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Does the photosynthetic response of *Asimina triloba* to low light contribute to its competitive advantage in forest understories compared with *Acer saccharum* and *Fraxinus quadrangulata*?[1]

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Abstract. *Asimina triloba* is replacing shade-tolerant *Acer saccharum* as the most abundant seedling in many *Ac. saccharum*-dominated forests in the midwestern USA. Selective browsing of *Ac. saccharum* by *Odocoileus virginianus* and avoidance of *As. triloba* contributes to this increased *As. triloba* abundance. However, shade tolerance may also be a factor contributing to increasing *As. triloba*. We tested our hypothesis that *As. triloba* is more shade tolerant than *Ac. saccharum. Fraxinus quadrangulata* is less shade tolerant than *As. triloba* and *Ac. saccharum*; however, other than *As. triloba*, it was the only species that increased stems per hectare in the seedling stratum from 2003 to 2008. We evaluated leaf photosynthetic traits to assess shade tolerance of these three species. Light response curves (LRCs) of *As. triloba*, *Ac. saccharum*, and *F. quadrangulata* saplings were measured under a dense *Ac. saccharum* canopy *in situ* using a portable infrared gas analyzer and were tested for fit to rectangular hyperbola, nonrectangular hyperbola, and exponential LRC models. Multivariate analysis of covariance, with estimated ambient irradiance and leaf temperature as covariates, tested interspecific differences in gas exchange properties: (R_d [dark respiration], α [LRC initial slope], and A_{MAX} [maximum photosynthetic rate]). Multivariate contrasts indicated that *F. quadrangulata* had significantly higher rates of photosynthesis than the two other species, indicating lesser shade tolerance, whereas *As. triloba* had greater initial light response (α values) than *Ac. saccharum*, which confers an advantage to *As. triloba* under low light conditions. These results implicate greater shade tolerance by *As. triloba* as another contributor to its increasing dominance in the understory.

Key words: deer browsing, gas exchange properties, hemispherical photography, leaf photosynthesis traits, light response curves, shade tolerance

This study investigates the photosynthetic responses of three common forest species to interpret their adaptation to low and high light conditions, that is, their shade tolerance. We predict that differing shade tolerance and photosynthetic response contribute to relative competitive ability in a mesophytic forest, Funk's Grove, in McLean County, central Illinois.

Ecological Characteristics of Focus Species. In the Central Hardwoods region of the midwestern and eastern USA (Fralish and Franklin 2002), which extends over an area of 51 million ha (Shifley and Thompson 2011), *Acer saccharum* Marsh. (sugar maple) is a dominant species in late-successional mesic areas (Peet and Loucks 1977; Adams and Anderson 1980; Whitney 1999; Nowacki and Abrams 2008). The success of *Ac. saccharum* seedlings and saplings in this environment is largely attributed to its ability to persist under the forest canopy at slow rates of growth until more favorable growth conditions become available (*i.e.*, tree mortality creates canopy gaps and light availability increases). Under low-light conditions, *Ac. saccharum* exhibits high survivorship by minimizing rates of carbon loss relative to other tree species (Walters and Reich 2000). In addition to these characteristics, which enhance survival under low-light conditions, *Ac. saccharum* adjusts its metabolic properties and growth pattern (*i.e.*, resource allocation) to take advantage of higher light conditions when they exist (Canham 1988; Bonser and Aarssen 1994; Lei and Lechowicz 1997, 1998).

In Canada *Ac. saccharum* was studied west, center, and east of Québec in 24 sites located between 45°51′–48°59′N and 70°21′–79°27′ W. In plots, density of sugar maple seedlings varied from 0.0 to 191.8, with a mean of 25.5 seedlings m^{-2} in circular plots; only 6% of the plots did not have sugar maple seedlings. It was suggested that

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seedling density increased with average July mean temperature of 19.5 °C; mean precipitation was 35 mm.

Four mast years were identified and produced large numbers of seeds. Mature sugar maple trees were positively related to maple saplings. However, saplings have a negative influence on sugar maple seedlings. The negative effects of saplings might have been caused by sugar maple leaves that reduce the amount of light available. Other factors that influence seedling presence and survival include climate variation, isolation of populations, abundance of seed predators, and seedling browsers, or changing light regime in forest gaps (Graignic *et al*. 2014).

Lee and Ibáñez (2021) followed seedlings of two understory trees, *Ac. saccharum* and *Quercus rubra* in a temperate forest in southeastern Michigan (Saginaw Forest [42°16′15.5172″N, 83°48′21.6786″W], Radick Forest [42°17′13.4988″N, 83°39′29.0016″W], and the E. S. George Reserve [42°27′25.5744″N, 84°1′12.813″W]). Seedlings of both species were planted in 2 years, totaling 290 *Ac. saccharum* and 320 *Q. rubra*. Seedling mortality was high for both species.

Seasonal assimilation of leaf carbon was monitored in spring, summer, and fall for *Ac. saccharum and Q. rubra* using hourly climate data that included temperature, vapor pressure deficit, soil moisture, and light (photosynthetically active radiation [PAR]). Carbon assimilation estimates were hourly and then summed over the duration of the growing season, which resulted in estimations of some net amount of the CO_2 assimilation by leaf tissue over the growing season (mol CO_2/yr) for each plant. The authors did not measure soil respiration or stem photosynthesis.

In spring, *Ac. saccharum* had higher foliar carbon assimilation (84.3% of annual total); in summer 15.9%; autumn –0.2%. In contrast, *Q. rubra* assimilated 52.5% in spring, 43.5% in summer, and 4.0% in autumn. Spring photosynthesis before canopy closure is clearly important for growth and survival of *Ac. saccharum*, but it may be different for other competing species.

