

Has Invasive Amur Honeysuckle (*Lonicera maackii* (Rupr.) Maxim) Met its Match? Interspecies Comparisons of Photosynthesis and Shoot Allocation in Heavy Shade

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Abstract

Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim) is a notorious invader of forests and forest edges throughout eastern North America. The species is difficult to exterminate and reestablishes readily. A perpetual presence of Amur honeysuckle in most forests is largely a forgone conclusion. Forests throughout the eastern U.S. are changing due to canopy closure after historical disturbance and long-term fire prevention. Fire intolerant species, especially sugar maple (*Acer saccharum* Marshall.), are coming to dominate forest canopies, creating shady understories and forest dynamics that pivot on shade tolerance. Two shade tolerant understory shrubs, pawpaw (*Asimina triloba* Adans.) and spicebush (*Lindera benzoin* Thunb.) compete with honeysuckle in maple understories. Based on field observations we hypothesized that these native species were more shade tolerant than invasive honeysuckle. We examined shade tolerance in honeysuckle, pawpaw, and spice bush by comparing photosynthetic light responses, leaf characteristics, and allocation to leaf area versus stem mass (leaf area ratio, LAR) in annual shoots. Honeysuckle had comparable light responses measured on a leaf area basis, but mass-based measurements show it is less efficient paying back carbon invested in leaf tissue. This arises because honeysuckle is unable to reduce specific leaf mass to the level of pawpaw and spicebush. LAR is distinctly higher in pawpaw and spicebush, suggesting an advantage in heavy shade. Since the great majority of photosynthesis in these species occurs under a closed canopy, we suggest honeysuckle will diminish in maple-dominated stands. Informal observations of greater height growth in pawpaw and spicebush in the field support this.

Introduction

Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim.), an introduced shrub native to lowland forests in eastern Asia, has emerged as perhaps the most widespread and problematic invader of forests throughout the eastern United States and adjacent Canada. The body of literature concerning this invasive is large and has been summarized/reviewed by Luken and Thieret (1996), Lieurance and Landisbergen (2016), and McNeish and McEwan (2016). The harm Amur honeysuckle inflicts on natural processes and native species populations is extensive, ranging from competitive exclusion of native plants (Collier and Vankat 2002, Loomis et al. 2015, Gorchoy 2005, Sena et al. 2021), to modification of herbivory patterns (Meiners 2007, Orrock et al. 2015), facilitation of pathogen vectors (Allana et al. 2010), modifications of soil (McEwan et al. 2012, Trammell et al. 2012), and modification of stream communities (McNeish et al. 2015). Despite an abundance of study, no truly time/cost-effective and ecologically appropriate technique has been devised to eliminate Amur honeysuckle from natural areas. Land managers seem to be resigned to its continued presence.

Scope of honeysuckle invasion over the last 30 + years is to a large extent a consequence of forest fragmentation and the degraded nature of regional forests. Commonly honeysuckle establishes in forest edges and damaged stands where the canopy is relatively open (Bartuszevige et al. 2006, Henken et al. 2013). High light conditions support rapid growth and copious seed production (Luken et al. 1997, Schulz and Wright 2015), with ready populations of animal vectors to disperse seed (Ingold and Craycraft 1983, Vellend 2002, Bartuszevige and Gorchoy 2006, Castellano and Gorchoy 2013). Because honeysuckle has a reasonable level of shade tolerance, it can persist in the understory and capitalize on natural canopy openings for further growth and establishment opportunities (Henken et al. 2013).

On mesic sites in eastern North America established honeysuckle are now experiencing a changing understory environment. Canopy closure is occurring in many formerly open canopy stands, reducing light availability. Additionally, throughout much of the eastern United States the process of “mesophication” (*sensu* Nowaki and Abrams 2008, Alexander *et al.* 2021) is under way. This involves replacement of fire tolerant species (e.g., *Quercus* L. spp., *Carya* Nutt. spp.) with highly competitive and fire intolerant species, especially sugar maple (*Acer saccharum* Marshall.). Active fire suppression has eliminated this constraint on the growth and spread of fire intolerant species. Maple forest understories are exceedingly dark and limit forest floor shrubs to a few shade tolerant species. For this reason, the capacity to survive and prosper in the forest understory will play a larger role for honeysuckle in the future. Part of this scenario is that honeysuckle will compete with other shade tolerant woody species.

