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The non-native plant *Rosa multiflora* expresses shade avoidance traits under low light availability¹

Daniel M. Dlugos³, Hilary Collins², Elise M. Bartelme², and Rebecca E. Drenovsky^{2,4}

PREMISE OF THE STUDY: Shade tolerance is a key trait promoting invasive plant performance in forest interiors. *Rosa multiflora* is a problematic invasive shrub in the northeastern United States, occurring in edge habitats and encroaching into forests. Our objective was to evaluate the shade tolerance of *R. multiflora* to assess how ecophysiological traits may facilitate its spread into forest interiors.

METHODS: In the field, we documented shrub and seed bank density, fecundity, phenology, and seasonal photosynthetic rates of *R. multiflora* in contrasting light environments. In the greenhouse, we exposed seedlings to simulated canopy treatments by altering spectral quantity and quality, mimicking habitats ranging from open fields to forest interiors.

KEY RESULTS: In the field, shrub density and fecundity of *R. multiflora* sharply increased with light availability. However, no differences were observed between forest edge and interior seed banks. *Rosa multiflora* initiated leaf growth earlier and retained leaves longer than canopy vegetation and tended to have higher photosynthetic rates in spring and fall. In the greenhouse, plants displayed shade-avoidance traits, decreasing relative growth rate and reducing branching, while increasing elongation and showing no change in light response curve parameters.

CONCLUSIONS: In deciduous forest understories, *R. multiflora* appears to make use of a lengthened growing season in spring and fall, and therefore, substantial growth and spread through intact forests appears dependent on canopy gaps. Management should focus on reducing edge populations to reduce spread into the interior and on monitoring newly created canopy gaps.

KEY WORDS deciduous forest; forest edge; functional traits; invasive plant; performance traits; Rosaceae

The success of a species in an environment is dependent on historical, physiological, and biological factors (Lambers et al., 2008). Can the species disperse to the area? Does the species express physiological and morphological traits that will support its performance? And finally, can the species compete with surrounding vegetation, protect itself from predators, and find necessary mutualistic partners? With non-native species, dispersal typically is initiated by humans, but subsequent spread and impact depends on the traits of the target species (Drenovsky et al., 2012). Therefore, understanding the ecophysiology of non-native species is a key first step to predicting their invasiveness in novel environments and targeting management.

Historically, intact forests were considered resistant to invasion by exotic species, due to the slow spread of shade-tolerant species (Naeem et al., 2000; Martin et al., 2009). However, more current

research clearly indicates that mature forests are vulnerable to plant invasions (Martin and Marks, 2006; Martin et al., 2009), despite a sharp decline in light availability from forest edges to forest interiors (<1% of full sunlight within 2 m of the forest edge; Brothers and Spingarn, 1992). Forest edges are often dominated by nonnative plants (Fraver, 1994; Ehrenfeld, 1997; Schulz and Gray, 2013), and if barriers to dispersal, germination, and recruitment do not exist, these edge populations can act as sources for further encroachment. Viable seed bank studies can determine whether a species has dispersed into the forest, the density of seeds in the seed bank, and whether seeds can potentially germinate and develop (Cochard and Jackes, 2005). Several studies report a significant percentage of invasive species within forest seed bank samples (Drake, 1998; Rogers and Hartemink, 2000; Honu et al., 2009). For invasive plants, seed bank longevity increases invasive potential because it improves the species' chances of founding and maintaining plant populations (Peroni and Armstrong, 2001; Lambers et al., 2005).

The presence of non-native species in the seed bank does not, alone, indicate their invasive potential in forested systems. Functional and performance traits associated with shade tolerance vs.

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shade avoidance are key factors associated with plant success in forest interiors (Martin et al., 2009; Heberling and Fridley, 2013). Invasive species that are shade avoiders may be gap dependent and thus spread more slowly into the forest (Martin et al., 2009). Typically, shade-avoiding species have traits that help them capture light when available and escape shaded microclimates (Lambers et al., 2008). For example, photosynthetic stems and phenology that promote early leaf flush and late leaf drop enable shade-avoiding species to photosynthesize in the “off” season, when deciduous forest canopies are open (Harrington et al., 1989; Robertson et al., 1994; Xu et al., 2007). Likewise, in reduced light, shade-avoiding plants typically decrease relative growth rate (RGR), limit biomass production, and change their morphology to promote internode elongation and decrease branching in search of more favorable light environments (Lee, 1988; Lee et al., 1996; Leicht and Silander, 2006; Lambers et al., 2008). In contrast, shade-tolerant species minimize carbon loss by having a low dark respiration rate and light compensation point (Gianoli and Saldana, 2013). In shade-tolerant species, rapid growth rates, even under shaded conditions, may be supported by high photosynthetic capacities (Pattison et al., 1998) and plasticity in the traits underlying RGR (e.g., leaf area ratio and net assimilation rate; Osunkoya et al., 2009), promoting success in forest interiors.

The invasive shrub *Rosa multiflora* Thunb. (Rosaceae) currently poses a threat to forests (Hunter and Mattice, 2002). When originally planted, *R. multiflora* was promoted by the United States Department of Agriculture to farmers as a living fence (Stevenson, 1946). Its use as a hedgerow species and for erosion control led to its widespread distribution, and it quickly naturalized into surrounding areas (Hill, 1983). While *R. multiflora* can occur in forests and grow in a wide variety of terrestrial ecosystems, it most often occurs in disturbed, open, and edge habitats (Hill, 1983; Brothers and Spingarn, 1992; Banasiak and Meiners, 2009). Its frequency and coverage in intact eastern deciduous forests has increased (Hunter and Mattice, 2002; Banasiak and Meiners, 2009; Christen and Matlack, 2009); therefore, understanding its ecophysiological requirements is integral to management of the species.