Asimina triloba (L.) Dunal (paw paw) is replacing shade-tolerant *Ac. saccharum* as the most abundant seedling in some *Ac. saccharum*-dominated forests in the midwesterm USA (Larimore et al. 2003; Slater and Anderson 2014). *Asimina triloba* trees reach a height of approximately 2.1 m after 10 yr of growth (Larimore *et al*. 2003), and a maximum height of approximately 9 m (Little 1988); thus they are an understory species as they typically do not reach the forest canopy. Historically, *As. triloba* was limited to wet areas as the species abundance is diminished by fire, and it can be locally extirpated by frequent or intense burns (Larimore *et al*. 2003; Holzmueller *et al*. 2009). However, fire can top kill mature *As. triloba* plants, but the roots can increase the number of *As. triloba* stems (Anderson and Schwegman 1991; Larimore *et al*. 2003). After the cessation of frequent prairie and savanna fires (Nowacki and Abrams 2008), the expansion of *As. triloba* in oak–hickory-dominated forests was facilitated by the understory conditions created by prior *Ac. saccharum* invasion and dominance of these forests (Larimore *et al*. 2003), which includes shadier and more moist conditions, or "mesophication" (Nowacki and Abrams 2008). Today, *As. triloba* tends to be restricted to moist, shady environments (Adams and Anderson 1980; Anderson and Mitsch 2003), at least within the northern portion of the species' range (Lagrange and Tramer 1985).

Fraxinus quadrangulata Michx. (blue ash) occurs on mesic to wet-mesic sites in our study area (Adams and Anderson 1980; Slater and Anderson 2014). Its native range is North America from Oklahoma to Michigan, the Midwest to Appalachia, and it is found in limestone glades (Baskin and Baskin 1996) and open forests (Bryant *et al*. 1980). It tolerates calcareous soils and high pH, reaching 15–23 m tall and spreading 10–18 m in the crown (Little 1988). Although this tree is not currently listed as endangered within the state, its population is declining because of an introduced insect pest, the emerald ash borer (*Agrilus planipennis* Fairmair). However, *F. quadranulata* appears to be more resistant to this insect pest than other native ash species (Tanis and McCullough 2012). In our 2009 study area, we did not see *Ag. planipennis*; however, they occurred in areas within 24 km. In our current research, *F. quadranulata* was the only species that was used for the first time for the study of photosynthesis. Currently, *Ac. saccharum, As. triloba*, and *F. quadrangulata* are described as very shade tolerant, shade tolerant, and moderately shade tolerant, respectively (Barnes and Wagner 2004). *Fraxinus quadrangulata* is less shade tolerant than *Ac. saccharum*; however, other than *As. triloba*, it is

the only species that increased stems per hectare in the seedling stratum at this site from 2003 to 2008 (Slater and Anderson 2014).

Additionally, the high availability of agricultural food resources and earlier legislation protecting deer (Pietsch 1954; Nixon *et al*. 1991; Nixon and Hansen 1992) have created large white-tailed deer (*Odocoileus virginianus*) populations. Before European settlement, density in central Illinois was estimated to be 22 deer/km^2 (Nixon *et al*. 1991). However, aerial surveys of deer in the Funks Grove area by the Illinois Department of Natural Resources in 2007 estimated a density $>$ 75 deer/km^2 (Smith 2004). Using the number of deer killed by hunters in McLean County as a surrogate for population density, the size of the deer herd may have increased 869% between 1984 and 2011. This rapid growth of the deer herd in our study area appears to have had a profound effect on tree reproduction. In a State of Illinois nature preserve adjacent to our study area, repeated random sampling of the same area in 1984, 1994, and 2011 showed that the relative density of *Ac. saccharum* seedlings declined sharply over time and was 69%, 26%, and 0% for the three samples, respectively. In contrast, relative density of *As. triloba* was 24, 52, and 92% for the same years, respectively (R. C. Anderson 2011, unpublished data). Although selective deer browsing may contribute to *As. triloba*'s increasing dominance at our study site (Slater and Anderson 2014), *As. triloba*'s competitiveness for light in the forest understory may also play a role.

Asimina triloba has several biochemical defense acetogenins, chemical compounds that inhibit deer negatively or lethally (Zhao *et al*. 1994; He *et al*. 1997). Consequently, deer tend to avoid browsing on *As. triloba* (Liang and Seagle 2002; Asnani *et al*. 2006; Slater and Anderson 2014), whereas *Ac. saccharum* and *Fraxinus quadrangulata* are readily browsed. In the midwestern USA, *As. triloba* appears to be benefitting from increased deer density; consequently, selective browsing by deer may be causing *As. triloba* to become an increasingly dominant species (Robertson *et al*. 1978; Asnani *et al*. 2006; Slater and Anderson 2014). Though *As. triloba* benefits from deer browsing (*i.e*., reduced competition from other species), it must survive conditions of low-light regimes under a dense *Ac. saccharum* canopy, suggesting that physiological shade tolerance may be an important factor determining its success and competitive ability in seedling and sapling strata.

Existing literature suggests that *As. triloba* is well adapted to low-light conditions in the forest understory (Augspurger *et al*. 2005; Hosaka *et al*. 2005), but the hypothesis that the photosynthetic response of *As. triloba* to varied levels of irradiance is an important factor contributing to its competitive ability and reproductive success in the forest understory remains to be tested. We hypothesized that *As. triloba* is less shade tolerant than *Ac. saccharum* but more shade tolerant than *F. quadrangulata*.

Photosynthesis, Irradiance, Sun and Shade Leaves. Shade tolerance is determined by ecophysiological properties of plants' light response curve (LRC). The daily accumulation of PAR in the 400- to 700-nm range is the limiting factor within the understory of a closed-canopy forest and is typically the driving factor in secondary succession in temperate forest ecosystems (Oliver and Larson 1996). Sun flecks occur $<$ 10% of the time and provide 10–80% of the light available for canopy and understory plants, respectively. Of this sunlight energy, 60–80% is utilized for photosynthesis by understory plants (Way and Pearcy 2012). Ultimately, a plant's success in this environment is determined by adaptation to low irradiance and energetic trade-offs among gas exchange, structural support, and biotic interactions (Givnish 1988).

Adaptation to various light regimes can be found among different plant species, plants within a single species, or even individual leaves of a single plant. Irradiance levels experienced by leaves during development influence the extent to which they develop sun or shade leaf characteristics (Boardman 1977; Lichtenthaler *et al*. 1981; Evans and Poorter 2001; Poorter *et al*. 2019); later, some of those properties can change as a function of light conditions to which mature leaves are exposed (Anderson *et al*. 1988; Chow *et al*. 1990).