In southern Illinois we have noticed three woody species are abundant in dark understories where honeysuckle is present: sugar maple, pawpaw (*Asimina triloba* Adans.) and spicebush (*Lindera benzoin* Thunb.). Maple and pawpaw appear to ultimately overtop honeysuckle, while dense spicebush stands crowd it significantly. This pattern might occur because of shade tolerance in these species, or priority effects. In this study we hypothesized that pawpaw and spicebush had greater shade tolerance than

honeysuckle. We focus only on these species because the extreme shade tolerance of maple is well known and has been more widely studied (e.g., Ellsworth and Reich 1992, Walters et al. 1993, Walters and Reich 1996, Sendall et al. 2015). Based on the ongoing expansion of pawpaw and spicebush we predicted higher rates of photosynthesis in shade, stronger manifestation of shade acclimation responses in leaf structure, and higher leaf area ratios (LAR, leaf area / plant mass) than in honeysuckle. To provide context for the performance of honeysuckle in shade, we also examined the photosynthetic performance of honeysuckle in edge habitats where it prevails. This was not possible for pawpaw and spicebush because they are absent from forest edges in our region.

Photosynthesis is a key aspect of shade tolerance. Early studies tended to treat acclimation or adaptation of photosynthesis to shade as the central element of shade tolerance (Bjorkman 1972, Boardman 1977, Chabot and Chabot 1977). Later work emphasizes patterns of resource allocation, respiratory load, and canopy architecture in conjunction with photosynthetic patterns as important determinants of shade tolerance (Givnish 1988, Lei and Lechowicz, 1990, Woodward 1990, Walters et al. 1993). Unfortunately, measuring, integrating, and interpreting these aspects is operationally challenging when studying seedlings in controlled environments, much less in the field using pre-existing plants. To make a practical, conceptually robust comparison between species, we interpret photosynthetic light responses in relative to the biomass invested in leaves and shoots. Annual production of leafy shoots by winter-deciduous species is essential to survival. Shoot production not only replaces the essential organs of photosynthesis and reproduction, but also provides the means to overtop and/or overspread competitors. We propose that species-level differences in the biomass costs and photosynthetic returns of shoots are very likely to affect the odds of persistence through time.

The background literature for the three study species varies in its depth. Photosynthesis/shade tolerance in Amur honeysuckle has been investigated by Luken et al. (1997), Fridley (2012), and Lieurance and Landsbergen (2016). Luken et al. (1997) examined the capacity to capitalize on increases in light intensity caused by canopy disturbance by transplanting small shade-grown shrubs to shade structures providing 1, 25, and 100% sunlight. Although the study relied on recently transplanted plants, it clearly showed preexisting leaves can acclimate to increased light. In addition, increased light stimulated production of new light-acclimated leaves and caused modification in tissue allocation patterns. Luken et al. (1997) conclude that honeysuckle is a habitat generalist with high phenotypic plasticity. Fridley (2012) compared estimates of carbon gain by native and exotic understory shrubs before the tree canopy expanded in spring and after the canopy opened in fall. Compared to most species, Amur honeysuckle obtained fairly little of its carbon during either period (total C < 15%), while many natives were more reliant on the light windows during early spring and late fall. Notably, shrubs of the genus *Lonicera* show wide variation in carbon gain patterns in spring and fall. The common tendency to generalize to Amur honeysuckle from the high rates measured by Harrington et al. (1989) in *L. X bella* Zabel is inappropriate (Fridley 2012). Lieurance and Landsbergen (2016) examined photosynthesis and allocation patterns across a light gradient (64–12% canopy openness) and concluded that high phenotypic and physiological plasticity allowed honeysuckle to “persist in all habitats”.

