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Seasonal Variation in Photosynthetic Rates Influences Success of an Invasive Plant, Garlic Mustard (*Alliaria petiolata*)

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ABSTRACT.—*Alliaria petiolata*, an invasive biennial plant, actively grows and achieves high maximum rates of photosynthesis in early spring during its second growing season, when many indigenous ground layer species are still dormant and high levels of irradiance reach the forest floor. *Alliaria petiolata* also extends its growing season into the summer through stem elongation and production of new leaves that are adapted to ambient irradiance levels, unlike native deciduous forest spring ephemeral species or summer forbs. Photosynthetic rates for two populations of *A. petiolata* in a forest ground layer were measured in summer and fall of the plant's first growing season (1998) and in spring of the second growing season (1999). During the second growing season, estimates of native ground layer cover were made at 3–4 wk intervals from early April to late May. Maximum photosynthetic rates (A_{Max}) were positively correlated ($r^2 = 0.791$, $df = 3$, $P = 0.0436$) with mid-day irradiance reaching the forest ground layer and were negatively correlated ($r^2 = 0.911$, $df = 3$, $P = 0.0116$) with percent ground layer cover. The highest A_{Max} (mean \pm SE) occurred on 6 April ($17.8 \pm 0.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and then declined during May, being $8.8 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $4.7 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ on 2 and 24 May, respectively. *Alliaria petiolata*'s pre-adaptation to achieve maximum rates of photosynthesis before the active growth of many native ground layer species when irradiance reaching the ground layer is high, and temperature and moisture conditions are favorable for the species, contributes to its successful spread and eventual domination of forest ground layers.

INTRODUCTION

CHARACTERISTICS OF INVASIVE SPECIES

Invasive plants are a major threat to native ecosystems (Baker, 1986; Hester, 1991; Randall, 1996; Spuhler and Harrington, 1996; Mack *et al.*, 2000), and frequently are more competitive than native species. These invasive species can successfully dominate the areas they invade, eliminating indigenous plants and reducing biodiversity (Randall, 1996; Vitousek *et al.*, 1996; Tilman, 1999). Davis *et al.* (2001) expressed concern about the dissociation of invasion ecology from succession ecology and noted that exotic invaders and local species that enter disturbed habitats following disturbance are both colonizers. They suggested that distinctions should not be made between native and alien invaders. Davis and Thompson (2000) proposed limiting the use of invader to species characterized by being novel to the area, having great impact on the new environment and with either short or long distance dispersal (their colonizer categories 4 and 8, respectively). Nonetheless, in general usage, the term invader is usually applied to nonindigenous species which establish persistent populations in new ranges where they cause environmental degradation as they increase in abundance and spread (Mack *et al.*, 2000), a definition we adopt for this paper.

Generalizations to predict relative community vulnerability to invasion are related to a variety of community characteristics, such as: (1) vacant niches or under utilized resources,

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release from biological controls, disturbance, species richness within communities (Mack *et al.*, 2000; Naeem *et al.*, 2000; Stohlgren *et al.*, 2002); (2) fluctuating availability of resources, such as photosynthate, water and nutrients, which can be limited in time and space (Davis *et al.*, 2000); and (3) temporal niche separation (Harrington *et al.*, 1989a, b; Zotz *et al.*, 2000). Characteristics contributing to success of invasive species include escaping competition from natural predators or disease, successfully competing with native species for limited natural resources (Mack *et al.*, 2000), evolving genotypes adapted to the new environmental conditions (Mack *et al.*, 2000; Mooney and Cleland, 2001), having a wide primary (native) latitudinal range (Rejmanek, 1995), setting seed under a wide range of temperature conditions and day lengths (Baker, 1965), using resources not used by natives (empty niches) or using resources when they are unavailable to natives (Vitousek, 1986; Harrington *et al.*, 1989a, b; Zotz *et al.*, 2000), using resources more efficiently than natives (Bazzaz, 1986; Williamson, 1996; Schmitz *et al.*, 1997; Pattison *et al.*, 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001) and expressing phenotypic plasticity (Byers and Quinn, 1998; Susko and Lovett-Doust, 2000). Some invasive plants also have high light-saturated photosynthesis (Pattison *et al.*, 1998; Baruch and Goldstein, 1999), wide environmental tolerances (Baker, 1965; Mulligan, 1965) and broad ecological niches (Bazzaz, 1986).

Despite efforts to characterize community susceptibility to invasion and the features of invasive species, various authors have indicated that generalizations regarding invasions are somewhat elusive (Lodge, 1993; Mack, 1996; Smith and Knapp, 2001). Consequently, improving our ability to make predictions about outcomes of invasions requires additional focused studies on specific potential invaders and communities (Lodge, 1993).