Sun- and shade-tolerant leaves differ in multiple ways, including leaf thickness, area, orientation, and chemical composition, especially nitrogen, which affect their photosynthetic response to different light levels (see Campany *et al*. 2016, Mathur *et al*. 2018 for details). Sun plants can have sun leaves at the top of the canopy and shade leaves at the lower portions of the tree canopy, whereas shade-tolerant plants have only shade leaves. (Mathur *et al*. 2018). Compared with sun-

tolerant leaves, shade-tolerant leaves have lower photosynthetic capacity, although increased light (*e.g.*, from sun flecks) can result in rapid upregulation of mesophyll conduction (Campany *et al*. 2016). Soil nitrogen (NO_3) and carbon make important contributions to the chloroplast structure, especially the enzyme rubisco, resulting in substantial differences between sun and shade chloroplasts (Mathur *et al*. 2018). These morphological and physiological differences can contribute to different photosynthetic responses to irradiance intensity (Campany *et al*. 2016).

The photosynthetic response of individual leaves of different species was the interest of several recent publications (Campany *et al*. 2016; Dickinson-Nelson and Van Aukin 2017; Poirier-Pocovir *et al*. 2018; Hopkins and Gravatt 2019; Idris *et al*. 2019; Xu *et al*. 2019) and is the focus of our study. To assess the shade-tolerance characteristics of *As. triloba* relative to other tree species (*Ac. saccharum* and *F. quadrangulata*), we developed a novel method to quantify and to compare gas exchange properties of leaves (dark respiration rates or R_d, initial slope of the LRC [α], and maximum photosynthetic rates or A_{MAX}) *in situ* under a forest canopy. We measured LRCs using a portable infrared gas analysis system (LI-COR 6400; LI-COR Biosciences, Lincoln, NE) and assessed varied ambient light conditions to which measured leaves were exposed using hemispherical canopy photography. We hypothesize that *Ac. saccharum*, *As. triloba*, and *F. quadrangulata* have LRCs corresponding to their different perceived shade tolerance. We predict that *Ac. saccharum*, the most shade-tolerant species, would have higher photosynthetic response to light than *As. triloba*, and *F. quadrangulata*, the least shade tolerant, would have the lowest photosynthetic response to light.

Materials and Methods. STUDY SYSTEM. Our study site (40°21.2′N, 89°7.7′W) was located within the 27-ha Thaddeus Stubblefield State of Illinois Land and Water Reserve, a mesic/wet-mesic forest located in Funks Grove, McLean County, central Illinois. Funks Grove is registered as a National Natural Landmark by the U.S. Department of Interior and is located 35 km southwest of Bloomington, IL. In the early 1800s, according to Government Land Office Records, this site was an oak-dominated savanna (Rodgers and Anderson 1979), but after the suppression of wildfires, with the introduction of European-style agriculture (*ca*. 1833), it has become a closed-canopy forest consisting primarily of *Ac. saccharum* with a few old-growth fire-resistant, shade-intolerant species (*Quercus macrocarpa* Michx., *Q. rubra* [Michx.] Farw., *Quercus muhlenbergii* Englem.) represented in the forest canopy (Arnold and Anderson 1994). The site currently exhibits a species composition that is characteristic of mesic/wet-mesic forests in central Illinois (Adams and Anderson 1980); tree, sapling, and seedling strata at this site are currently dominated by *Ac. saccharum*, *Ac. saccharum*, and *As. triloba*, respectively (Smith 2004; Slater and Anderson 2014).

SAMPLING DESIGN. For measurement of photosynthetic LRCs, 2- to 5-m-tall saplings of *Ac. saccharum*, *As. triloba*, and *F. quadrangulata* were selected across the range of tree canopy conditions under which they occurred at the study site. No seedlings of *A. saccharum* and not enough of *F. quadrangulata* were present for measurement. Leaves of *Ac. saccharum* and *As. triloba* are 9–14 cm long and wide, 18–25 cm long, and 7.5–13 cm wide, respectively, and *F. quadrangulata* leaflets are 6–11 cm and 2.5–4.1 cm long and wide, respectively (Little 1988). Photosynthetic light response measurements were made on leaves 1–2 m above the ground surface that were not shaded by other leaves on the branch to which they were attached. Measurements of leaf temperature and photosynthetic rates were made on one leaf of each sapling. There were 19, 19, and 17 saplings for *Ac. saccharum*, *As. triloba*, and *F. quadrangulata*, respectively. One leaf or leaflet per sapling large enough to fill the 2- × 3-cm chamber was selected.

We used the LRC program and the light-emitting diode red–blue light source of the LI-COR 6400 portable photosynthesis system (LI-COR Biosciences) with the following settings: flow rate 500 μmol s^{-1} and CO_2 concentration 400 μmol mol^{-1}. Leaves were subjected to their species' saturation irradiance level (1,000 or 800 μmol m^{-2} s^{-1} PAR) until readings of net photosynthesis stabilized; then measurements of net photosynthesis were taken at progressively decreasing quantities of PAR: 1,000, 800, 600, 400, 300, 200, 100, 50, 25, 10, 5, and 0 μmol m^{-2} s^{-1} PAR when the coefficient of variation (sum of ΔCO_2, ΔH_2O, Δflow in μl s^{-1}) was $< 1\%$ after the minimum stabilization time of 60 s or the maximum time of 120 s was reached. Initially, all species were light

saturated at 1,000 μmol m^{-2} s^{-1} PAR; however, subsequent measurements for *Ac. saccharum* and *As. triloba* saplings were not made at 1,000 and 800 μmol m^{-2} s^{-1} because these species exhibited signs of photoinhibition at these levels of irradiance. We found that from about 9:00 am to 3:30 pm Central Daylight Time usually was the best time for measuring photosynthesis. All measurements were made after canopy closure (from June 12 to July 2, 2009).