While invasive species in forests, such as *R. multiflora*, originally were described as rare and stunted, their numbers are increasing rapidly (Brothers and Spingarn, 1992; Ehrenfeld, 1997). It is unclear whether their slow rate of invasion is due to an inability to grow under canopy or more simply a lack of rapid seed dispersal (Martin and Marks, 2006; Martin et al., 2009). A study to assess plant fecundity and seed banking as well as to measure the success of *R. multiflora* seedlings under various light conditions is needed to determine this particular species' level of success in forests compared with open areas. Determining the shade tolerance of plants, especially younger plants, could impact where to focus management efforts in natural areas (McAlpine and Jesson, 2007).

The objective of this study was to determine the shade tolerance of *R. multiflora* by assessing how canopy shading (both natural and simulated) influences its growth, morphology, reproduction, and photosynthetic performance. Field objectives were to document plant density, fecundity, phenology, instantaneous field photosynthetic rates, and spectral quality and quantity differences between light environments of *R. multiflora*. Plant relative growth rate (RGR) as well as other morphological and physiological responses to shading were assessed in the greenhouse and compared with traits known to be associated with shade tolerance. If *R. multiflora* is shade tolerant, it should be able to maintain its RGR, produce

flower and fruits, not alter its morphology, and minimize respiratory losses under decreasing light quality and quantity. In contrast, if *R. multiflora* is a shade-avoiding species, it should express decreased relative growth rate, increased internode elongation, reduced branching, decreased flowering and fruiting, and higher respiratory costs under decreasing light quality and quantity. Together, this suite of traits should help us understand the physiological strategy for its invasion into forest interiors and potential methods to manage *R. multiflora* in eastern deciduous forests.

MATERIALS AND METHODS

Species description—*Rosa multiflora* is a large shrub native to Asia. It is present in 39 states in the conterminous United States and is listed as problematic in 12 states (<http://www.plants.usda.gov>). It is common to forest edges, along streams (Merriam, 2003; Magee and Ahles, 2007), and in fallow fields but more recently has been documented in interior forests (Rhoads and Block, 2007; Voss and Reznicek, 2012; Kurtz and Hansen, 2013). *Rosa multiflora* can reproduce vegetatively and sexually (Rosene, 1950; Christen and Matlack, 2009; Jesse et al., 2010). Each plant can produce $\approx 500\,000$ seeds annually (Amrine, 2002), which are dispersed via birds, streams (Rosene, 1950; Merriam, 2003), rodents (Shahid et al., 2009), and deer (Myers et al., 2004) and may be viable in the seed bank for up to 20 yr (Amrine, 2002).

Site description—Field data for plant density, fecundity, and soil seed banks were collected within Cuyahoga Valley National Park (hereafter, CVNP; $81^{\circ}33'30.72''\text{W}$, $41^{\circ}15'48.18''\text{N}$), ≈ 35 km southeast of Cleveland, Ohio, USA. Mean annual temperature is 9.8°C ; mean annual precipitation, 990.6 mm; and mean annual snowfall, 1549.4 mm (<http://www.nps.gov/cuva/learn/nature/weather.htm>). The majority of the park is mixed mesophytic deciduous forest (Burls and McClaugherty, 2008). Although some sections of contiguous forest remain, much of the landscape is highly fragmented, creating a significant proportion of edge habitat. *Rosa multiflora* is one of the most common non-native plants in the park, being found in approximately 80% of transects surveyed (Djuren and Young, 2007).

Because of intensive management of invasive species (targeting *R. multiflora*) the year after our initial measurements, further field sampling in CVNP was not possible. Therefore, field sites for hip collection, phenology, and seasonal photosynthesis were located in the North Chagrin ($41^{\circ}34'12.63''$, $81^{\circ}25'11.77''$), South Chagrin ($41^{\circ}27'13.80''$, $81^{\circ}24'28.21''$), and Euclid Creek ($41^{\circ}33'38.58''$, $81^{\circ}31'58.80''$) Reservations of the Cleveland Metroparks system, just east of Cleveland, Ohio, USA. These sites are similar in plant community composition, climate, and anthropogenic impacts to the CVNP.

Light levels and shrub density—During May 2010, three sites were located in the CVNP with high *R. multiflora* density at the forest edge (≈ 14 stems $\cdot\text{m}^{-2}$). Forest edges were defined as the point at which the habitat changes from herbaceous annuals to primarily trees (Robertson et al., 1994). All sites were similar in aspect, slope, forest species composition, distance from roads (>20 m) and distance from streams (>20 m). Interior plots were >20 m from canopy gaps. At each site, five 3×10 m plots were established lengthwise along the forest edge parallel to five plots of the same size in the forest interior (>100 m between edge and interior plots).

Within a site, sets of paired edge and interior plots were separated by 110 m.

In late May/early June, following canopy closure, we measured photosynthetic photon flux density (PPFD, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at chest height (≈ 1.5 m) above *R. multiflora* shrubs within all plots at each site (LI-1000, LI-COR, Lincoln, Nebraska, USA). Each plot was divided into quarters, and triplicate measurements were made above each shrub at 15 s intervals; all subsamples within a plot were averaged before statistical analysis. Approximately one-third of the forest interior quarters had no *R. multiflora* shrubs. In these cases, PPFD was measured above the nearest *R. multiflora* shrub, if one was < 20 m from plot's center and > 100 m away from forest edges ($n = 15$ averaged measurements for edge habitats; $n = 12$ for interior habitats). Using the same plots, we assessed plant density with the point-center quarter method. If no *R. multiflora* shrubs were detected within 20 m of the plot's center, no data were collected for this quarter. To account for low sampling densities in the interior, plant density was calculated as described by Warde and Petranka (1981).