The invasive biennial *Alliaria petiolata* (garlic mustard) invades eastern deciduous forest in North America and can dominate the ground layer (Cavers *et al.*, 1979; Nuzzo, 1991, 1999; Anderson *et al.*, 1996; McCarthy, 1997; Meekins and McCarthy, 1999; Blossey *et al.*, 2001). In this study, we focused on potential mechanisms that would enable *A. petiolata* to gain an advantage over native species. The biennial's second growing season is of particular interest because, during this time, *A. petiolata* experiences its most rapid growth rates (Anderson *et al.*, 1996). We studied seasonal variation in *A. petiolata*'s photosynthetic rates during its first and second years of growth. We assessed its ability to produce new leaves adapted to changing levels of irradiance in forest ground layers and growing actively in early spring when most native species are dormant and availability of resources such as inorganic nutrients is high (Jones *et al.*, 1997). The phenological niche separation between garlic mustard and indigenous ground layer species and seasonally fluctuating availability of resources, (Davis *et al.*, 2000) may explain the success of garlic mustard in invading deciduous forest ground layers.

The study species.—*Alliaria petiolata*, a species indigenous to Eurasia, was introduced on Long Island, New York, USA in 1868 (Clapman *et al.*, 1952). It subsequently colonized most of northeastern United States and southeastern parts of Canada (Haber, 1996) and now occurs south to northern Georgia and as far west as Kansas, Nebraska and Oklahoma. Isolated occurrences of the species have been reported in Idaho, Oregon, Utah and Washington (Nuzzo, 1991, 1999; Blossey *et al.*, 2001). Following the classification scheme for colonizers proposed by Davis and Thompson (2000), *A. petiolata* would fall into either category 4 or 8 (novel to the area and causing undesirable ecological effects—a “true invader”), depending upon how dispersion is viewed, short (category 4) or long (category 8). *Alliaria petiolata* occurs in habitats with irradiance levels varying from deep shade, such as forest ground layers, to sites receiving nearly full sunlight, such as forest edges, trails and openings (Cavers *et al.*, 1979; Nuzzo, 1991; Dhillion and Anderson, 1999). It has traits associated with successful invasive plants, such as use of generalized pollinators (Bazzaz,

1986; Cruden *et al.*, 1996) and phenotypic plasticity (Byers and Quinn, 1998; Susko and Lovett-Doust, 2000). Roberts and Anderson (2001) presented evidence that the non-mycorrhizal garlic mustard produces chemical(s) that interfere with the formation of mycorrhizal associations which may reduce the competitive abilities of native deciduous forest ground layer plants, of which 71–84% are mycorrhizal.

During its first year, *Alliaria petiolata* occurs as a basal rosette (Clapman *et al.*, 1952; Anderson *et al.*, 1996). First-year plants have high mortality rates in forests during the late spring and summer apparently due to drought conditions in summer (Anderson *et al.*, 1996), reduced irradiances and/or competition with other ground layer plants. Following seed germination, which occurs from mid to late-February to early to mid-April, in central Illinois about 75% of the seedling mortality occurs in the first 3 mo (Anderson *et al.*, 1996). However, mortality rates greatly decrease for second-year plants and about 8 to 10% of the seedlings survive to maturity and produce seeds (Anderson *et al.*, 1996; Byers and Quinn, 1998). Thus, during the second year *A. petiolata* seems to attain a competitive advantage over native ground layer species (Byers and Quinn, 1998).

In the forest ground layer, *Alliaria petiolata* is exposed to a wide range of irradiance because it grows in the winter and early spring before the canopy is developed and in the late spring and summer when the canopy is fully developed. In many species, leaves that develop in full sunlight (sun leaves) have different morphological and physiological characteristics than those developing in shaded conditions (shade leaves). Sun leaves differ from shade leaves by generally having higher rates of photosynthesis, higher light compensation points, thicker leaves, greater stomatal densities, higher chlorophyll a/b ratios, lower chlorophyll content (mg/g), more developed palisade and mesophyll regions and reach saturation at higher irradiances than shade leaves (Nobel, 1976; Patterson *et al.*, 1978; Givnish, 1988; Skillman *et al.*, 1996; Muraoka *et al.*, 1997). *Alliaria petiolata* plants produce leaves with physiological characteristics of sun or shade leaves depending upon the irradiance levels under which they were grown (Meekins and McCarthy, 2000; Myers, 2000) and achieve maximum photosynthetic rates at irradiances comparable to those under which they developed and reached maturity (Dhillon and Anderson, 1999). Because *A. petiolata* is exposed to varied light regimes, the plant potentially can develop new leaves adapted to the changing irradiance conditions of the forest ground layer and use light efficiently.

Native eastern deciduous forest herbs known as spring ephemerals (Curtis, 1971; Graves, 1990), which include trout lily (*Erythronium americanum*), Dutchman's breeches (*Dicentra cucullaria*), spring beauty (*Claytonia virginica*) and other species, also achieve full leaf expansion in the early spring before the tree canopy is fully developed. These plants use the high levels of radiation on the forest floor and experience reduced photosynthetic rates as the tree canopy develops (Taylor and Pearcy, 1976). The ephemeral species, and others such as May apple (*Podophyllum peltatum*) and wood nettle (*Laportea canadensis*) that develop later in the spring, potentially compete with garlic mustard for resources. We hypothesize that *Alliaria petiolata* demonstrates phenological niche separation from native ground layer plants. The purpose of our study was to determine if *A. petiolata*: (1) develops new leaves adapted to changing levels of irradiance reaching the forest ground layer in response to the developing tree canopy and (2) grows most actively in the early spring when many native ground layer plants are dormant. These mechanisms could contribute to the success of *A. petiolata* in invading deciduous forests. The specific questions addressed in this study were: (1) Does the rate of photosynthesis and A_{Max} (maximum photosynthetic rates) of *A. petiolata* in natural populations vary in response to seasonal changes in the level of irradiance reaching the forest floor? and (2) Does *A. petiolata*

achieve maximum rates of photosynthesis in the early spring before the native herbaceous ground layer is well developed?