To account for the effect of ambient light conditions on variation in photosynthetic rates, hemispherical canopy photographs were taken at the location of each sampled leaf utilizing a Canon PowerShot G10 digital camera with a Raynox circular fish-eye conversion lens in 2009. The camera was mounted vertically on a standard tripod; the lens was located as close to the original leaf location as possible and leveled before image capture. Images were captured between 4:30 and 6:30 am Central Standard Time (from July 26 to July 29) to achieve minimum variance in backlighting conditions and maximize the contrast between the forest canopy and open sky (Rich 1990; Roxburgh and Kelly 1995).

Available moisture and ambient temperature may influence photosynthetic response (Hew *et al*. 1969; Juan *et al*. 2009). To assess possible climate effects on the experimental measurements, we analyzed temperature and precipitation recorded for May through August, summer months surrounding the period of photosynthesis measurements, for comparison of 2009 with the 30-yr record of 1990 to 2020, excluding 2009 (Appendix 1). Data were obtained from the National Oceanic and Administration weather station nearest the study site, Normal 4 NE, Normal, IL, 24 km north of the study site, with the exception of one missing record that was obtained from the Chenoa, IL station, 35 km farther north. Temperatures were analyzed for May through August. Rainfall was summed for those months. All monthly and seasonal data were tested for normality on the basis of the Shapiro–Wilk W statistic before analysis with one-sample *t* test (Sokal and Rohlf 1995). Analyses were performed in SAS (SAS Institute, Inc.) with PROC UNIVARIATE and PROC TTEST.

Statistical Analysis. Our first step in analyses was to determine which of the three functions that may describe the photosynthetic light response provides the best description of the data for each species. LRCs were fitted to rectangular hyperbola, nonrectangular hyperbola, and exponential models (Table 1; Thornley 1976; Gomes et al. 2006; Lambers et al. 2008; Lambert et al. 2011) for each sampled leaf, using nonlinear least-squares regression (PROC NLIN, SAS Institute 2003). Because the physiological mechanisms of photoinhibition (Björkman 1981; Demming-Adams and Adams 1992) are different from those that determine the portion of the LRC of interest to this study, measurements of leaf photosynthetic rates that exhibited evidence of photoinhibition (> 5 % decrease at higher light intensities from that leaf's maximum measurement) were eliminated before analysis. The best model for each species was determined using Akaike's information criterion (AIC) calculated from PROC NLIN output, as described by Motulsky and Arthur (2004). Error terms for each model were pooled by species and the model selected for that species. Ecophysiological parameters ($R_{d,}$ α, and A_{MAX}) for each leaf were assigned using parameter estimates from this model.

Our second step in the analysis was to compare among species the estimated parameters of the best photosynthetic curves. To do this, estimates of direct and diffuse solar irradiance were obtained from the analysis of hemispherical photographs at each leaf location using gap light analyzer software (Frazer *et al*. 1999). Daily total irradiance and daily maximum irradiance (direct light + direct diffuse light, for each) averaged for the closed-canopy portion of the growing season and averaged for the 2-wk period preceding LRC measurements were evaluated to determine the best measure of ambient light conditions (Björkman 1981; Chow *et al*. 1990). Maximum solar irradiance (direct + diffuse light) averaged for the 2 wk preceding LRC measurement demonstrated the strongest correlation with observed variation in LRC properties. This 2-wk average of maximum solar irradiance was analyzed by one-way analysis of variance (ANOVA) to compare the species. Ambient light and leaf temperature measurements were then used as covariates in a multivariate analysis of covariance (MANCOVA; Sokal and Rohlf 1995) of the ecophysiological parameter estimates of the LRCs (R_d, α, and A_{MAX}). The parameter estimates for leaf dark respiration (R_d) were square root transformed to meet test assumptions of normality and homogeneity of residual variation. Post hoc comparisons between

Table 1. Formulae used for calculation of light response curves. Model selected for each species indicated in bold type.

Model description and formula		Akaike information criterion and r^2 values (means ± SE) by species	
1. Rectangular hyperbola (Thornley 1976; modified, *e.g.*, Marshall and Biscoe, 1980)			
$P = \frac{\alpha I A_{MAX}}{\alpha I + A_{MAX}} - R_d$	*Acer*	−24.94 ± 1.24	0.9930 ± 0.0009
	Asimina	−17.63 ± 1.78	0.9857 ± 0.0019
	Fraxinus	−34.54 ± 1.65	0.9960 ± 0.0007
2. Nonrectangular hyperbola (Thornley 1976; modified, *e.g.,* Marshall and Biscoe, 1980)			
$P = \frac{\alpha I + A_{MAX} - \sqrt{[(\alpha I + A_{MAX})^2 - 4\theta\alpha I A_{MAX}]}}{2\theta} - R_d$	*Acer*	−25.79 ± 1.85	0.9969 ± 0.0005
	Asimina	−18.70 ± 2.94	0.9965 ± 0.0007
	Fraxinus	**−38.35 ± 1.42**	**0.9982 ± 0.0003**
3. Exponential (Thornley 1976; modified, *e.g.*, Iqbal *et al*. 1997)			
$P = \{A_{MAX}[1 - e^{\left(\frac{-\alpha I}{A_{MAX}}\right)}]\} - R_d$	***Acer***	**−31.61 ± 1.32**	**0.9962 ± 0.0005**
	Asimina	**−27.11 ± 2.30**	**0.9944 ± 0.0010**
	Fraxinus	−33.60 ± 1.56	0.9962 ± 0.0005

* P is the photosynthetic rate, I is the light flux density, α is the initial slope of the P:I curve, A_{MAX} is the asymptotic value of P as I→∞, and R_d is the dark respiration rate; θ is a convexity parameter that only appears in the nonrectangular hyperbola.

all species pairs were conducted using multivariate contrasts with Bonferroni correction ($P < 0.05/3 = 0.0166$).

Results. DETERMINING THE BEST FUNCTIONS. On the basis of AIC scores (Table 1), leaf R_d, α, and A_{MAX} were estimated using the exponential model for *As. triloba* and *Ac. saccharum* and the nonrectangular hyperbola for *F. quadrangulata*. All models provided excellent fits to the data ($r^2 > 0.985$; Table 1).