Assessment of plant fecundity and soil seed banks—During summer 2010, the central-most shrub in each plot was selected to count the number of flowers and hips produced per plant. During May 2010, six cores, 6 cm in depth and 5.5 cm in diameter, were taken from each plot and composited ($n = 15$ cores from each light environment; $n = 30$ cores total) for the seed bank study. Following Honu et al. (2009), field soils were sieved, mixed with sterilized potting soil, stratified in cold storage for 6–8 weeks then placed in germination trays in the greenhouse. No *R. multiflora* germinated after 2 months; therefore, each sample was passed through a series of sieves (3–0.5 mm) followed by sight identification to detect ungerminated *R. multiflora* seeds. Seeds were positively identified under a dissecting microscope using flora (Holmgren, 1998) and reference *R. multiflora* seeds from our research laboratory. Due to time constraints, nine of the 15 composite samples per light environment were randomly selected for sieving. Seed number was expressed on an area (sampled per plot) basis.

Plant phenology and seasonal photosynthesis—Phenological observations of leaf lifespan were made at the North Chagrin Reservation during the 2013 growing season. Three, large *R. multiflora* populations within the park were monitored for first date of budburst, leaf initiation, full green leaf-out, and leaf senescence and abscission.

Leaf photosynthesis was measured using a LI-6400XT IR gas analyzer (LI-COR) at three times across two growing seasons—20 June 2013 (following canopy closure), 30 October 2013 (following partial canopy leaf drop), and 25 May 2014 (before canopy closure). Poor weather conditions after full canopy leaf drop prevented further photosynthetic measurements. Five to 11 plants were randomly selected at each edge and interior habitat (defined as previously). Plants were > 10 m apart to minimize sampling clones, and different plants were measured at each sampling time. Measurements were made midday during cloudless conditions using a clear top chamber. Chamber CO_2 concentration was set to $400 \mu\text{mol}\cdot\text{mol}^{-1}$ and flow to $500 \mu\text{mol}\cdot\text{s}^{-1}$. Mean PPFD ranged from 223.9 to $869.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in interior habitats and 1593.1 to $1695.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in edge habitats across the three sampling periods; PPFD tended to be more variable in forest interiors. For each plant, three subsample measurements were made at 15-s intervals following equilibration inside the chamber; these subsamples were averaged before statistical analysis.

Seed collection—*Rosa multiflora* seeds were collected in the Cleveland Metroparks system, 4–5 March 2013. Seeds from ≈ 2000 hips representing 25 maternal plants found in open ($n = 5$), open/edge ($n = 11$), and edge ($n = 9$) habitats were extracted, sorted, and composited, with approximately equal numbers of seeds per maternal plant, for the greenhouse experiments.

Greenhouse shade-tolerance experiments—Two greenhouse studies were conducted to (1) estimate RGR and biomass allocation and (2) assess plant architecture and photosynthetic responses under contrasting light conditions. In May 2013, seeds were treated in a 1:1 solution of household bleach and water, rinsed with deionized water, and immediately planted. One seed was sown per pot (SC7 Ray Leach Cone-Tainers: 3.8 cm diameter by 14 cm deep; D40 deepots: 6.4 cm diameter by 25 cm deep; Stuewe and Sons, Tangent, Oregon, USA). Smaller pots were used for early-harvest plants (0 and 10 d following emergence of first true leaves), whereas larger pots were used for subsequent harvests. Soil was a 6:3:1 mixture of potting soil, seed starter mix, and calcined clay. After 41 d of dark, cold stratification, pots were transferred to the John Carroll University greenhouse; after germination, plants were placed under 30% shade cloth until experiment initiation.

After seedlings developed their first true leaves (July 2013), 130 plants were randomly selected for the RGR experiment. Plants ($n = 120$) were individually assigned to one of four light treatments (ambient control, open edge, edge, and interior; Appendix S1, see Supplemental Data with the online version of this article) simulating different canopy conditions in a complete randomized design; an additional 10 plants were randomly assigned to the initial harvest. “Ambient control” plants were surrounded with clear film (Lee 130 Clear; Lee Filters, Andover, UK), simulating open field conditions in both light quantity and quality. The remaining treatments were made in decreasing increments of light quantity with a flat reduction of light quality using a combination of light-filtering films (Lee 121 Lee Green) and shade cloth (40% or 80%). Since edge habitats vary in light availability based on canopy density and aspect, we constructed treatments that mimicked a more open (“open edge”) and more closed (“edge”) forest edge environment. “Open edge” plants experienced only the light-filtering green film, whereas “edge” plants were shaded by film and 40% shade cloth. “Interior” plants had the lowest light environment and were shaded by film and 80% shade cloth. Structures were applied to individual plants ($n = 120$ total across treatments and harvests) and were open-ended to minimize build-up of heat and humidity but were sufficiently tall to ensure plants were consistently shaded (data not shown).

Four destructive harvests were conducted. The first harvest ($n = 10$) took place after the emergence of first true leaves, when treatments were initiated (0 d), with one set of plants harvested every 10 days following (10, 20, 30 d; $n = 10$ per treatment per harvest). Soil was kept at field capacity using tap water, with 10% modified Hoagland's solution (Epstein, 1972) applied at germination and once between each harvest. During harvests, plants were separated into roots, stems, and leaves. Leaves and cotyledons were placed in a cooler on ice until their area was measured (WIN Rhizo image analysis software; Regent Instruments, Saint-Foy, Quebec, Canada). Roots were sieved from soil (0.65 cm) and rinsed in water to remove debris. Samples were oven-dried at 60°C for ≥ 48 h, and masses were recorded.

Relative growth rate (RGR) was calculated for each harvest interval using an online RGR calculator (Hunt et al., 2002) according

to the recommendations of Causton and Venus (1981) for ungraded and unpaired harvests. These values were averaged to obtain an overall RGR across the first 30 d of growth. Total biomass and allocation traits (leaf area ratio, LAR; leaf mass ratio, LMR; root mass ratio, RMR; and specific leaf area, SLA) were calculated for plants of the last harvest only; in this way, replicate values were obtained for statistical analysis (which is not possible with data processed across paired harvests).