Pawpaw is an abundant clonal shrub/subcanopy tree distributed across the southeastern U.S. on deep, moist soils. Clones may largely shade the forest floor, and individual ramets can achieve heights of 3–12 m (Immel 2001), reaching stem diameters of 25 cm (K. Schulz, pers. obs.). Thus, it is functionally both a large shrub and a subcanopy tree capable of overtopping honeysuckle (maximum height 5.2 m) or spicebush (maximum height 3–5 m) (PLANTS Database 2022). In southwestern Illinois, the location of this study, pawpaw is restricted to the forest interior, where it produces a low canopy of large, horizontally oriented leaves 10–30 cm long (Immel 2001). Larger individuals flower and produce banana-like berries 7–16 cm long (Immel 2001) in early fall. A number of mammals consume pawpaw fruits and disperse the seeds, although most stands likely consist of large clones (Rogstad et al. 1991, Larimore et al. 2003). White-tailed deer (*Odocoileus virginianus* Zimmermann), common understory browsers, do not browse on pawpaw foliage (Slater and Anderson 2014). In commercial forests pawpaw is regarded a significant competitor with tree seedlings (Olson and Keeley 2018). Baumer and Runkle (2010) demonstrated strong competitive ability in pawpaw against very tolerant sugar maple and moderately tolerant black cherry (*Prunus serotina* Ehrh.). Tree seedlings under pawpaw were less abundant and smaller than in surrounding locations. Accounts of the photosynthetic behavior of pawpaw are seemingly absent in the literature.

Spicebush is a dioecious clonal species of moist forest interiors and has a range similar to pawpaw. It achieves height and spread comparable to forest-grown honeysuckle (1–3(5)) m tall, Nesom 2002). The leaves are moderately large, 6–14 cm long. It is an

aggressive competitor in the understory, but evidence is mixed concerning its ability to capitalize on canopy gaps (see below). Female shrubs produce shiny red, oily drupes in early fall. These are favored by birds and disappear far earlier than honeysuckle fruits. Spicebush seeds are ca. 3 mm in diameter and germinate easily after stratification. Seeds persist in the litter layer for a number of years (Nesom 2002), but most shrubs arise from clonal reproduction (Nesom 2002). Deer and other mammalian herbivores appear not to browse on spicebush foliage (Schulz, pers. obs.).

Luken et al. (1997) compared light acclimation responses of spicebush to honeysuckle and observed marked differences. Unlike honeysuckle, spicebush transplanted to 25 and 100% sunlight weakly expressed plastic responses to high light (plants grown at 1% sunlight failed to thrive). Davidson (1966) examined growth responses of six shrub species maintained in growth chamber simulating open (14% full sun) and closed canopy (3% full sun) forest light levels. Spicebush was distinctive among species because it gained height faster and produced more leaves under closed canopy, suggesting it was a shade specialist. In contrast to Luken et al. (1997), Niesenbaum (1992) observed greater leaf area and annual branch growth in spicebush exposed to 20% vs. 1% full sun in natural habitats. Moreover, Veres and Pickett (1982) observed substantially greater leaf area, leaf biomass, branch biomass, and primary stem production in high light (4300 foot candles, estimated as ca. 43% full sun) vs. low light (300 foot candles, estimated as 3% full sun) habitats.

Methods And Materials

Studies were conducted in late midsummer (August and early September) in a ca. 50 year-old upland successional forest and a south-facing forest edge on the Campus of Southern Illinois University (38.78° N, 90.00° W), in Madison County, southwestern Illinois USA. The soils are moderately acid Menfro Silt loam, containing ca. 22% clay in the surface horizons (Leeper 2004). Dominant forest trees include sugar maple, several oak species (*Quercus rubra* L., *Q. michauxii* Nutt., *Q. macrocarpa* Michx.), walnut (*Juglans nigra* L.), slippery elm (*Ulmus rubra* Muhl.), green ash (*Fraxinus pennsylvanica* Marshall.), and persimmon (*Diospyros virginiana* L.). The tree canopy is somewhat broken, supporting a heavy subcanopy of maple seedlings and pawpaw ca. 3–6 m tall. Mean (SD) midsummer light levels in the forest understory estimated from canopy photographs were < 13.3 (0.06)% of available photosynthetically active radiation. The edge site was dominated by cottonwood (*Populus deltoides* Marshall.), green ash, and sycamore (*Platanus occidentalis* L.). No light measurements of were made at the edge site but an appropriate sun path diagram shows the site received ca. 10 h. direct sunshine daily during summer.

Understory study shrubs were selected as sets of adjacent honeysuckle, spicebush, and pawpaw shrubs 0.7–1.2 m tall and < 1.5 m apart. All individuals were apparently healthy and unstressed. Sets were located under similar, representative canopy conditions. We chose this approach to ensure comparable environments among study plants and for use as a blocking variable. Although this is not *per se* a random sample, it follows widespread practice in plant ecophysiology. Edge habitat shrubs were selected haphazardly at intervals of 5 m along the shrub line.