COMPARING PARAMETERS AMONG SPECIES. Ambient light conditions (maximum daily irradiance, 2-wk average) had a mean ± SE of 0.946 ± 0.085 μmol PAR cm^{-2} s^{-1}, indicating very low light levels. One-way ANOVA indicated no significant difference among the species in ambient light conditions ($F_{2,52} = 0.25$, $P = 0.776$). Ambient light conditions and leaf temperature met the test assumptions for covariates with these LRC parameters. The overall MANCOVA results demonstrate significant differences in the LRC parameters of the species tested, along with a significant effect of the covariate light, but not of the covariate temperature (Table 2). Both eigenvectors for species were significant ($F_{6,90} = 5.01$, $P < 0.001$ and $F_{2,46} = 5.30$, $P < 0.01$) and they accounted for 66% and 34% of the variation, respectively. For the species effect, standardized canonical coefficients for R_d, α, and A_{MAX} for the first canonical function (Table 2) indicated that A_{MAX} contributed most to the interspecific differences on the first canonical axis. The same coefficients for the second canonical function (Table 2) indicated that α contributed most to interspecific differences on the second canonical axis. Least-squares mean parameter values, adjusted to common ambient light and temperature conditions (Fig. 1), confirm the large interspecific differences in maximum photosynthetic rate, A_{MAX}, and the initial slope, α. Unexpectedly, the values of dark respiration (R_d) were similar for all three species (Fig. 1). These mean parameter estimates R_d, α, and A_{MAX} (Fig. 1) were used in the exponential or nonrectangular hyperbola equations to generate the LRCs for the three study species (Fig. 2). These curves illustrate the substantial differences in maximum photosynthetic rates (*i.e.*, the asymptotes) and the initial slope of the LRC among species (Fig. 2). In addition, the approximate light saturation points for *F. quadrangulata*, *Ac. saccharum*, and *As. triloba* were 1,000, 300, and 200 μmol PAR m^{-2} s^{-1}, respectively.

Table 2. Multivariate analysis of covariance results (overall model) testing for species difference in ecophysiological parameters of the light response curve (R_d, α, A_{MAX}). Both eigenvectors for species were significant ($F_{6,90} = 5.01$, $P < 0.001$ and $F_{2,46} = 5.30$, $P < 0.01$), accounting for 66% and 34% of the variation among species, respectively. Standardized canonical coefficients for the species effect for R_d, α and A_{MAX} were –0.331, –0.177, and 1.525, respectively, for the first canonical function, and –0.877, 1.372, and 0.831, respectively, for the second canonical function.

	Wilk's Λ	F value	P value
Species	0.5622	$F_{6,90} = 5.01$	< 0.0002
Light	0.4945	$F_{3,45} = 15.33$	< 0.0001
Temperature	0.8702	$F_{3,45} = 2.24$	0.10

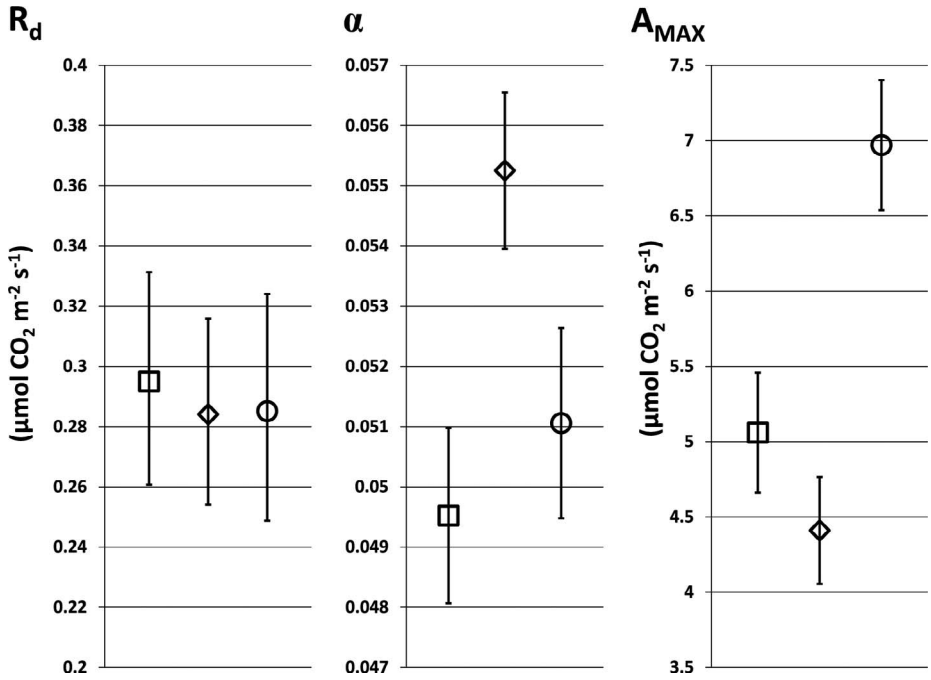

FIG. 1. Light response curve parameters—dark respiration rate (R_d, back transformed), initial slope of the light response curve (α), and maximum photosynthetic rate (A_{MAX})—of *Acer saccharum* (□, $n = 19$), *Asimina triloba* (◇, $n = 19$), and *Fraxinus quadrangulata* (○, $n = 17$) leaves. Values (means ± SE) represent leaf parameters after adjustment to common ambient light conditions and leaf temperatures resulting from multivariate analysis of covariance.

Multivariate linear contrasts of LRC parameters were significant between all species (Table 3). For the contrast between *Ac. saccharum* and *As. triloba* (Table 3), the standardized canonical coefficients indicate that α made the greatest contribution to the difference between these species (Fig. 1), with a lesser contribution from R_d, which was negatively correlated with α for this species pair. In contrast, for both *Ac. saccharum* and *As. triloba* comparisons with *F. quadrangulata*, A_{MAX} was the variable with the largest standardized canonical coefficient (Table 3, Fig. 1). For the *As. triloba* and *F. quadrangulata* contrast, standardized canonical coefficients indicated that α and R_d were relatively minor contributors negatively correlated with A_{MAX} for this species pair (Table 3, Fig. 1). The *Ac. saccharum* and *F. quadrangulata* contrast differed from the *As. triloba* and *F. quadrangulata* comparison in that the standardized canonical coefficients indicated that α was positively correlated with A_{MAX} and R_d was negatively correlated with both of these variables across this species pair, with both α and R_d making some contribution to the multivariate difference between this species pair (Table 3, Fig. 1).