A second set of plants, grown under experimental conditions for approximately 2 months, was used to collect physiological data and describe plant architecture. In late July 2013, 10 unshaded plants approximately 2.5 wk old were randomly assigned to either the ambient control or open edge treatment ($n = 5$ per treatment); these plants were used to generate light response curve data and assess plant architecture responses to shade treatments. Approximately 10 d later, a second block of 10 plants of similar age were randomly assigned to the same treatments to increase replication for plant architecture measurements. On 23–25 August 2013, photosynthetic light response curves were generated on the initial 10 plants ($n = 5$ ambient control, $n = 5$ open edge) using the LI-6400XT IR gas analyzer fitted with a red-blue LED light source (LI-COR). Sample CO_2 was set to $380 \mu\text{mol}\cdot\text{mol}^{-1}$; block temperature, 26°C ; and target reference relative humidity, 45%. Based on preliminary data, ambient control plants were assessed at light values of 900, 700, 500, 250, 100, 50, 25, and $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; open edge plants were assessed at 700, 600, 500, 250, 100, 50, 25, and $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Scatterplots indicated dynamic photoinhibition occurred for some individual ambient control plants above $700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and for open edge plants above $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; these data were omitted from further analyses. Data were fit to the Mitscherlich and Michaelis–Menten equations (Lachapelle and Shipley, 2012) and analyzed by nonlinear regression to estimate dark respiration rate, maximum photosynthetic rate, apparent quantum yield, and the light compensation point. On 25 and 27 September 2013, the number of branches, height, average internode length, and number of nodes were measured on the full set of 20 plants.

Statistical analyses—Field studies in Cuyahoga Valley National Park and Cleveland Metroparks—One-way ANOVAs were used to compare PPFD, shrub density, and seed bank data between edge and interior plots, as neither plot nested within location nor location were significant. Linear regression was used to assess the relationship between shrub density and PPFD, fitting the data to a quadratic polynomial equation. Paired t tests were run to compare the number of flowers and fruits in edge vs. interior plots. A two-way ANOVA was used to compare seasonal photosynthetic rates with habitat (interior vs. edge) and season as predictor variables and photosynthetic rate as the response variable. Normality and homogeneity of variance were assessed with the Shapiro–Wilks test and Levene’s test, respectively. Data for PPFD and number of flowers and fruits were log-transformed for analysis (Zar, 2010).

Greenhouse studies of shade tolerance—Comparisons of functional traits between light treatments were assessed using one-way ANOVAs with light environment (ambient control, open edge, edge, interior) as the predictor variable and biomass, allocation traits and light response curve parameters as the response variables. Morphological data were analyzed using a randomized complete block design to account for plants assigned to treatments at different dates, with light environment (ambient control, open edge) and block as

the main effects. Data were tested for equal variance and normality using Levene’s test and Shapiro–Wilks test, respectively. Total biomass and branching data were log-transformed to improve normality (Zar, 2010). All data were analyzed using SAS version 9.2 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Forest light environments, shrub density, fecundity, and soil seed bank

PPFD readings directly above *R. multiflora* shrubs were significantly higher along the forest edge than the forest interior, with a 20-fold difference between these habitats ($F_{1,24} = 39.25$, $P < 0.0001$; Table 1). Shrub density was not significantly different between the forest edge and the forest interior, due to large variability among sites and small sample sizes ($F_{1,4} = 4.82$, $P = 0.09$). However, there was a trend for higher density of *R. multiflora* at the forest edge than the forest interior (edge: 0.42 ± 0.32 shrubs m^{-2} ; interior: 0.01 ± 0.01 shrubs m^{-2} ; data means \pm SD, $n = 3$) and a significant increase in shrub density with increasing PPFD ($F_{2,3} = 35.63$, $P = 0.008$; Fig. 1). Fecundity was significantly lower in the forest interior than at the forest edge, as indicated by paired t tests (flowers: $t_{14} = 5.7$, $P < 0.0001$; fruits: $t_{14} = 5.7$, $P < 0.0001$; Table 1). In forest interiors, flower and fruit production were $\approx 4\%$ of that produced per plant along forest edges.

No *R. multiflora* seeds germinated during the greenhouse portion of the seed bank study. Most seedlings that did germinate were ruderal, weedy species (e.g., *Oxalis stricta* L., *Plantago major* L.). Following soil sieving, relatively few *R. multiflora* seeds were found in the seed bank, even in samples from the forest edge where fruit production and shrub density were high. Additionally, despite the fact that edge shrubs produced significantly more flowers and fruits than interior shrubs, the number of seeds in the edge soil samples did not differ from the interior samples (65.9 seeds $\cdot\text{m}^{-2}$ of soil; $P > 0.05$).

Leaf phenology and seasonal photosynthetic rates of field-established plants

For *R. multiflora*, budburst began early April 2013 (well before canopy leaf-out), leaf initiation by late April, and full green leaf-out by late May. Fall leaf senescence of canopy trees and *R. multiflora* began mid-October. By late October, all canopy leaves were senescing, and about half had abscised, although *R. multiflora* plants still retained most of their leaves. As late as mid-December, a few green leaves could still be located on isolated *R. multiflora* individuals, well after canopy trees had senesced and abscised.

Photosynthetic rate differed significantly between edge and interior plants ($F_{1,36} = 5.76$, $P = 0.022$). Averaged over the three measurement points, edge plants had photosynthetic rates twice that of those in

TABLE 1. Mean photosynthetic photon flux density (PPFD) ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and fecundity of shrubs in edge and interior habitats in Cuyahoga Valley National Park, Ohio, USA. Data are back-transformed means and asymmetric 95% confidence intervals.

