass than natives and this early advantage may partially explain its successful invasion in the deciduous forest understory. Similar to *A. petiolata*, *B. thunbergii* displayed sun-leaf characteristics before canopy closure in the spring and shade-leaf characteristics under closed canopy conditions.

Alliaria petiolata appears to benefit from underutilization of resources in early spring by native species and its apparent preadaptation to exploit these resources. Invasive species may be pre-adapted to take advantage of available irradiance or other resources at different times than native species, because life history characteristics evolved at different times under different selective pressures (White 1983, Zotz et al. 2000, Mack 2003, Davis et al. 2010). Similarly, Mack (2003) proposed that some plant invasions represent life forms that did not appear within the local or regional flora, because of apparent phylogenetic constraints or failure of that life form to arise in or reach a given community. Natural selection typically results in a match between the phenology of a species and environmental conditions to maximize its fitness (Stenseth and Myrsetrud 2002), which should favor native over novel species. Godoy et al. (2009) concluded that the

flowering phenology of alien invasive species in the continental Mediterranean ecosystems of Spain was genetically determined and was little modified in the novel habitat. Flowering of native species and invasive species of Mediterranean origin occurred in spring. However, invasive species of temperate and tropical origin had peak flowering in summer and benefited from recent human activities that reduced the strength of summer droughts, which allowed invasives to have reduced competition with natives for resources.

In contrast, Willis et al. (2010) reported that non-native species and invasive species were far better than native species in adjusting their flowering time to climate change in the novel environment. Thus, under changing conditions invasive species may gain an advantage over native species, if they are preadapted to the altered environment or they adjust to the changing conditions more effectively than native species (Facon et al. 2006). Our results indicate that in its second year of growth *Alliaria petiolata* has reduced competition from many native species, especially summer dominant species, because it is phenologically separated from these species. Whether this phenological niche separation displayed by *A. petiolata* is a recently derived characteristic, was a genetically fixed phylogenetic trait before the species arrived in North America, or is related to climate change is yet to be determined.

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