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Research Article

Physiological responses to light explain competition and facilitation in a tree diversity experiment

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Abstract

1. Ecologists often invoke interspecific facilitation to help explain positive biodiversity–ecosystem function relationships in plant communities, but seldom test how it occurs. One mechanism through which one species may facilitate another is by ameliorating abiotic stress. Physiological experiments show that a chronic excess of light can cause stress that depresses carbon assimilation. If shading by a plant's neighbours reduces light stress enough, it may facilitate that plant's growth. If light is instead most often a limiting factor for photosynthesis, shading may have an adverse, competitive effect.
2. In a temperate tree diversity experiment, we measured stem growth rates and photosynthetic physiology in broadleaf trees across a gradient of light availability imposed by their neighbours. At the extremes, trees experienced nearly full sun (monoculture), or were shaded by nearby fast-growing conifers (shaded biculture).
3. Most species had slower growth rates with larger neighbours, implying a net competitive effect. On the other hand, the two most shade-tolerant species (*Tilia americana* and *Acer negundo*) and the most shade-intolerant one (*Betula papyrifera*) had faster stem growth rates with larger neighbours. The two shade-tolerant species had the greatest increases in photoinhibition (reduced dark-acclimated F_v/F_m) across the gradient of increasing light availability, which suggests they are more vulnerable to chronic light stress. While most species had lower carbon assimilation rates in the shaded biculture treatment, *T. americana* had rates up to 25% higher. *T. americana* also dropped its leaves 3–4 weeks earlier in monocultures, curtailing its growing season.
4. We conclude that although large neighbours can cause light limitation in shade-intolerant species, they can also increase growth through abiotic stress amelioration in shade-tolerant species. Finally, in shade-intolerant *B. papyrifera*, we find a pattern of stem elongation in trees with larger neighbours, which suggests that a shade avoidance response may account for the apparent positive trend in stem volume.
5. *Synthesis*. Both positive and negative species interactions in our experiment can be explained in large part by the photosynthetic responses of trees to the light environment created by their neighbours. We show that photosynthetic physiology can help explain the species interactions that underlie biodiversity–ecosystem function relationships. The insights that ecologists gain by searching for such physiological mechanisms may help us forecast species interactions under environmental change.

KEYWORDS
biodiversity and ecosystem function, facilitation, light competition, photoinhibition, photoprotection, shade tolerance, species interactions, tree diversity

1 | INTRODUCTION

The sun's light powers photosynthesis—the chain of reactions through which plants turn carbon dioxide into the living matter they use to grow and reproduce. A common view in plant ecology is that light is often a limiting resource, such that competition for scarce light can govern the fate of plant species (Braun-Blanquet, 1932; Canham et al., 1994; Dybzinski & Tilman, 2007; Hautier et al., 2009; Monsi & Saeki, 2005). But physiologists have also shown that plants often absorb light beyond their capacity to use it for photosynthesis (Demmig-Adams & Adams, 1992; Long et al., 1994). Beyond an initial linear rise with increasing light, photosynthesis begins to saturate, and additional light contributes little to the plant's carbon gain (Figure 1). Any factor that limits photosynthesis can exacerbate the excess of light, including photosynthetic downregulation and environmental stresses such as water limitation, cold temperatures or nutrient-poor conditions (Demmig-Adams & Adams, 1992; Long et al., 1994).

Light is thus both an essential resource and a potential stressor. A chronic excess of light can cause plant cells lasting oxidative damage, especially to Photosystem II (PSII). Such damage reduces the efficiency of photosynthesis and can be costly to repair, but plants can avoid it using mechanisms of photoprotection (Murchie & Niyogi, 2011). These mechanisms include biochemical pathways that safely dissipate excess light as heat—most notably, the xanthophyll cycle. They also include structural means to avoid absorbing too much light, such as self-shading canopies, reflective leaves or steep leaf angles (Kothari, Cavender-Bares, et al., 2018; Lovelock & Clough, 1992; Streb et al., 1997). In general, plants use such photoprotective mechanisms most under environmental conditions that put them at high risk of damage, including high light (Montgomery et al., 2008) and cold or dry climate (Cavender-Bares, 2007; Ramírez-Valiente et al., 2015; Savage et al., 2009; Wujeska et al., 2013). Under such conditions, plants need strong photoprotection to prevent even more costly damage.