METHODS

Study sites.—The study was conducted using populations of *Alliaria petiolata* occurring in two second-growth hardwood forests located approximately 25 km north of Normal, Illinois: the 60 ha Sears-Davis site and the ParkLands Foundation Merwin Nature Preserve, a 284 ha nature preserve. The Sears-Davis site is located 1 km northeast of the ParkLands site. Both sites occur on upland areas on soils belonging to the Strawn Series, which is a well-drained, fine-loamy, mixed, mesic, Typic Hapludalf (Windhorn, 1998). *Alliaria petiolata* plants are dispersed throughout the sites at varying densities.

At both sites, plants were chosen and permanently marked for study using stratified random sampling. Fifteen plants were randomly selected at 5 m intervals along a 75 m transect at the Sears-Davis site and ten plants were randomly selected every 5 m along a 50 m line transect at the ParkLands site.

Photosynthesis was measured for first-year plants at the Sears-Davis site in 1998 on 31 July–12 August 1998 (referred to as August) and 5–6 November 1998 and for second-year plants in 1999 on 24–26 March, 6–7 April, 2–3 May and 27–28 May 1999. Measurements were made at the ParkLands site on 13 April and 11 May 1999 during the time when preliminary data collected in 1998 had shown that *Alliaria petiolata* achieved its seasonally highest photosynthetic rates. These measurements were made for comparison with those made at the Sears-Davis site. Photosynthetic measurements in November, March and April were made when trees lacked leaves and in early May, late May and August under nearly closed or closed canopy conditions.

Photosynthetic rate, leaf and air temperatures, vapor pressure deficits (Vpd) and intercellular leaf CO₂ concentrations (C_i) were measured using the LI-COR 6400 infrared gas analysis system between 9 A.M. and 3 P.M. central standard time (CST). Light response curves were created by measuring photosynthesis at 1800, 1600, 1400, 1200, 1000, 800, 400, 200 and 100 μmol m⁻² s⁻¹ PPFD. Irradiances were generated by the LI-COR 6400 LED red/blue light source using the auto light curve program of the LI-COR 6400 with the following settings: flow rate (500 μmol s⁻¹) and CO₂ concentration (400 μmol mol⁻¹). Our objective was to determine the rate of photosynthesis at a seasonal state rather than the maximum photosynthetic rate of an individual leaf during its development. Measurements were made on the most recently developed leaves that would fill the 2 × 3 cm chamber, except in March when some leaves were slightly smaller than the chamber area. However, these smaller leaves were selected over older leaves because they had developed under the current irradiance conditions unlike the older leaves lower on the rosette. A single leaf was measured on each plant. The LI-COR 6400 was run at ambient relative humidity and temperature conditions and was calibrated once a week when measurements were made.

Solar irradiance measurements were recorded on clear days between 11 A.M. and 1 P.M. at each individual plant location at the approximate height of the upper leaves of *Alliaria petiolata* (a total of 15/d). Irradiance measurements were made at the Sears-Davis site using the external hemispherical irradiance sensor on the LI-COR 6400, which measures red and blue light, on days when photosynthesis was measured. The 15 irradiance measurements made on each day were averaged.

Characterizing the forest community.—Woody overstory vegetation was sampled in 10 m wide belt transects centered on the 75 m and 50 m transects, at the Sears-Davis and ParkLands sites, respectively, along which *Alliaria petiolata* plants used to measure photosynthesis were

located. The dbh (diameter at breast height) was measured for trees over 9 cm (dbh) and recorded by species. In 1999, total herbaceous ground layer plant cover was estimated using 50 cm \times 50 cm quadrats located 1 m north and south of each *A. petiolata* plant on 6 April, 3 May and 28 May at the Sears-Davis site and on 13 April and 11 May at the ParkLands site. Ground layer cover estimates for the quadrats were averaged for each date by site.

Data analysis.—To characterize the woody vegetation of the two sites, tree data collected in the belt transects were converted to trees and basal area (m^2) per ha by species for each site. From this information, total tree density and basal area and an Importance Value (IV) for each species (relative density + relative dominance/2) were calculated.

A repeated measures analysis with a Helmert contrast that compares mean photosynthetic rate at given irradiance to the mean of subsequent irradiances was used to test for differences among dates in photosynthesis measured at selected irradiances separately for each population. Irradiance levels and dates were used for the repeated variables (SAS Institute, 1989). All statistical tests involving multiple comparisons were adjusted with a Bonferroni correction. To address the question of how A_{Max} varied seasonally, one-way ANOVAs were used with Ryan's test as a follow up to analyze the relationship between date and A_{Max} for the ParkLands population.