Photosynthetic light response curves were measured on eight individuals of each species during midsummer (late July and August 2016) at midday with a LI-COR Li6400XT gas exchange system (LI-COR Biosciences, Lincoln, NB USA). Chamber conditions (means with SD) were maintained at levels typical for forest conditions in summer. CO₂ concentration in the chamber was 396 (2.78) ppm. Leaf temperature was 30.0 (0.0844) °C and leaf to air vapor pressure deficit (VPD) was 1.12 (0.198) kPa, corresponding to ca. 70–75% relative humidity, which approaches the operating limit of the photosynthesis system. Before light curves were taken leaves were acclimated to a previously determined saturating light intensity (500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the understory site; 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for edge shrubs). PAR levels were then stepped downward: 400, 300, 250, 200, 150, 100, 75, 50, 25, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for understory shrubs; 1600, 1400, 1200, 1000, 800, 600, 400, 300, 200, 150, 100, 50, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for edge shrubs. Measurements were recorded after stable gas exchange rates were achieved at each light level. Respiratory rates at PAR 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are means of four samples because respiratory measurements are of low magnitude and in practice have greater temporal variability. Leaf areas were determined from photographs of pressed leaves using ImageJ. Leaf mass was measured to a resolution of 0.0001 g on specimens dried at 65 °C. Rates of gas exchange are expressed on both a leaf area basis and a leaf dry weight basis. Leaf chlorophyll contents were measured from leaf disks using the DMSO method (Hiscox and Israelstam 1979).

To assess the leaf area and biomass allocation in shoots of shaded shrubs, 12–14 leafy shoots were collected from the study plants and other comparable individuals in the study area. Leaf areas and the masses of leaves and stems were determined as above.

Photosynthetic light responses were compared using repeated measures ANOVA. Comparisons of leaf traits and biomass allocation in shade were made by 1-way ANOVA followed by Tukey's HSD. In some cases, biomass data did not conform to theoretical assumptions and Kruskal-Wallis nonparametric ANOVA followed by the Dwass-Steel-Christchlow-Fligner Test for all pairwise comparisons were substituted. Comparisons of honeysuckle leaf traits in sun and shade were made using unequal variance t-tests. All analyses were conducted using Systat 13 (Systat Software, San Jose, CA USA).

Results

Understory Photosynthesis, leaf area basis

Light response curves were similar across species (Fig. 1a), saturating at ca. $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ with maximum rates of photosynthesis (A_{max}) ranging $3.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in pawpaw to $4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in spicebush. Repeated measures ANOVA showed that overall photosynthetic rates were significantly higher in spicebush, but the patterns of light response (PAR x species interaction) were the same among species (Table 1). A_{max} and respiratory rate (R) did not differ significantly among species (Table 1). Stomatal conductance (g_w), intrinsic water use efficiency (A_{max}/g_w , with g_w measured in μmol), and internal CO_2 concentration were tested by 1-way ANOVA, with and without VPD as a covariate. Neither stomatal conductance (mean = 75.4 , SE = $5.81 \text{ mmol m}^{-2} \text{s}^{-1}$), intrinsic water use efficiency (mean = 54.1 , SE = 3.24), nor internal CO_2 (mean = 299 , SE = 5.09 ppm) varied significantly.

Understory Photosynthesis, leaf mass basis

Photosynthesis calculated on a leaf mass basis presented a different picture. Repeated measures ANOVA showed that honeysuckle had markedly lower rates of photosynthesis overall (Fig. 1b, Table 1) and responded to increasing light ($0\text{--}100 \mu\text{mol m}^{-2} \text{s}^{-1}$) much more slowly than spicebush and pawpaw (Fig. 1b, Table 1). The light responses of spicebush and pawpaw were nearly identical. A_{max} in honeysuckle was 45% lower than in the two other species (Fig. 1b, Table 2). Respiratory CO_2 release in pawpaw was significantly (ca. 20%) smaller in honeysuckle and spicebush (Table 2).