Depending on how well protected a plant is, prolonged exposure to excess light can still cause enough damage to reduce carbon assimilation rates (Murchie & Niyogi, 2011). Consistent with Long et al., (1994), we use the term 'photoinhibition' to describe a drop in carbon assimilation caused by either photodamage or sustained biochemical photoprotection. Bright sunlight causes photoinhibition directly by exposing leaves to more radiation, but it also acts indirectly by altering other microclimatic conditions such as temperature, soil moisture and vapour pressure deficit (VPD; Björkman & Powles, 1984). For example, high VPD can cause stomata to close, which limits the use of light for photosynthesis; without an energetic sink, the resulting excess of light can cause photoinhibition, which limits photosynthetic capacity even further. Alternately, limitation in water or other resources may arrest tissue expansion and cause carbon sink limitation (Tardieu et al., 2014); in response, plants may downregulate photosynthesis and initiate sustained photoprotection (Adams et al., 2013). Such scenarios may be worsened by belowground competition for resources. Because such stresses vary along environmental gradients, photoinhibition and photoprotective strategies could affect the distribution and persistence of plant populations (Külheim et al., 2002).

Given that excess light can cause stress, it may be that one plant species can facilitate another through shading. Whether a plant receives net costs or benefits from its neighbours' shade depends on the balance resulting from (a) the increasing frequency and severity of light limitation and (b) the avoidance of chronic light stress. We can describe these effects in the terms of Monteith et al., (1977), who defined light-use efficiency (LUE) as net photosynthesis divided by the amount of photosynthetically active radiation (PAR) absorbed. Consider a typical light–response curve that plots photosynthesis (*y*-axis) against PAR (*x*-axis; Figure 1). Chronic photoinhibitory stress may change the shape of the curve by lowering LUE, and thus photosynthesis, at any given amount of PAR. By relieving photoinhibition, shading may raise LUE. But shading would also move the *x*-coordinate leftward along the curve such that the leaf will be in the light-limited portion more often. Whether shade helps or harms the plant depends on whether, integrated across time, the gain of avoiding chronic stress exceeds the loss caused by potential light limitation.

The species interactions that result from shading could help to explain the results of experiments that manipulate biodiversity, including tree diversity. Research has shown that biodiversity often promotes ecosystem functions such as productivity (Tilman et al., 2014). In forests, this trend has been shown in both experimental (Grossman et al., 2017; Huang et al., 2018; Potvin & Gotelli, 2008; Tobner et al., 2016; Williams et al., 2017; Zemp et al., 2019) and observational (Gamfeldt et al., 2013; Liang et al., 2016; Oehri et al., 2017) data, across temperate (Grossman et al., 2017; Tobner et al., 2016; Williams et al., 2017), subtropical (Huang et al., 2018) and tropical (Potvin & Gotelli, 2008; Zemp et al., 2019) biomes. These positive relationships are robust to variation in climate, successional stage and other factors (reviewed in Ammer, 2019; Grossman et al., 2018).

One of the potential drivers of positive biodiversity–productivity relationships is interspecific facilitation (Barry et al., 2019; Wright et al., 2017). In biodiversity experiments, patterns of productivity within species or functional groups can sometimes serve as evidence for facilitation (Mulder et al., 2001; Fichtner et al., 2017; Wright et al., 2021), but they cannot tell us the physiological mechanisms that cause one species to facilitate another. Ecologists may need to understand these mechanisms to forecast species interactions and