Trait	Habitat	Mean	Lower 95% CI	Upper 95% CI	n
PPFD	Edge	721.7	448.1	1162.3	15
	Interior	35.9	17.2	75.3	12
No. flowers per shrub	Edge	41.6	16.9	102.5	15
	Interior	1.8	0.9	3.7	15
No. fruits per shrub	Edge	28.1	10.4	76.0	15
	Interior	1.1	0.9	1.4	15

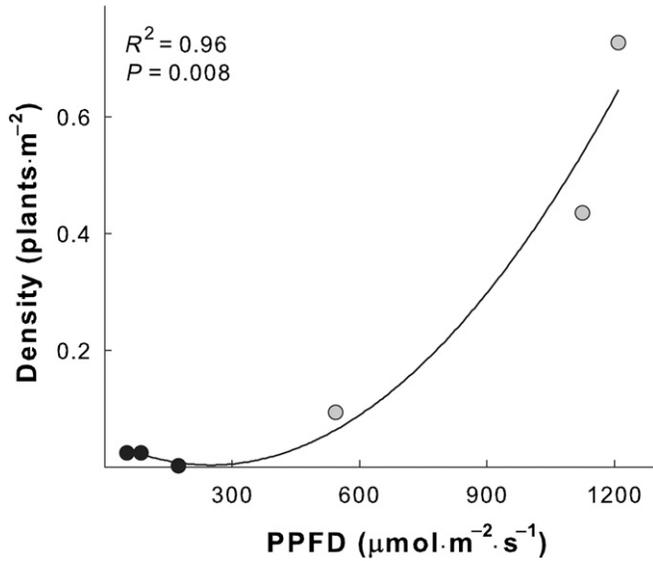


FIGURE 1 Relationship between shrub density and photosynthetic photon flux density (PPFD). Shrub density was determined by the point center quarter method in forest edges and interiors at three sites within Cuyahoga Valley National Park, Ohio, USA. PPFD readings represent averages for each light environment by site combination. Black circles represent data from interior sites; gray circles represent data from edge sites.

the interior (Fig. 2). Although not significant, photosynthetic rate tended to be higher in May and October than in June, irrespective of light environment ($F_{2,36} = 2.59, P = 0.089$). There was not a significant interaction of month by location ($P > 0.05$).

Greenhouse shade-tolerance experiments—When averaged across all harvest periods, the RGR of *R. multiflora* decreased linearly with lower available light (Fig. 3A). After thirty days, survivorship was 100% for ambient control and open edge treatment plants, 90% for edge treatment plants, and 60% for interior treatment plants. In the

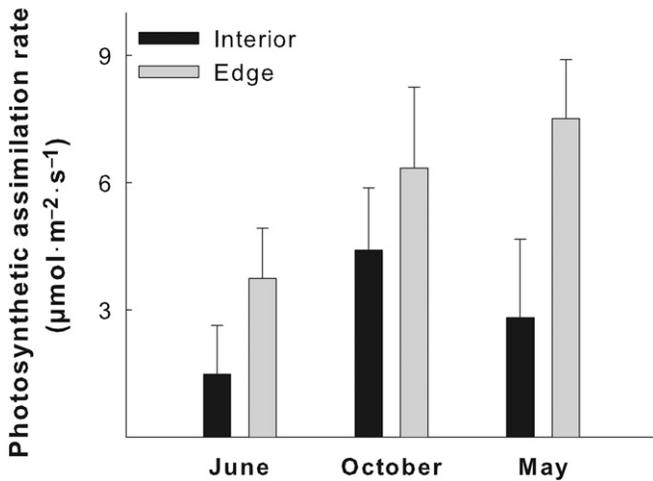


FIGURE 2 Photosynthetic assimilation rate of *Rosa multiflora* at interior and edge locations for June 2013, October 2013, and May 2014 sampling dates. Data are means and standard error. June interior ($n = 10$), June edge ($n = 11$), October interior ($n = 5$), October edge ($n = 5$), May interior ($n = 5$), May edge ($n = 6$).

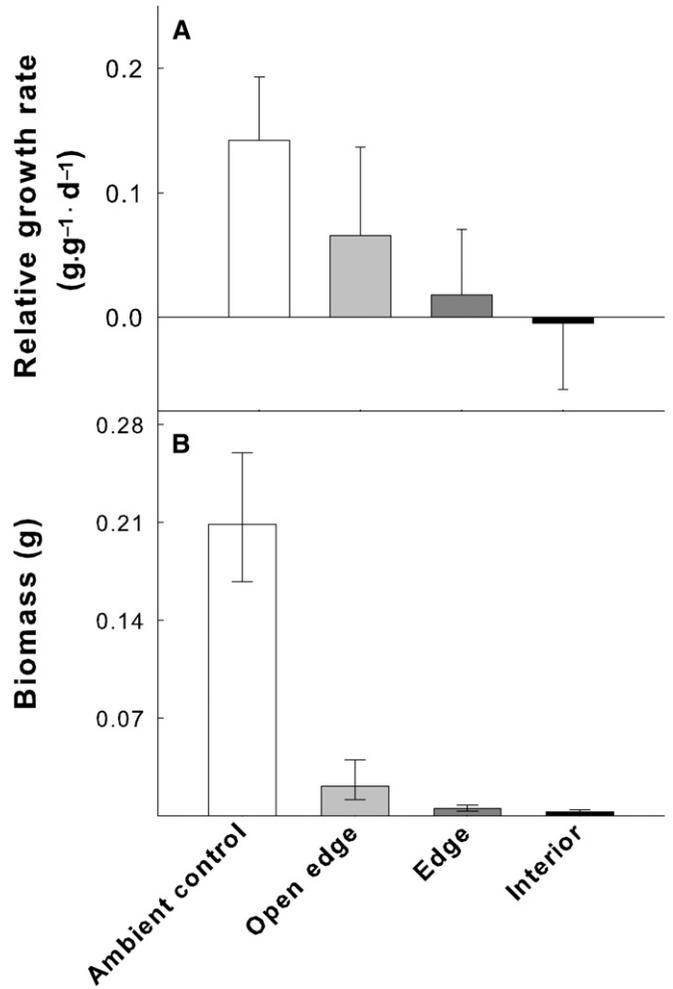


FIGURE 3 (A) Relative growth rate of *Rosa multiflora* grown in four greenhouse shade treatments averaged across four harvest periods over 30 d. Data are overall means with standard error. At each harvest, $n = 10$ for each treatment harvest combination except for interior plants of the third harvest ($n = 9$), edge plants of the fourth harvest ($n = 9$), and interior plants of the fourth harvest ($n = 6$). (B) Total biomass per plant of *Rosa multiflora* exposed to four greenhouse shade treatments for 30 d. Data are back-transformed means with 95% confidence intervals for biomass. For total biomass, ambient control and open edge ($n = 10$), edge ($n = 9$), interior ($n = 6$).