Nonparametric Kruskal-Wallis one-way ANOVAs were used to determine differences in A_{Max} among dates for the Sears-Davis population because the variances were not homogeneous and could not be transformed to meet this criterion. To address the question of how photosynthesis of *Alliaria petiolata* was affected by seasonal variation in irradiance reaching the forest floor, a Pearson correlation analysis was performed on the irradiance levels and A_{Max} of *A. petiolata* for the Sears-Davis population for the five sampling dates when irradiance was measured. Pearson correlations were calculated between mean A_{Max} , averaged for each sampling date and mean vapor pressure deficits based on leaf temperatures (VpdL), intercellular CO_2 concentration (C_i) and leaf temperature to assess variation in A_{Max} attributable to these variables. We used a *t*-test to determine whether leaves measured in March 1999, which did not fill the leaf chamber of the LI-COR 6400, had a significantly different A_{Max} than leaves that filled the chamber. To address the question, how do seasonal changes in photosynthetic rate relate to ground layer forb development, a Pearson correlation analysis was used to examine the relationship between A_{Max} and estimated ground layer cover of both populations combined. All statistical analyses were performed using SAS software (SAS Institute, 1989).

RESULTS

Site characterization.—The Sears-Davis site had a tree density of 371 trees/ha, about one-half of the 610 trees/ha at the ParkLands site. However, the tree basal areas of the Sears-Davis and ParkLands sites were nearly the same (27.8 m^2 /ha vs. 24.5 m^2 /ha). At the Sears-Davis site, the three species with the largest IV's were *Prunus serotina* (IV = 30.4), *Quercus rubra* (16.4) and *Ulmus rubra* (13.4), and at ParkLands, *Q. alba* (24.7), *U. americana* (20.5) and *Fraxinus americana* (17.0) were the most important species.

Seasonal variation in light response curves.—Repeated measures analysis indicated a significant effect of irradiance level on photosynthetic rate (Wilk's Lambda $_{9,76} = 0.028$, $F = 288.4$, $P < 0.0001$). There was also a significant interaction (Wilk's Lambda $_{45, 343} = 0.0389$, $F = 8.13$, $P < 0.0001$) between irradiance and date of measurement, and significant differences were found among dates for photosynthetic rates at all levels of irradiance (Table 1). At the Sears-Davis site, the April sample had significantly higher rates of photosynthesis than all other samples across irradiances ranging from 400 to 1800 $\mu\text{mol m}^{-2}$

TABLE 1.—Sears-Davis site repeated measures analysis with a Helmert contrast for photosynthetic rates across irradiances levels ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF) with dates grouped. For all irradiances listed in table $df = 5, 84$ and $P < 0.0001$

| Irradiance | MS | | F-value |
|------------|-------------|-------|---------|
| | Mean Square | Error | |
| 1800 | 435.2 | 5.219 | 83.38 |
| 1600 | 426.9 | 5.104 | 83.64 |
| 1400 | 403.2 | 4.892 | 82.41 |
| 1200 | 381.9 | 4.613 | 82.79 |
| 1000 | 340.6 | 4.421 | 77.04 |
| 800 | 298.4 | 3.832 | 77.88 |
| 600 | 235.3 | 3.373 | 69.75 |
| 400 | 143.3 | 2.822 | 50.78 |
| 200 | 37.66 | 2.314 | 16.27 |
| 100 | 25.92 | 2.184 | 11.87 |

s^{-1} PPF) (Table 2, Fig. 1) and there were other significant differences among samples (Table 2). At 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, the April and early May samples were significantly higher than all other samples and the late May sample was significantly higher than the March sample. The March sample was significantly higher than all other samples at the lowest irradiance, 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (Table 2, Fig. 1).

At the ParkLands site, the photosynthetic response of garlic mustard was essentially the same as that of the Sears-Davis population so the results for the ParkLands site are summarized here but are given in more detail in Myers (2000). Repeated measures analysis indicated a significant effect of irradiance level on photosynthetic rate (Wilk's Lambda $_{9,10} = 0.001$, $F = 1961$, $P < 0.0001$) and a significant interaction (Wilk's Lambda $_{9,10} = 0.007$, $F = 147.5$, $P < 0.0001$) between irradiance level and date. There were significant differences in photosynthetic rates between the two dates at all levels of irradiance. Photosynthetic rates in April were significantly higher than in early May at all measured irradiances except for 100 and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, at which levels, the early May sample was significantly higher than the April. The A_{Max} for the ParkLands population on April 13 was 13.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which is lower than the A_{Max} of 17.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ measured for the Sears-Davis population on April 6–7. Canopy closure at the two sites occurred within about a week of each other.