Table 1
Repeated measures ANOVA for photosynthetic light response curves. PAR
is photosynthetically active radiation

Leaf Area Basis					
Between Subjects					
Source	SS	df	MS	F-Ratio	<i>P</i>
Species	24.1526	2	12.0763	3.96	0.0334
Error	70.2114	23	3.0527		
Within Subjects					
Source	SS	df	MS	F-Ratio	<i>P</i>
PAR	425.4770	10	42.5477	314.97	0.0000
PAR*Species	5.5950	20	0.2798	2.07	0.0057
Error	31.0693	230	0.1351		
Leaf Mass Basis					
Between Subjects					
Source	SS	df	MS	F-Ratio	<i>P</i>
Species	0.3469	2	0.1735	32.28	0.0000
Error	0.1236	23	0.0054		
Within Subjects					
Source	SS	df	MS	F-Ratio	<i>P</i>
PAR	0.6920	10	0.0692	373.94	0.0000
PAR*Species	0.0687	20	0.0034	18.56	0.0000
Error	0.0426	230	0.0002		

Shade Leaf Characteristics

All three species exhibit similar levels of chlorophyll measured on a leaf area basis and have statistically indistinguishable chlorophyll a:b ratios (Table 2). Leaf mass per unit area (specific leaf mass, SLM) in honeysuckle is nearly twice that in pawpaw and spicebush (Table 2). This results in significantly lower levels of total chlorophyll per unit mass in honeysuckle.

Table 2

Characteristics of sun and shade-grown honeysuckle, pawpaw, and spicebush. $A_{\max}$, maximum light-saturated photosynthetic rate; R, dark respiration rate; QUE, quantum use efficiency (slope of light response curve 0 to 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$); LAR, leaf area ratio. Comparisons of sun and shade honeysuckles are denoted by capital letters (unequal variance t-test); comparisons of shade honeysuckle, pawpaw, and spicebush are denoted by lower case letters (1-way ANOVA followed by Tukey's HSD). Values followed by the same letter do not differ at $P < 0.05$.

	Honeysuckle (sun)			Honeysuckle (shade)			Pawpaw		Spicebush			
Leaves	Mean	SE		Mean	SE		Mean	SE		Mean	SE	
Total chlorophyll (g m ⁻²)	0.378	0.025	A	0.258	0.009	B a	0.242	0.013	a	0.241	0.010	a
Total chlorophyll (g g ⁻¹)	3.94	0.18	A	6.58	0.45	B a	12.67	0.76	b	11.01	0.79	b
Chlorophyll a:b ratio	11.86	1.77	A	3.11	0.33	B a	4.00	0.38	a	4.63	0.57	a
Specific leaf mass (g m ⁻²)	96.3	6.8	A	40.3	2.3	B a	19.3	0.9	b	22.3	0.9	b
A _{max} (μmol m ⁻² s ⁻¹)	16.58	0.82	A	3.56	0.26	B a	3.44	0.20	a	4.23	0.29	a
A _{max} (μmol g ⁻¹ s ⁻¹)	0.1760	0.0157	A	0.0916	0.0092	B a	0.1808	0.0116	b	0.1903	0.0120	b
R (μmol m ⁻² s ⁻¹)	-1.29	0.07	A	-0.34	0.06	B a	-0.31	0.07	a	-0.25	0.03	a
R (μmol g ⁻¹ s ⁻¹)	-0.0137	0.0014	A	-0.0083	0.0015	B a	-0.0157	0.0033	b	-0.0114	0.0011	a
QUE (μmol C (μmol photons) ⁻¹)	0.0230	0.0005	A	0.0339	0.0032	B a	0.0396	0.0016	a	0.0421	0.0016	a
Light Compensation Point (μmol m ⁻² s ⁻¹)	23.9	4.0	A	6.6	4.7	B a	3.1	2.4	a	1.5	0.8	a
Shoots												
Leaf area (m ²)				0.0234	0.0019	a	0.0792	0.0094	b	0.0385	0.0038	c
Stem mass (g)				0.291	0.036	a	0.279	0.071	a	0.204	0.034	a
Leaf mass (g)				0.995	0.081	a	1.567	0.203	b	1.031	0.108	a,b
LAR (m ² g ⁻¹)				0.02369	0.00065	a	0.05460	0.00760	b	0.03755	0.00073	c

Edge vs. Understory Photosynthesis for Honeysuckle

Forest edge and understory honeysuckle showed large and statistically significant differences in photosynthetic measures and leaf characteristics (Table 2). $A_{\max}$ in high light honeysuckle was 4.5-fold greater than in shade honeysuckle; R was 3.5-fold greater; LCP was 3.6-fold higher; QUE (quantum use efficiency: the slope of light response curve 0 to 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was 0.7 of the value in shade. Total chlorophyll on an area basis was 1.5-fold higher, but only 0.6-fold as high on a mass basis.