Rainfall and temperature for 2009 were unlikely to have resulted in unusual conditions affecting

Table 3. Multivariate pairwise contrasts among species.

	Asimina vs. Acer	*Asimina vs. Fraxinus*	*Acer vs. Fraxinus*
P value	$P = 0.015$	$P < 0.001$	$P < 0.01$
F-test from Wilk's Λ	$F_{3,45} = 3.89$	$F_{3,45} = 6.68$	$F_{3,45} = 4.79$
Wilk's Λ	0.7941	0.6919	0.7579
Eigenvalue	0.2593	0.4452	0.3194
Standard canonical coefficients			
R_d (square root transformed)	−0.6113	−0.3491	−0.8229
α	1.2887	−0.1494	0.7588
A_{MAX}	−0.0008	1.5413	1.6986

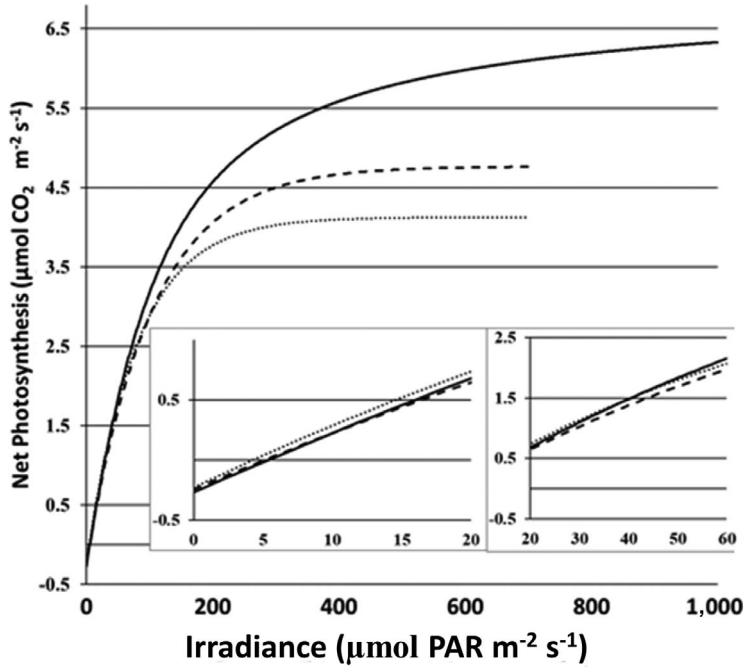

FIG. 2. Projected light response curves of *Asimina triloba* (dotted line), *Acer saccharum* (dashed line), and *Fraxinus quadrangulata* (solid line), adjusted to common ambient light conditions and leaf temperatures. Light response curves were generated by inputting species' mean parameter values (R_d, α, A_{MAX}; Fig. 1) into the exponential or nonrectangular hyperbola equation used to generate them. The species' mean value of θ (0.501, SE $\pm$ 0.002), a dimensionless constant that ascribes the convexity of the curve for the nonrectangular hyperbola, was used for *F. quadrangulata*.

photosynthesis. Mean monthly temperatures in 2009 for May, June, July, and August were 16.3, 21.7, 20.4, and 20.9 °C, respectively, compared with 30-yr average temperatures for the same months of 16.7, 22.1, 23.8, and 22.7 °C, respectively. Mean rainfall for the 4 months was summed for analysis. Total rainfall for May through August 2009 was 47.8 cm compared with the 30-yr average of 43.0 cm. All monthly and seasonal data were normally distributed on the basis of the Shapiro–Wilk W statistic. *t* tests reported that 2009 temperature for May, June, and August did not significantly differ from the long-term trend ($t = 0.24$, $P = 0.51$; $t = 0.38$, $P = 0.71$; $t = 1.18$, $P = 0.24$, respectively). July temperatures were significantly cooler than the long-term trend ($t = 2.33$, $P = 0.02$). Summer rainfall was greater than the long-term average, but not significantly different. ($t = -0.39$, $P = 0.70$).

Discussion. IMPLICATIONS OF TARGETED SPECIES LIGHT RESPONSE CHARACTERISTICS. Our results show that there are significant overall differences in photosynthetic properties among the three study species, indicating differences in shade tolerance. The standardized canonical coefficients in the comparisons of *F. quadrangulata* with the other two species indicate that these differences are strongly influenced by the higher maximum photosynthetic rates of *F. quadrangulata* leaves. In addition, data for *F. quadrangulata* were best fit by the nonrectangular hyperbola, whereas the other two species were best fit by the exponential curve. The main difference in these two functional forms is that for the same parameters, the nonrectangular hyperbola rises more slowly and approaches its asymptote gradually compared with the exponential curve, which approaches the asymptote rapidly and flattens more abruptly (see Fig. 2). High values of A_{MAX} and light saturation point indicate that *F. quadrangulata* is adapted to higher light regimes than *Ac. saccharum* and *As. triloba*. These results conform to the observation that *F. quadrangulata* saplings appeared to be present at locations with greater light availability within the study site than the other two species, and to other data suggesting

it is an intermediate shade-tolerant species (Abrams and Kubiske 1990). The status of *F. quadrangulata* as an intermediate shade-tolerant species likely means that it will be restricted to locations with lower canopy closure and higher ambient light.

Fraxinus quadrangulata is a low-use browse species, and its present success in seedling recruitment appears to be largely due to the exclusion of other species by intense deer browsing at this site (Slater and Anderson 2014). Slater and Anderson (2014) report that *F. quadrangulata* was browsed about the same proportion as its presence in this site; however, University of Illinois Extension reports that *Fraxinus* species as a group are not favored by deer (Illinois Extension 1997). Similar results would thus be expected at sites with similar growing conditions and high deer densities.