Seasonal variation in photosynthesis (A_{Max}) and irradiances.—For the five dates when irradiance measurements were made [August (1998), and in March, April, early and late

TABLE 2.—Results of repeated measures analysis for different dates in mean photosynthetic rates measured at selected irradiances ($\mu \text{mols m}^{-2} \text{ s}^{-1}$ PPF) at Sears-Davis site. Means with the same letter for a given irradiance are not significantly different across the dates (see Fig. 1)

| Irradiance | August 1998 | November 1998 | March 1999 | April 1999 | Early May 1999 | Late May 1999 |
|------------|----------------|------------------|---------------|---------------|-------------------|------------------|
| 100 | A | A | B | A | A | A |
| 200 | AD | AD | A | C | C | D |
| 400 | A | A | A | B | C | A |
| 600 | A | A | BD | C | B | AD |
| 800–1800 | A | A | B | C | B | A |

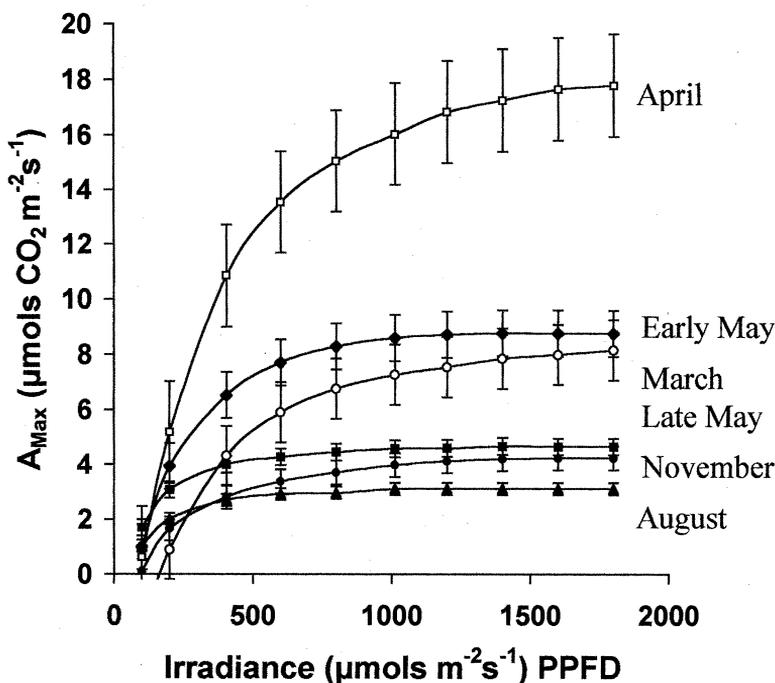


FIG. 1.—Seasonal variation in mean photosynthetic rates ± 1 SE measured at selected irradiances at the Sears-Davis site

May (1999)] there was a significant positive correlation ($r^2 = 0.791$, $df = 4$, $P < 0.044$) between mean A_{Max} of *Alliaria petiolata* and irradiance level reaching the forest floor at the Sears-Davis site (Fig. 2). At the Sears-Davis site, the A_{Max} for April ($17.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was significantly higher and the August sample ($3.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was significantly lower than all other samples (Table 3, Fig. 3). The March vs. early May samples and the November vs. late May samples were not significantly different. Ryan's test indicated that for the ParkLands population A_{Max} was significantly higher for the April sample ($13.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than the May sample ($8.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $P < 0.05$).

Within leaf chamber conditions.—Mean intercellular CO_2 concentration (C_i) for the eight samples varied from $318 \pm 11 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Sears-Davis, early May 1999) to $371 \pm 7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Sears Davis, Nov. 1998) (Table 4) and was not significantly correlated ($r^2 = 0.038$, $df = 6$, $P = 0.643$) with mean A_{Max} . For the August 1998 and April 1999 samples, when the lowest and highest A_{Max} were recorded at the Sears-Davis tract, respectively, mean C_i was almost identical, being $351 \pm 7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in April and $353 \pm 7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in August. Sample date mean vapor pressure deficits based on leaf temperature (VpdL) (Table 4) varied from 0.60 ± 0.01 kPa (Sears-Davis, November 1998) to 2.75 ± 0.15 kPa (Parklands, May 1999). During August 1998 mean VpdL was 1.24 ± 0.05 kPa indicating that plants in August were not experiencing more desiccating atmospheric conditions than plants measured at some other times during the year. The April 1999 samples had relatively low VpdL (Parklands = 1.30 ± 0.04 kPa and Sears Davis = 0.77 ± 0.09 kPa). The Pearson correlation between VpdL and A_{Max} was not significant ($r^2 = 0.0392$, $df = 6$, $P = 0.638$). There was a significant negative correlation ($r^2 = 0.607$, $df = 6$, $P = 0.025$) between C_i and VpdL. Mean leaf and air