Chlorophyll a:b ratio was 3.8-fold higher and SLM was 2.4-fold higher. When $A_{\max}$ and R are expressed on a mass basis, high light shrubs have 1.9 and 1.6-fold higher rates, respectively.

Comparison of potential carbon gain by shoots

Comparisons of biomass and leaf area allocation were complicated by widely differing variances between species which precluded standard ANOVA, even after multiple attempts to transform the data. Kruskal-Wallis nonparametric ANOVA (KW) followed by the Dwass-Steel-Christlow-Fligner Test for all pairwise comparisons were substituted. The ratio of leaf to stem biomass was similar for pawpaw and spicebush (6.5 and 6.9, respectively), but significantly less for honeysuckle (3.5, both comparisons significant at $P < 0.0200$). Leaf area per shoot differed among the three species (Table 2). Leaf areas were greatest for pawpaw, followed by spicebush, and then honeysuckle. Consequently, leaf area ratio (LAR), the ratio of leaf area per unit shoot mass, varied greatly across species in the order spicebush = pawpaw, > honeysuckle (Table 2).

If photosynthetic rates (area basis) at a representative PAR level are multiplied by LAR, one obtains an approximation of potential daytime carbon gain per gram of biomass investment in shoots. Figure 2a illustrates the approximate photosynthetic “payback” across PAR levels typical of forest understories. In all cases honeysuckle obtains far less carbon per unit of biomass investment than spicebush and pawpaw.

A problem with this analysis is that nighttime respiration is a drain on carbon gain. To partially correct this, payback estimates were adjusted by subtracting an estimate of dark respiration. Leaves and stems were assumed to have the same mass-based respiratory rate which was adjusted to typical cooler conditions at night (25 °C, using $Q_{10} = 2$). We assumed that the duration of the daily photosynthetic period under a canopy would be ca. 12h. This attempt to account for respiration overnight reveals much lower levels of carbon gain (Fig. 2b), but species differences and the pattern of response to light remain.

Discussion

Area-based photosynthetic rates for honeysuckle in this study can be compared with the more detailed work of Lieurance and Landsbergen (2016). Honeysuckle in our study achieved half their maximum photosynthetic rate in shade, and 10% higher rates in the sun. Patterns in the light response and leaf characteristics were concordant with greater acclimation to shade, suggesting our shade site was darker and the sun site brighter than in that published account. Luken et al. (1997) observed about 10% lower maximum rates for sun honeysuckle, but twice the maximum rate for spicebush, again suggesting our sites were more extreme. Until this study is replicated in brighter shade environments, our conclusions are limited to deep shade.

Studies of shade tolerance and photosynthesis have traditionally measured photosynthetic rates on a leaf area basis, not a mass or shoot basis as was done here. Here, different impressions were gained depending on whether measurements were area-based or mass/shoot-based. On an area basis all three species show comparable light responses and rates of photosynthesis. This would suggest that honeysuckle has the acclimation capacity to sufficiently compete with native woody understory plants. In a short survey of studies examining invasive understory shrub photosynthesis [e.g., Harrington et al. 1989, Luken et al. 1997, Pattison *et al.* (1998), Lieurance and Landsbergen (2016), Dornbos *et al.* (2016)], none except Xu (2007) deviate from area-based measurements. This is significant because mass-based measurements reference photosynthesis to the approximate carbon cost of leaf construction and the “profitability” of leaves; area-based measurements reference photosynthesis to the efficiency of the receptive surface of whatever carbon cost.