In comparison, *As. triloba* possesses gas exchange properties (A_{MAX} and R_d) similar to those of *Ac. saccharum*, which is considered to be a highly shade-tolerant species. Furthermore, the higher α values (Fig. 1) of *As. triloba*, which were the principal factor in contributing to statistically significant differences between the LRC parameters of these two species, suggest that it is even more shade tolerant than *Ac. saccharum*. A steeper initial slope of the LRC would confer an advantage to *As. triloba* in dark, closed-canopy situations, as carbon gain increases rapidly with small increases at intermediate levels of light (Fig. 2), above the light compensation point, but below the light saturation point (Ögren 1993), which are typical within the forest understory (Canham 1988). The absolute difference in the parameter α for these species is small (Fig. 1), but this small difference has a profound impact on photosynthetic performance at low light levels typical of the understory. From irradiance values from 60 to 8 μmol m^{-2} s^{-1}, predicted photosynthetic rates for *As. triloba* are 6% to 59% greater than those of *Ac. saccharum* (see insets for Fig. 2). Thus, at the lowest light levels we expect photosynthetic performance of *As. triloba* to be much better than that of *Ac. saccharum*. It is the combination of these shade-tolerance characteristics and avoidance by deer as a browse species (Slater and Anderson 2014) that are likely causing the large relative increase of this species in Funks Grove. One caveat to this interpretation is that the gas exchange properties assessed in this study are only one component of these species' growth strategies, and further analysis of the influence of these strategies on long-term carbon balances is warranted before making any definitive assessments regarding the status of *As. triloba*'s shade-tolerance characteristics relative to *Ac. saccharum* for several reasons, as follows.

First, it has been suggested that the ability of *Ac. saccharum* to survive in low-light conditions is not necessarily attributable to the carbon gain acquired by its leaves, but rather to the minimization of carbon loss (*i.e.*, low metabolic rates) by all plant structures (leaves, shoots, and roots) during low-light or nighttime periods (Walters and Reich 2000). Therefore, the shade-tolerance properties of *Ac. saccharum* or other plant species may not be adequately summarized by only addressing the characteristic LRC properties of leaf tissues. Our data show that dark respiration rates of leaves of all three species are similar, suggesting similar overall carbon loss rates, at least in leaf tissues. A thorough assessment of shade tolerance will require measurement of carbon exchange rates and a generalized daily carbon budget at the whole-plant level (Givnish 1988; Walters and Reich 2000; Leonardos and Grodzinski 2016).

Second, previous work suggests that the annual patterns of carbon gain for these two species are quite different. *Acer saccharum* seedlings and saplings growing in the forest understory initiate bud break before canopy trees, allowing leaf expansion and photosynthesis to occur before canopy closure (Augspurger *et al*. 2005). Most annual carbon assimilation occurs during this time, whereas the carbon balance is essentially neutral for *Ac. saccharum* trees growing in the understory during the rest of the year (Kwit *et al*. 2010; Lee and Ibáñez 2021). This period of carbon gain before tree canopy closure is apparently critically important for *Ac. saccharum* trees to maintain annual and long-term positive carbon budgets. Augsburger (2008) demonstrated that without this initial deposit, *Ac. saccharum* trees exhibit high rates of mortality. In contrast, *As. triloba* does not exhibit leaf expansion before canopy closure (Augspurger *et al*. 2005); therefore, it must acquire its entire annual carbon budget while growing under the reduced light conditions of the closed-canopy forest understory. *Acer saccharum* and *As. triloba* occupy different photosynthetic niches temporally. Our results indicate that *As. triloba* achieves greater photosynthesis rates in response

to low light than does *Ac. saccharum* and this may contribute to increasing dominance in the understory.

Clonal growth of *As. triloba* allows sharing of resources among ramets. Shaded ramets can receive photosynthate from ramets growing in higher light conditions, which decreases the risk of mortality to individual ramets (Hosaka *et al*. 2005, 2008). Annual variability of carbon acquisition and resource sharing within *As. triloba* colonies further complicate the assessment of carbon budgets and shade-tolerance characteristics of these species because annual carbon budget analysis requires nondestructive sampling of plant tissues in assessing carbon exchange rates. Although the techniques to conduct these types of analyses are still in their infancy (Leonardos and Grodzinski 2016), the methods outlined in this experimental procedure may serve to progress work being done in this field of study.

We do not assume that seedling photosynthetic rates are identical to sapling photosynthetic rates. Forest reproduction is influenced by relative growth rates, which are in turn influenced by many factors, including photosynthetic capacity, climate, presence or absence of masting, seed, seedling and sapling predators and herbivores, diseases, forest structure and tree-fall gaps, fire history, and human utilization of forest resources. This study represents one aspect of tree reproduction and survival relative to shade tolerance.

Greater photosynthetic capacity of *As. triloba* than *Ac. saccharum* in June and July in this study is congruent with results reported by Augsperger *et al*. (2005), who tracked phenology and maximum photosynthetic capacity of *Ac. saccharum* and *As. triloba* individuals 2–4 m tall, comparable with this study. *Acer saccharum* juveniles leafed out about 27 days before 50% canopy closure, whereas *As. triloba* individuals leafed out simultaneously with overstory canopy. Maximum photosynthetic capacity in *Ac. saccharum* occurred at the time of initial leaf expansion (approximately mid-March) and declined after mid-May through the summer. *Asimina triloba* had greatest photosynthetic capacity at leaf-out at a higher rate than *Ac. saccharum*, about mid-May, and remained higher until mid-August. No *Fraxinus* species were included in that study and we have found no other references to photosynthetic rates in *F. quadrangulata*.