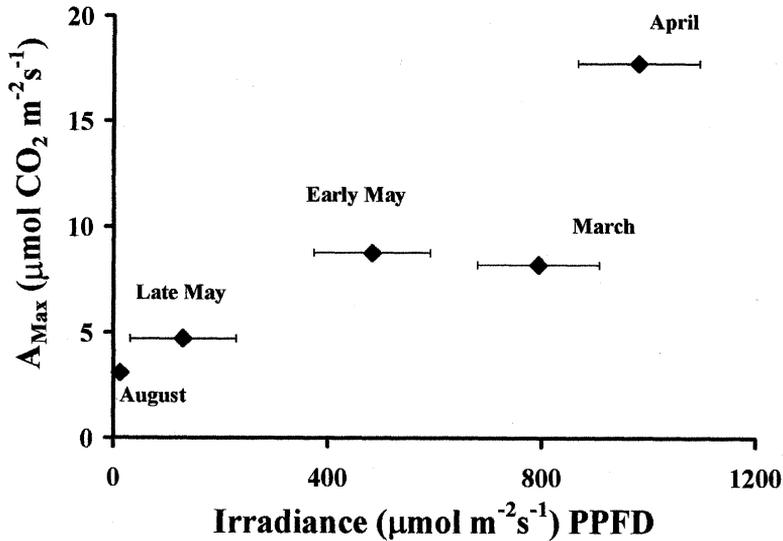


FIG. 2.—Relationship between mean irradiance level ± 1 SE reaching forest floor and A_{Max} (maximum photosynthetic rates) for the Sears-Davis site in 1999, irradiance SE for August was $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD and for the remaining dates SE varied from 99 to $114 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD

temperatures (Table 4) were strongly correlated [$r^2 = 0.995$, $df = 6$, $P < 0.0001$, Y (Leaf temperature) = $1.030X - 0.382$] with leaf temperature being about 0.3 C cooler than air temperature. The Pearson correlation between leaf temperatures and A_{Max} was not significant ($r^2 = 0.0001$, $df = 6$, $P = 0.983$). However, a second-degree polynomial regression had the strongest correlation with the temperature data ($R^2 = 0.56$, $df = 2, 5$, $F = 3.19$,

TABLE 3.—Results of Kruskal Wallis analysis for comparison of A_{Max} for all dates at the Sears-Davis site $df = 1$ for all comparisons. Multiple comparisons were adjusted with a Bonferroni correction ($P < 0.0033$ for significance) (see Fig. 3)

| Comparison/Dates | Chi-square | Prob > CHISQ |
|--------------------|------------|--------------|
| April–August | 21.79 | 0.0001 |
| April–November | 21.78 | 0.0001 |
| April–March | 19.53 | 0.0001 |
| April–Early May | 21.78 | 0.0001 |
| April–Late May | 21.78 | 0.0001 |
| August–November | 1.71 | 0.0001 |
| August–March | 12.88 | 0.0003 |
| August–Early May | 21.78 | 0.0001 |
| August–Late May | 6.72 | 0.0095 |
| November–March | 9.05 | 0.0026 |
| November–Early May | 19.51 | 0.0001 |
| November–Late May | 0.80 | 0.3725 |
| March–Early May | 0.59 | 0.4427 |
| March–Late May | 6.94 | 0.0084 |
| Early May–Late May | 21.39 | 0.0001 |

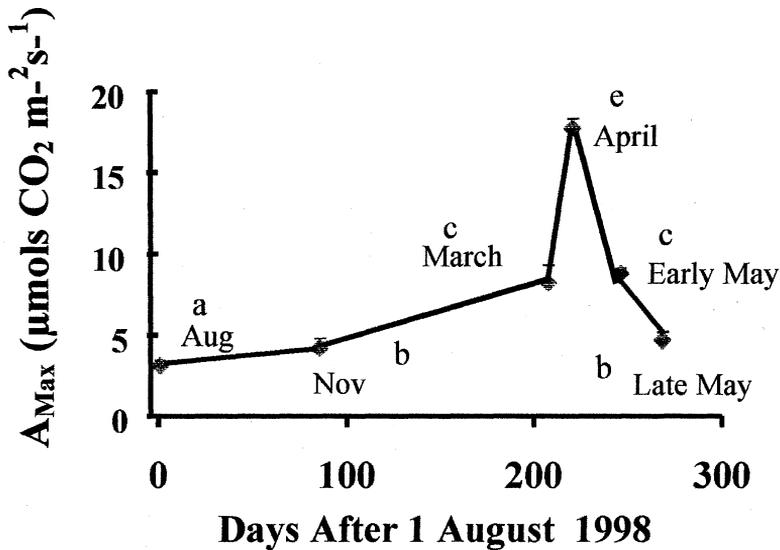


FIG. 3.—Seasonal variation in A_{Max} (maximum photosynthetic rates) for the Sears-Davis site. Means with different letters are significantly different from each other

$P > F = 0.128$). Based on the predicted values from the regression equation [$Y (A_{Max}) = -19.865 + 3.587x - 0.097x^2$], photosynthesis would be optimized at leaf temperatures around 18–19 C with an A_{Max} of $13.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The April and March samples had mean leaf temperatures close to the predicted optimum temperatures for photosynthesis.

Ground layer development and A_{Max} .—In 1999 ground layer cover increased 55.8% from 12.4% in early April to 78.2% in late May at the Sears-Davis site, while measured A_{Max} of *Alliaria petiolata* declined from 17.8 to $4.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during the same time. There was a significant negative correlation between A_{Max} and ground layer cover for all sample dates in April and May ($r^2 = 0.911$, $df = 3$, $P = 0.0116$; Fig. 4) for the Sears-Davis and ParkLands sites combined. At the Sears-Davis tract, bare ground and litter covered 88.1% of the ground on 6 April and the three leading herbaceous species, spring beauty (*Claytonia virginica*), Dutchman's breeches (*Dicentra cucullaria*) and wake robin (*Trillium recurvatum*), had 1.4, 1.1 and 0.9% cover, respectively. Spring beauty was in flower at this time and Dutchman's breeches was beginning to flower. Garlic mustard began to bolt on this date and the only tree species that was beginning to leaf out was Ohio buckeye (*Aesculus glabra*) in the understory. By 27 May 1999 bare ground and litter was reduced to 21.6% of the forest floor surface and the three dominant ground layer plants were wood nettle, May apple and Virginia waterleaf (*Hydrophyllum virginianum*), with cover percentages of 43.9, 22.9 and 13.0%, respectively.