30-day-harvest plants, total biomass per individual declined significantly with decreasing light availability ($F_{3,31} = 93.15, P \leq 0.0001$; Fig. 3B). Ambient control plants had the greatest biomass of any treatment group, producing 10 times more biomass than the open edge treatment and over 100 times more biomass than either the edge or interior treatment plants. Surprisingly, biomass allocation did not vary based on treatment, with neither root mass ratio nor leaf mass ratio differing among treatments ($P > 0.05$; data not shown). Both leaf area ratio (LAR) and specific leaf area (SLA) differed among treatments ($F_{3,31} = 3.34, P = 0.032$ and $F_{3,31} = 4.00, P = 0.016$; Fig. 4A, B), with both variables showing maximal values in the open edge and edge treatments.

When grown under simulated habitat conditions in a greenhouse setting, the ambient control and open edge plants had similar

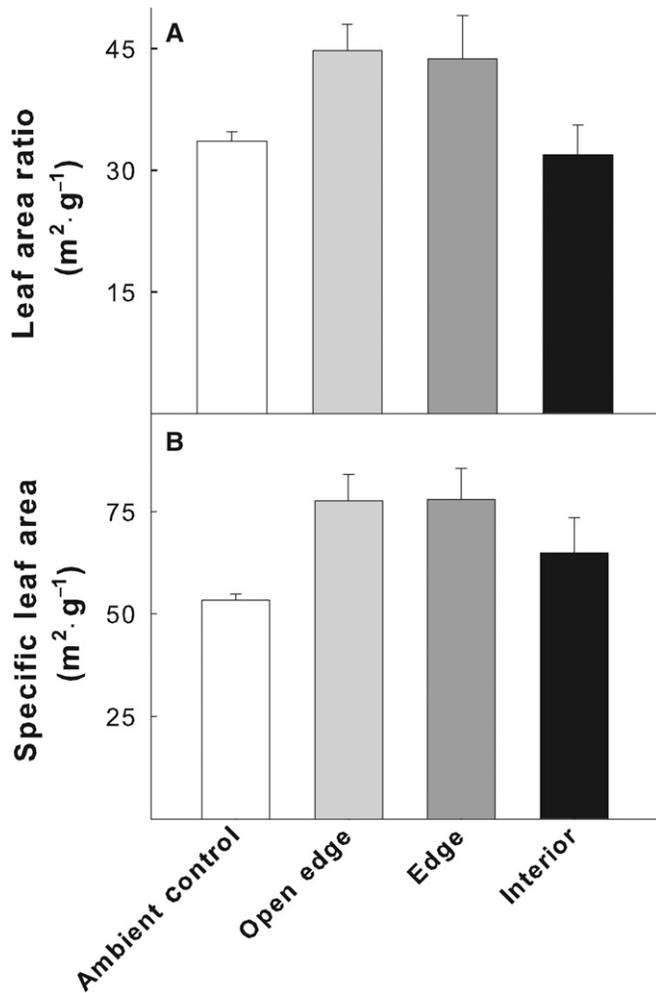


FIGURE 4 (A) Leaf area ratio, and (B) specific leaf area of *Rosa multiflora* exposed to four greenhouse shade treatments for 30 d. Data are means with standard error. Ambient control and open edge ($n = 10$), edge ($n = 9$), interior ($n = 6$).

light response curves (Fig. 5). As a result, most of the parameters derived from the curves (R_d , A_{max} , q_{lcp}) were not significantly different between treatments (Table 2; $P > 0.05$). There was a trend for a slightly lower light compensation point in the open edge plants relative to the ambient control plants ($F_{1,7} = 3.81$, $P = 0.09$). Morphologically, plants grown in the two treatments differed in their architecture (Fig. 6). Plants in the more shaded open edge treatment were nearly 1.5-fold taller than those of the ambient control ($F_{1,17} = 5.52$, $P = 0.031$; Fig. 6A). Those in the open edge also produced half as many branches as plants in the ambient control treatment ($F_{1,17} = 7.76$, $P = 0.013$; Fig. 6B). Open edge plants produced longer internodes ($F_{1,17} = 6.97$, $P = 0.017$; Fig. 6C) but produced a similar number of nodes per plant ($P > 0.05$; Fig. 6D).

DISCUSSION

Rosa multiflora continues to pose a problem for land managers and is continually cited as one of the most frequently observed invasive plant species in the northeastern United States, often occurring at

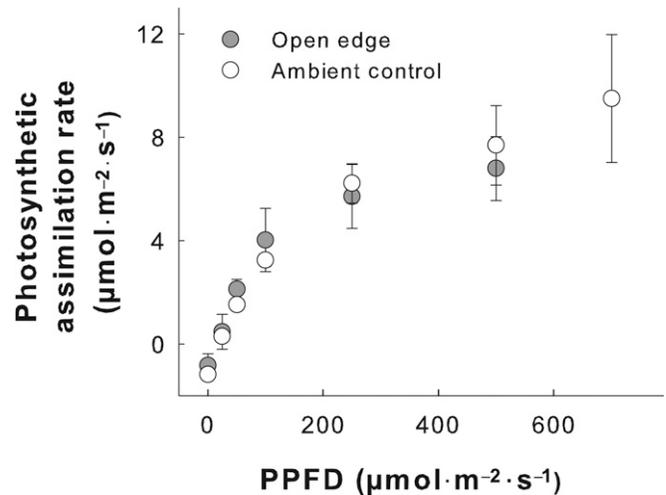


FIGURE 5 Light response curves of photosynthetic assimilation across varying photosynthetic photon flux densities for *Rosa multiflora* plants grown under ambient control ($n = 5$) and open edge ($n = 5$) greenhouse shade treatments. Data are means and standard error. Open edge plants were not measured at the highest light level ($700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) due to likelihood of photoinhibition.

very high densities (McDonald et al., 2008; Kelly et al., 2009; Matlack and Schaub, 2011; Schulz and Gray, 2013). This invasion has clearly advanced into forested areas (Fraver, 1994; Banasiak and Meiners, 2009), even in established, hundred-year-old forests (Matlack and Schaub, 2011). Our work used observational field studies and manipulative greenhouse experiments to determine the extent of *R. multiflora* shade tolerance and to increase understanding of the species' strategy for spread into forest interiors. On the basis of the suite of traits measured in this study, it appears that *R. multiflora* expresses the traits of a shade-avoiding species, indicating its success in forest interiors is, at least in part, gap dependent.