Evaluated, on a leaf mass or shoot basis, honeysuckle in deep shade is distinctly inferior to the two native species. Higher allocation to leaf mass per unit area is a well-known trait of plants in high light environments (e.g., forest edge honeysuckle in this study), however this is a liability when light is very limiting and mass per unit area cannot be sufficiently adjusted downward to support larger leaf areas. SLM for honeysuckle in sun was about twice that for shade honeysuckle, but SLM for shade honeysuckle is still twice as large as for pawpaw and spicebush. Plastic responses in honeysuckle clearly cannot duplicate the behavior of the more shade-specialized pawpaw and spicebush. The profoundly higher performance for honeysuckle leaves in sun suggests its presence in the forest understory is an expression of wide niche breadth, not adaptation to shade *per se* as seen in pawpaw and spicebush. Based on gas exchange data and leaf characteristics, honeysuckle clearly finds near optimal habitat

along forest edges. This supports Schulz and Wright's (2015) suggestion that control of edge shrubs should be a conservation priority.

From the perspective of shoot allocation, the lower capacity of honeysuckle to adjust SLM in shade is reinforced by a greater allocation to stem tissue and lower LAR. Presuming leaf orientation is similar between the species, in a very shady environment honeysuckle shoots cannot repay the cost of shoots as quickly as pawpaw and spicebush. Naturally, it would be informative to compare whole plant respiratory costs, but obtaining these data is out of practical reach.

A concern in any photosynthesis study involving *Lonicera* spp. is the relative importance of summer photosynthesis under a closed canopy versus spring/fall photosynthesis under more open canopies. There is a tendency to generalize from Harrington et al. (1989) that high spring photosynthetic rates seen in *L. X bella* apply to Amur honeysuckle. Fridley (2012), using photosynthesis measurements in a model, showed that *spring* photosynthetic gains for *L. X bella* were clearly meaningful, but that Amur honeysuckle achieved low gains in spring and modest gains in fall. Phenological observations like those made by McEwan et al. (2009) are fertile ground for speculation, but do not include photosynthesis measurements in light of photosynthetic capacity, or considerations of low leaf area and near-vertical leaf orientation for much of spring (Schulz, pers. obs.). Photosynthesis in fall might be significant (Fridley 2012), but frequent phenological mismatches between tree canopy senescence (last half of October), hard frost which causes honeysuckle leaves to senesce, and generally declining photosynthetic capacity are also probable. Records of fall weather patterns in nearby St. Louis, MO USA show high interannual variation in the first date of frost. The mean date is November 1, but one standard deviation from this date spans the period October 16 to November 17 (NOAA 2022a). Anecdotally, in 2020 we noted honeysuckle leaf senescence at the start of November; in 2022 leaf senescence was delayed into early December (Schulz, pers. obs.). For these reasons the value of the fall light window may be quite intermittent for understory shrubs. In the long term, phenological differences between the three species are probably of limited importance given the large performance gap between honeysuckle and the two natives. Any phenological advantage would be difficult to overcome in a few weeks of a mean 208 day (range 159–260) growing season (NOAA 2022b).

This finding should be taken as a suggestion that pawpaw and spicebush may replace honeysuckle over time in forest types driven by shade tolerance. Naturally the abundance and distribution of pawpaw and spicebush in any given situation will affect this process. Ironically, management plans which seek the re-imposition of fire will greatly reduce the abundance of maple, pawpaw, and likely spicebush, however they may only top kill honeysuckle and, absent repeated fire, leave stands more invisable (Nyboer and Edgin 2017). We have noticed that both pawpaw and spicebush are increasing in local forests. This may be caused by higher shade tolerance as regional forests recover from anthropogenic disturbance, but it also reflects the fact that deer do not browse either species and competitors have declined (Slater and Anderson 2014). We note that honeysuckle is subject to moderate deer browsing, which is a disadvantage. Nonetheless, we periodically observe that honeysuckle overtopped by pawpaw shows signs of decline, as do honeysuckle under closing maple canopies.

Certainly, this analysis of photosynthetic patterns and the structure of shoots is not a comprehensive study of whole plant shade tolerance. However, we submit that the capacity to produce shoots that have a higher level of net primary production in shade is a meaningful element of the larger problem. A recent visit back to the study site several years after this work supports these findings. Pawpaw and spicebush, which were originally comparably sized, are now almost twice as tall as honeysuckle.

Declarations

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Kurt Schulz conceived the project, collected, and analyzed the data, and wrote the manuscript. Special thanks to Anh Nguyen (Southern Illinois University Edwardsville) for considerable assistance with field data collection.