DISCUSSION

The success of *Alliaria petiolata* in invading forest ground layer occurs in part because it produces new leaves adapted to the prevailing light regime. In early spring of the second growing season, *A. petiolata* leaves are adapted to high light conditions and achieved high A_{Max} , thus acting as sun leaves. For example, in central Illinois, before canopy closure in

TABLE 4.—Mean \pm SE (Ci) Intercellular CO₂ concentration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), VpdL (Vapor Pressure Deficit based on leaf temperature, kPa) and leaf and air temperature (degrees C)

| Site | Date | Ci | VpdL | Tair | Tleaf |
|-------------|----------------|--------------|-----------------|------------------|------------------|
| ParkLands | April 1999 | 329 \pm 10 | 1.30 \pm 0.04 | 21.67 \pm 0.33 | 20.73 \pm 0.34 |
| | May 1999 | 317 \pm 13 | 2.75 \pm 0.15 | 28.01 \pm 0.46 | 27.02 \pm 0.43 |
| Sears-Davis | August 1998 | 353 \pm 7 | 1.24 \pm 0.05 | 27.15 \pm 0.19 | 27.11 \pm 0.17 |
| | Nov. 1998 | 371 \pm 7 | 0.60 \pm 0.01 | 8.42 \pm 0.12 | 8.42 \pm 0.14 |
| | March 1999 | 320 \pm 25 | 1.41 \pm 0.07 | 16.67 \pm 0.42 | 17.22 \pm 0.48 |
| | April 1999 | 351 \pm 7 | 0.77 \pm 0.09 | 21.65 \pm 0.89 | 21.31 \pm 0.92 |
| | Early May 1999 | 318 \pm 11 | 1.97 \pm 0.08 | 26.72 \pm 0.74 | 26.50 \pm 0.91 |
| | Late May 1999 | 338 \pm 13 | 1.93 \pm 0.06 | 26.41 \pm 0.57 | 26.51 \pm 0.55 |
| Grand Mean | | 337 | 1.50 | 22.09 | 21.85 |

March, the level of mid-day irradiance reaching the forest ground layer on clear days was (mean \pm SE, range) 822 \pm 30, 421 to 1404 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD. However, following canopy closure in May, the mean irradiance reaching ground layer plants declined to 189 \pm 93, 13 to 1400 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD.

However, a confounding factor in determining the cause for seasonal variation in photosynthesis is the developmental stage of the leaves. Developing and senescing leaves have lower photosynthetic rates than physiologically active mature leaves (Miyaji *et al.*, 1997; Muraoka *et al.*, 1997; Miyazawa and Terashima, 2001). Differences in leaf developmental stage could cause the seasonal variation in photosynthetic rates we have observed rather than production of leaves adapted to the varying levels of irradiance on the forest floor. Based on their size, we considered the possibility that our March sample may have included some leaves that were not fully mature. However, the mean A_{Max} was not significantly different ($t=0.05$, $P=0.958$, $df=13$) between leaves that were larger ($8.27 \pm 1.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) or smaller ($8.16 \pm 1.48 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than the leaf chamber. Moreover, the newly formed leaves had higher photosynthetic rates than those lower on the rosette. We

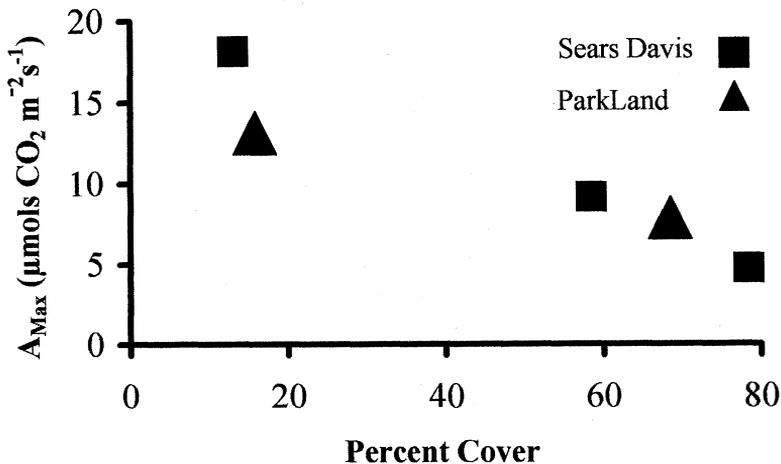


FIG. 4.—Relationship between A_{Max} of *Alliaria petiolata* and percent cover for Sears-Davis and ParkLands sites

concluded that leaf development was not the primary cause for the moderately low photosynthetic rates in March. Additionally, *Alliaria petiolata* adds new leaves more slowly in summer and fall than in the spring. Consequently, it is possible that the low photosynthetic rates during August and November 1998 (Fig. 1) are due to the plants having older leaves than in the spring. However, the rapid decline in photosynthetic rates from early April to early May, when the plant is actively growing, suggests that production of shade adapted leaves rather than leaf senescence results in a decline in photosynthetic rates in August and November. Nonetheless, the influence of leaf development on seasonal variation in leaf photosynthesis warrants further investigation.