We observed an exponential increase in plant density with increased light availability, as well as significantly higher fecundity at forest edges than in forest interiors. Few shrubs produced flowers in forest interior habitats, and most flowers did not result in fruit production. In contrast, a shade-tolerant invasive plant such as *Berberis thunbergii* can produce fruit in <4% of full sunlight (Silander and Klepeis, 1999). Other studies of forest invaders have suggested reduced fecundity in forested interiors. For example, the invasive

TABLE 2. Parameters of the light response curves for ambient control treatment ($n = 5$) and open edge treatment ($n = 5$).

Trait	Treatment	Mean	SD
A_{max}	Ambient control	8.18	3.54
	Open edge	6.37	1.53
q_{lcp}	Ambient control	0.55	0.01
	Open edge	0.07	0.02
LCP	Ambient control	19.47	5.04
	Open edge	13.00	4.86
r_d	Ambient control	1.29	0.37
	Open edge	1.04	0.40

Notes: A_{max} is the light saturated rate of CO_2 assimilation ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Quantum yield (q_{lcp} , $\mu\text{mol CO}_2\cdot\mu\text{mol}^{-1}$ photons) indicates how efficiently absorbed photons are used to assimilate carbon. LCP is the light compensation point ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and indicates the light quantity at which carbon lost through respiration is equivalent to carbon gained through photosynthetic assimilation. r_d = dark respiration rate ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

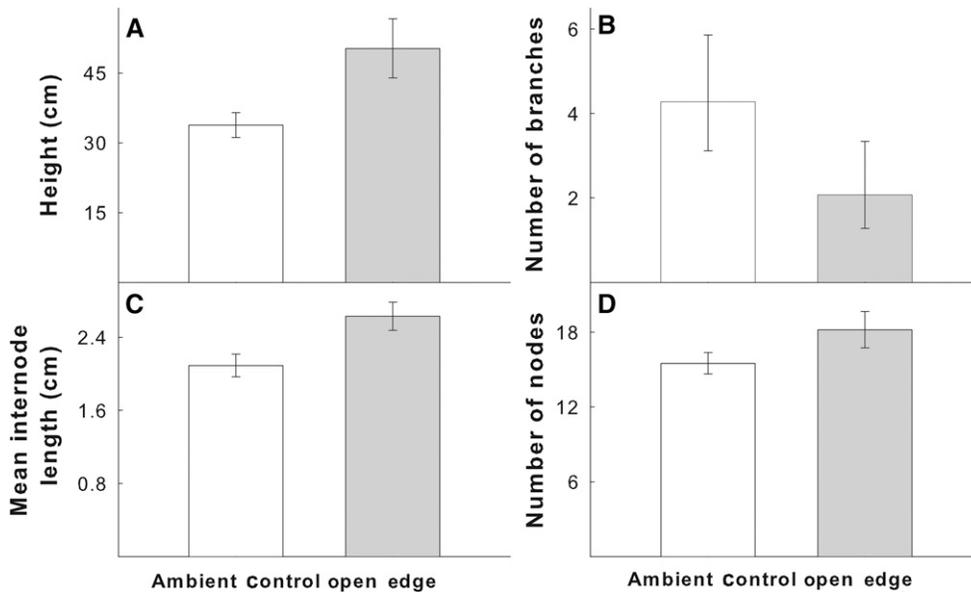


FIGURE 6 Morphological traits of *Rosa multiflora*: (A) height, (B) branching, (C) mean internode length, and (D) number of nodes characterized after growth in ambient control ($n = 10$) and open edge ($n = 10$) greenhouse shade treatments. Data for A, C, and D are means and standard error. Data for B are back-transformed means and 95% confidence intervals.

grass, *Microstegium vimineum* (Trin.) A. Camus (Huebner, 2010), the invasive forb *Hypericum perforatum* L. (Buckley et al., 2003), as well as the invasive vines, *Vincetoxicum rossicum* (Kleopow) Barbarich and *V. nigrum* (L.) Moench (Averill et al., 2011) have lower fecundity in shade than in higher light areas. Shade-intolerant invasive plants may have lower fecundity in reduced light because more resources must be dedicated to vegetative growth for light harvesting and because lower photosynthetic rates in shade may decrease the carbon resources needed for seed production (Lambers et al., 2008). In our work, *R. multiflora* had a lower RGR, increased LAR and SLA as well as lower photosynthetic rates under shaded conditions, suggesting that growth and fecundity were carbon-limited despite increased leaf area relative to total plant or leaf mass. In some forest interior areas and certainly in canopy gaps, however, it appeared that *R. multiflora* was successful at vegetative reproduction (H. Collins, personal observation). In support, genetic analyses of *R. multiflora* shrubs in shaded or partially shaded habitats in Iowa suggest that smaller patches may rely more heavily on asexual reproduction than sexual reproduction (Jesse et al., 2010).