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Figures

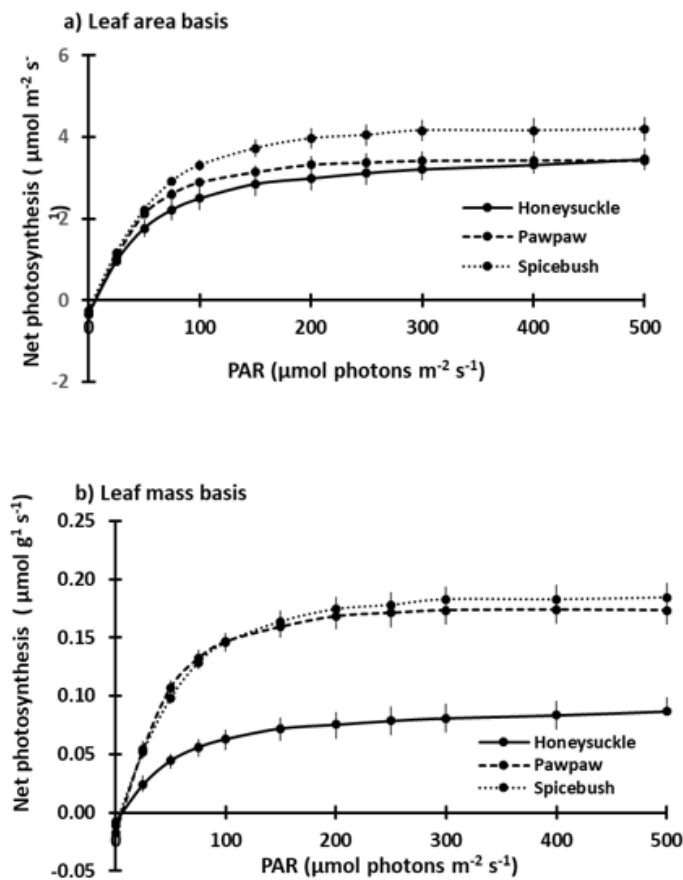


Figure 1

a,b. Photosynthetic light response curves (means and SEs) of honeysuckle, pawpaw, and spice bush. a) measured on a unit leaf area basis; b) measured on a leaf mass basis. For leaf area-based comparisons spicebush has significantly higher rates of photosynthesis. For leaf mass-based comparisons honeysuckle has significantly lower rates of photosynthesis and a differently shaped response curve (Table 1.)

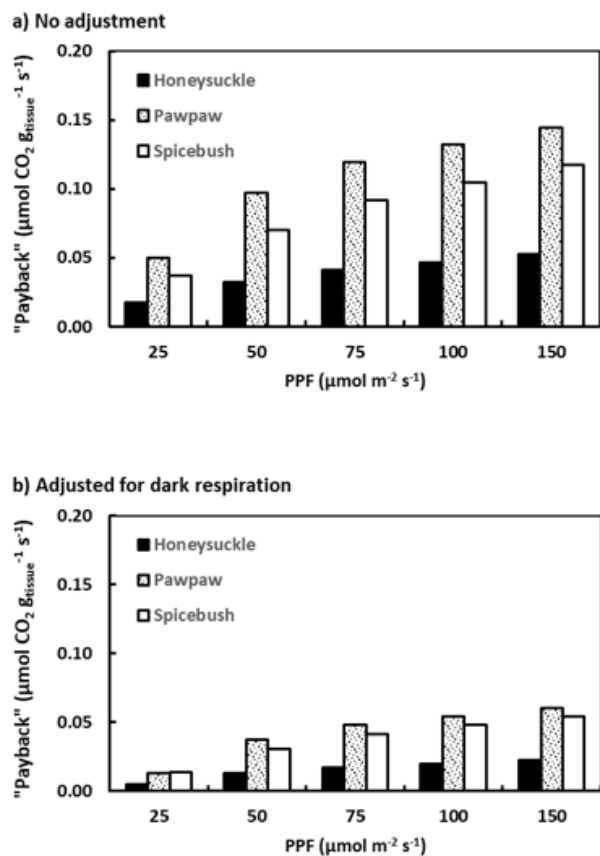


Figure 2

a,b. Photosynthetic gains per unit shoot mass at common understory light levels. a) daytime only, no adjustment for dark respiration; b) adjustment for dark respiration assuming all shoot tissue respire at the rate of leaves.