Other researchers have also reported a positive correlation between A_{Max} and irradiance levels in mature plants and seedlings (Burton and Bazzaz, 1995; Johnson *et al.*, 1997; Muraoka *et al.*, 1997) and a negative relationship between native ground layer biomass and tree canopy cover (Tappeiner and Zasada, 1993; Huffman *et al.*, 1994; Gonzalez-Hernandez *et al.*, 1998). Similarly, the ability to photosynthetically adapt to seasonal variation in irradiance levels due to canopy closure has been reported for ground layer herbs (Taylor and Pearcy, 1976; Yoshie and Kawano, 1986; Yoshie and Yoshida, 1987; Graves, 1990). However, invasive species compete more successfully for irradiance than native species by several mechanisms. For example, *Bischofia javanica*, an invasive tree species in forests in Bonin Island of Japan, acclimates to increased irradiance by having greater increases in maximum photosynthesis of shade leaves than native species and by the production of newly formed sun leaves (Yamashita *et al.*, 2000). The invasive *Bunias orientalis*, a herbaceous species, which has expanded its range in central Europe, displays phenological niche separation and achieves nearly one-half of its carbon gain between early September and December, when competition for light from other species is low (Zotz *et al.*, 2000). Invasive shrubs in temperate deciduous forests have been shown to develop leaves sooner and retain them longer than indigenous shrubs (Harrington *et al.*, 1989a, b). Annual carbon gains for the two invasive shrubs, *Rhamnus cathartica* and *Lonicera X bella*, before the indigenous shrub, *Cornus racemosa*, began leaf emergence was 29% and 35% for the two species, respectively (Harrington *et al.*, 1989a, b). Similarly, *Alliaria petiolata* displays phenological niche separation with a period of active growth in early spring that provides it with a "window of opportunity" to become established in the forest ground layer, with little or no competition from the dormant or slowly developing, native ground layer plants. This active growth of *A. petiolata* occurs at times when other workers indicate that the availability of inorganic nutrients and soil moisture are high (Jones *et al.*, 1997) and our study suggests leaf temperatures should be favorable for high photosynthetic rates. These conditions, coupled with high levels of irradiance reaching the forest ground layer, are important in enhancing April photosynthetic rates at both of our sites.

Taylor and Pearcy (1976) reported that near Albany, New York, the early spring native species trout lily and wild leek (*Allium tricoccum*) had high A_{Max} (19.2 and 12.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively) on 23 April. However, A_{Max} declined after this time and these species were photosynthetically active only before canopy closure. These native species are potential competitors of garlic mustard and they have maximum photosynthetic rates that are comparable to the A_{Max} of garlic mustard. However, garlic mustard is photosynthetically active and increases leaf area and biomass before spring ephemerals begin to emerge in the forest ground layer (Anderson *et al.*, 1996). Additionally, even though many of the spring ephemerals are actively growing by early April, they covered a small percentage (12.4%) of the forest floor when garlic mustard reached its A_{Max} on 6 April. As the canopy closes, second-year *Alliaria petiolata* plants experience rapid shoot elongation, which averaged 1.9 cm/day between 18 April and 13 May in central Illinois (Anderson *et al.*, 1996) and produce leaves adapted to the reduced

irradiance in the ground layer. Native species that dominate the late spring and summer of the forest ground layer, such as May apple and wood nettle, are larger than the ephemerals. However, *A. petiolata* has a well-established shoot and has completed most of its reproductive cycle when these species become dominant (Cavers *et al.*, 1979; Anderson *et al.*, 1996).

In answer to the questions initially posed in this research, it can be concluded that for *Alliaria petiolata*, A_{Max} and photosynthesis at selected irradiances were related to seasonal variation in irradiance reaching the forest floor and ground layer development. Additionally, the period of time in spring during which *A. petiolata* reaches A_{Max} coincides with low moisture stress and temperatures that are favorable for maximizing photosynthesis in this species. Our findings provide insight into the ecology of *A. petiolata* and indicate an additional mechanism by which it may invade forest ground layers through phenological niche separation. The basal rosette of leaves is efficient in capturing light on the forest floor when irradiance levels are high and there is little competing ground layer vegetation. As the canopy closes and native species begin to increase in cover and height, the elongating shoot of *A. petiolata* supports shade-adapted leaves at higher levels where they could more effectively compete with native species. Thus, *A. petiolata* grows in the early spring before most native species are actively growing, and extends its growing season into the summer through stem elongation and production of new leaves that are adapted to ambient irradiance levels unlike native ephemeral species or summer forbs. The fluctuating availability of resources (Davis *et al.*, 2000), especially irradiance, when native species are not using them, and a phenological niche separation, favors the invasive *A. petiolata*.

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