Despite shrubs at forest edges having significantly higher fecundity than shrubs in forest interiors, the number of seeds retrieved from soil seed banks was similar between these two light environments. Although patchy seed dispersal and low sample size may have limited our ability to detect significant differences, on the basis of repeated observations made throughout each season, we hypothesize that seeds are deposited randomly and far from the parent plants due to frequent harvesting from animal dispersers such as birds (McCay and McCay, 2009; Greenberg and Walter, 2010), rodents (Shahid et al., 2009), and white-tailed deer (*Odocoileus virginianus*) (H. Collins, personal observation). As a result, animal dispersal may help promote spread of this invasive shrub away from the maternal plants and into forest interiors.

Phenologically, *R. multiflora* plants in the field initiated spring growth before surrounding woody vegetation and maintained

leaves longer in autumn. Interior plants, in particular, tended to retain leaves longer in autumn, while edge plant leaves senesced. Although yearly carbon assimilation was not calculated in this study, *R. multiflora* had an extended growing season in both spring and fall with a trend toward seasonal photosynthetic differences. Lengthened leaf span in spring and fall with a trend toward higher photosynthetic rates in those seasons could account for a large portion of yearly carbon gains (Harrington et al., 1989; Xu et al., 2007; Fridley, 2012). Additionally, we did not examine winter photosynthetic rates, although the semi-evergreen stems of *R. multiflora* could provide an additional source of carbon gain (Robertson et al., 1994).

In contrast to shade-tolerant plants, which maintain their growth rate as light availability decreases (Valladares and Niinemets, 2008), *R. multiflora* linearly decreased its overall RGR with increased shade. Relative biomass al-

location patterns between leaves and roots were not altered by shading. However, the area of leaves increased in relation to leaf and plant mass (SLA and LAR) as light availability decreased. Both LAR and SLA had mirrored increases from ambient control to open edge and edge treatments followed by a decrease for interior treatments. As shade-tolerant plants characteristically have low LAR, LMR, and SLA (Walters and Reich, 1999, 2000), the increasing LAR and SLA in shading further supports the lack of shade tolerance in *R. multiflora*. Decreased LAR and SLA in the interior treatments were likely linked to poor growth and low survivorship under limited light availability instead of an acclimation response; these plants produced little leaf area beyond the first set of true leaves.

It is hypothesized that shade-tolerant plants will minimize carbon loss while less-tolerant plants favor light capture (Gianoli and Saldana, 2013). By decreasing the light compensation point and dark respiration rate, plants can decrease carbon loss (Walters and Reich, 1999; Sterck et al., 2013). When open edge and ambient control plants are compared, light response curves indicated no change in the dark respiration rate but a trend toward a lower light compensation point in more shaded plants. This difference in light compensation point in shade may suggest plasticity to minimize carbon loss in *R. multiflora*; however, curves were only generated on the least shaded treatments as well as having been generated on young plants instead of adult plants. Additionally, open edge treatment plants differed in growth patterns and morphology relative to the full-sun control plants, having longer internodes, greater height, and decreased branching. These morphological changes demonstrate a lack of tolerance to shade (Valladares and Niinemets, 2008) because stem elongation and reduction of branching serve as foraging mechanisms in shade-sensitive plants searching for light (Lambers et al., 2008).

In this study, *R. multiflora* did not display shade-tolerance traits either in the field under natural forest interior light conditions or when exposed to simulated canopy shading as seedlings in the greenhouse. This lack and its poor survivorship under increasingly

shaded greenhouse conditions suggest that *R. multiflora* is not shade tolerant. It appears that *R. multiflora* is able to survive in eastern deciduous forests through shade avoidance by having a longer growing season with its semi-evergreen habit. The lengthened growing season and stems with potential to photosynthesize, coupled with its possible plasticity in light compensation point, may allow *R. multiflora* to assimilate a large proportion of carbon in the “off” season and then significantly slow down activity in the summer when shaded, minimizing carbon losses due to respiration. In support, studies comparing distributions of the invasive shrub *Berberis thunbergii* and *R. multiflora*, shade-tolerant *B. thunbergii* is able to grow in evergreen forests, while *R. multiflora* is more limited to deciduous forests (Kelly et al., 2009). An open canopy during at least part of the year may be necessary for *R. multiflora* to persist.

These shade-avoiding traits of *R. multiflora* have implications for management. Although seed germination does not appear to be influenced by light availability, the lack of shade tolerance during seedling establishment, extreme differences in seedling biomass accumulation, and low seedling survivorship in simulated forest treatments suggest that *R. multiflora* recruitment by seed will be low in forested areas. Since *R. multiflora* has low seedling recruitment even in highly suitable areas but can spread clonally over distances (Patterson, 1976; Christen and Matlack, 2009; Jesse et al., 2010), it is possible that plants in shaded areas are offshoots of individuals in more open areas. Gap openings in forests also could contribute to its spread. Invasive understory plants, including *R. multiflora*, can exist in a lag phase until suitable conditions arise (Martin and Marks, 2006; Banasiak and Meiners, 2009). Gap closure can take as long as 9 years (Himes and Rentch, 2013), allowing sufficient time for seeds or clones of *R. multiflora* to establish or nearby plants to flourish. Based on our work, current management techniques should focus on removal of edge populations, which serve as potential sources of spread into younger forests with more open canopies. High seed production at forest edges combined with the ability to form a seed bank may promote the spread of *R. multiflora* into forest interiors, as observed for other gap-dependent invasive species (Vanhellemont et al., 2010). Once canopy gaps exist, areas should be monitored regularly to prevent new plants from becoming established and building reserves, since *R. multiflora* success in the understory is strongly linked to an open canopy (Matlack and Schaub, 2011) and declines with canopy growth (Banasiak and Meiners, 2009). In particular, areas experiencing disturbance or nutrient inputs should be monitored. *Rosa multiflora* appears to perform better on nutrient-rich soils, promoting its success in forest understories (McDonald et al., 2008; Huebner et al., 2014). This study provided no evidence for shade tolerance. However, *R. multiflora* continues to be one of the most problematic weeds in the northeastern United States. By targeting its ecophysiological strategy of shade avoidance, managers may more effectively control *R. multiflora*, which is crucial to the health of eastern deciduous forests.

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