Asimina triloba sapling patches form very dense shade that inhibits tree seedling survival under the canopy. Baumer and Runkle (2010) found that tree seedlings of *Ac. saccharum* survived outside *As. triloba* canopy about 1.5 times greater than under the canopy, *Prunus serotina* survived about 3 times greater outside the canopy, and *Fraxinus* sp. survived no differently under or outside *As. triloba* canopy. Graignic *et al*. (2014), in a widespread study of *Ac. saccharum* in forests of eastern Canada, found that *Ac. saccharum* seedling density was positively correlated with basal area of all trees and of *Ac. saccharum* trees. Larger trees produced more seedlings. In addition, *Ac. saccharum* seedlings were negatively associated with *Ac. saccharum* sapling density, presumably because of shading. The presence of *As. triloba* saplings in our study area may be inhibiting *Ac. saccharum* seedling survival by shading. It is probable that *F. quadrangulata* seedlings are less affected by shading, similar to the study of Baumer and Runkle (2010). These effects would be magnified in the presence of deer browsing.

ANALYSIS AND POTENTIAL EXPANSION OF THE EXPERIMENTAL PROTOCOL. Hemispherical photography has been used in conjunction with analysis of leaf photosynthetic properties (*e.g*., Walters and Field 1987; Newell *et al*. 1993; Poorter and Oberbauer 1993; Brooks *et al*. 1996; Valladares *et al*. 1997; Lee and Ibáñez 2021); however, these studies have typically analyzed single measurements and have used hemispherical photography to make categorical generalizations of light conditions. This experiment is unique in that it uses multivariate statistical analysis of leaf photosynthetic traits in conjunction with hemispherical photography to quantify the ambient light conditions to which those leaves are exposed. Because significant results were obtained using this protocol, further development of this system may prove useful in future studies.

The current experimental design was intended to study the difference in photosynthetic light response parameters among the target species. The techniques have been applied to quantify plant carbon balances (Heberling *et al*. 2019a, b; Lee and Ibáñez 2021) relative to phenological escape and the importance of spring avoidance of shade by understory herbs, invasive species, understory life stages of tree species, projected climate change, and other ecological questions. We used hemispherical photography to isolate varied ambient light conditions among leaves as a covariate that, unmeasured, would increase variability in

photosynthetic responses unrelated to intraspecific differences. The combination of LRCs and light availability yields the value of net carbon gain or loss experienced by leaf tissues (Walters and Reich 2000; Kwit *et al*. 2010), and fluctuations in light availability assessed by canopy photograph analysis would be useful in estimating daily carbon budgets. Furthermore, hemispherical photographs and LRC measurements taken over the course of the growing season would account for changes in the forest canopy and leaf physiology, permitting annual carbon budgets to be calculated. Combining these predictions with computer models that simulate plant crown architecture (Pearcy and Yang 1996; Muraoka *et al*. 2003; Pearcy *et al*. 2005; Laurans and Vincent 2016; Leonardos and Grodzinski 2016; Brauner *et al*. 2018; Chianucci 2019; Brüllhardt *et al*. 2020) can yield estimates of carbon gains at the whole-plant level. Such an expanded model applied to our species would provide further insight into the annual carbon balances of plants growing under the forest canopy. This type of analysis would be required before making a final assessment of the shade-tolerance characteristics of *As. triloba* and its ability to compete in the absence of other interactions such as deer browsing. In this study we have demonstrated that analysis of leaf photosynthetic traits using LRCs can distinguish differences among similarly shade-tolerant species. We have demonstrated novel analyses with testing to fit photosynthetic response curves to rectangular hyperbola, nonrectangular hyperbola, and exponential LRC models. We believe this method contributes to analyses of hypotheses regarding growth, survival, and physiological niches within forests.

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Appendix

Mean monthly temperature and total summer precipitation for 30 yr recorded at National Oceanic and Atmospheric Administration weather stations in Normal, IL and Chenoa, IL from 1990 to 2020. Shapiro–Wilk probabilities > 0.05 indicate that data do not significantly depart from normal distribution. t-tests reported that 2009 temperatures for May, June, and August did not differ significantly from the long-term trend ($P > 0.05$ for all 3 months). July temperatures were significantly cooler than the long-term trend ($P = 0.02$). Values for 2009 and 30-yr means are presented in bold type.

	Mean monthly temperature, °C				Total precipitation, cm
Year	May	June	July	August	May through August
1990	15.06	22.83	22.83	22.33	59.99
1991	19.89	24.06	24.06	23.44	27.13
1992	15.72	20.33	20.33	19.44	43.64
1993	16.72	20.50	20.50	22.78	70.41
1994	15.61	23.00	23.00	20.78	25.20
1995	14.56	22.83	22.83	26.61	54.48
1996	15.56	21.61	21.61	23.28	31.19
1997	13.61	21.28	21.28	21.11	33.40
1998	19.56	21.83	21.83	23.56	48.59
1999	17.72	22.44	22.44	21.67	52.65
2000	18.11	20.89	20.89	23.61	44.50
2001	17.89	20.94	20.94	23.72	36.45
2002	14.56	23.28	23.28	23.39	51.03
2003	16.44	20.50	20.50	23.89	45.16
2004	18.83	21.50	21.50	20.33	46.84
2005	16.17	24.39	24.39	23.94	22.28
2006	16.17	21.39	21.39	22.44	40.89
2007	19.17	21.72	21.72	24.83	28.32
2008	13.06	22.39	22.39	20.89	45.09
2010	17.00	22.94	22.94	24.56	47.93
2011	15.33	21.56	21.56	22.94	41.15
2012	19.61	21.83	21.83	22.72	24.89
2013	17.61	21.78	21.78	22.39	34.42
2014	17.11	22.28	22.28	23.06	50.17
2015	17.94	21.78	21.78	22.00	64.29
2016	15.61	23.33	23.33	24.06	59.87
2017	15.06	22.33	22.33	20.44	37.01
2018	21.11	23.22	23.22	23.56	36.09
2019	16.61	21.44	21.44	21.89	53.54
2020	15.78	22.89	22.89	22.11	35.81
2009	**16.28**	**21.67**	**20.40**	**20.89**	**47.88**
Statistics					
30-yr mean	**16.70**	**22.10**	**23.80**	**22.70**	**43.08**
SD	1.90	1.00	1.40	1.50	12.23
$t =$	0.24	0.38	2.33	1.18	-0.39
$P =$	0.81	0.70	0.02	0.24	0.70
$W =$	0.98	0.97	0.97	0.97	0.98
$P =$	0.84	0.64	0.74	0.81	0.85