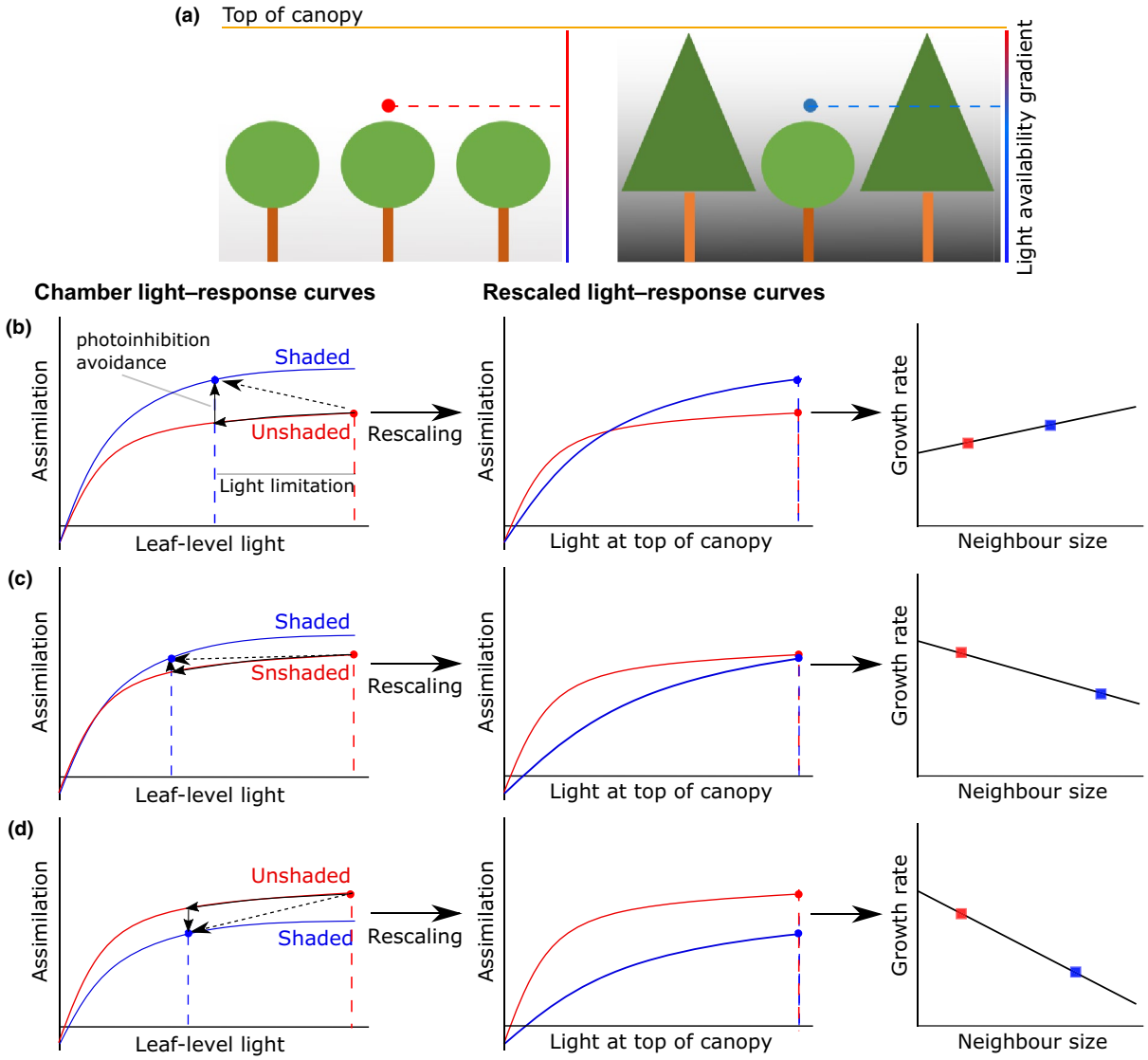

FIGURE 1 (a) Imagine the same slow-growing broadleaf species (round) found in two communities: a monoculture (left) and a biculture (right) with a faster growing conifer (triangular). In the absence of shading by neighbours, all trees would receive the amount of light available at the top of the canopy (yellow line). We define a tree's relative light availability (RLA) as the fraction of this light that the tree's top leaves receive. In monoculture, most broadleaf trees have an RLA close to 1. In shaded biculture, they are shaded by their larger conifer neighbours, so their RLA is much less than 1. These trees may be more likely to suffer from light limitation, but they are also at less risk of photoinhibition. (b) For a single leaf, carbon assimilation tends to increase along a saturating curve as light intensity at the leaf surface increases. Consider two hypothetical photosynthetic light–response curves (left) of leaves from shaded (blue) and unshaded (red) plants. However much light reaches the top of the canopy, the unshaded plant's top leaves receive nearly the full amount (red dashed line) while the shaded plant only receives a corresponding fraction determined by its RLA (blue dashed line). Along a given light–response curve, a reduction in light reduces photosynthesis (represented by the small black arrow along the red curve). But if shading spares the plant from photoinhibition, it can change the shape of the curve such that photosynthesis at any given light level is greater (represented by the small black vertical arrow). The balance (represented by the large dashed arrow) may either increase or reduce carbon assimilation. To compare assimilation rates as a function of light at the top of the canopy, we can rescale the blue light–response curve along the *x*-axis by the inverse of its RLA, making the two dashed lines coincide (middle). In this case, after rescaling, the shaded plant has higher assimilation rates except when there is little light at the top of the canopy. When shaded plants have higher assimilation integrated over time, they may have faster growth, so growth rates increase with larger neighbours (right). In this framework, shading benefits trees most, or harms them least, when light at the top of the canopy is abundant: the risk of photoinhibition is greater, and the proportional cost of a given percentage decline in light is lower. (c) We can imagine another tree species in which photoinhibition has a smaller effect (the shaded and unshaded chamber light–response curves are more similar) and the RLA in the shade is lower (the blue dashed line is at a lower light level) such that shading has greater costs and smaller benefits. Here, rescaling to account for light limitation makes it clear that the shaded plant has lower photosynthesis at any given level of light at the top of the canopy (middle), so plants shaded by large neighbours may have lower growth rates (right). (d) Finally, if the shaded tree has lower carbon assimilation for any given light intensity at the leaf surface, it will be at an even greater disadvantage after accounting for light limitation. Hence, it may grow much more slowly than the unshaded tree

TABLE 1 Characteristics of species in FAB. Except for *Betula papyrifera*, broadleaf species tended to grow slower than needleleaf conifers. Shade tolerance is drawn from Niinemets and Valladares (2006), who evaluated it along a 1–5 scale where higher values indicate an ability to maintain growth under lower light

Scientific name	Species code	Common name	Family	Leaf form	Mean RGR in monoculture, 2013–2016 (year^{-1})	Shade tolerance	Partner in shaded biculture
Acer negundo	ACNE	Box elder	Sapindaceae	Broadleaf	0.039	3.47	None
Acer rubrum	ACRU	Red maple	Sapindaceae	Broadleaf	0.379	3.44	*Pinus banksiana*
Betula papyrifera	BEPA	Paper birch	Betulaceae	Broadleaf	1.272	1.54	*Pinus banksiana*
Juniperus virginiana	JUVI	Eastern redcedar	Cupressaceae	Needleleaf	0.975	1.28	NA
Pinus banksiana	PIBA	Jack pine	Pinaceae	Needleleaf	2.288	1.36	NA
Pinus resinosa	PIRE	Red pine	Pinaceae	Needleleaf	1.619	1.89	NA
Pinus strobus	PIST	White pine	Pinaceae	Needleleaf	1.722	3.21	NA
Quercus alba	QUAL	White oak	Fagaceae	Broadleaf	0.735	2.85	*Pinus strobus*
Quercus ellipsoidalis	QUEL	Northern pin oak	Fagaceae	Broadleaf	0.722	NA	*Pinus strobus*
Quercus macrocarpa	QUMA	Bur oak	Fagaceae	Broadleaf	0.547	2.71	*Betula papyrifera*
Quercus rubra	QURU	Northern red oak	Fagaceae	Broadleaf	0.505	2.75	*Pinus strobus*
Tilia americana	TIAM	American basswood	Tiliaceae	Broadleaf	0.724	3.98	*Pinus strobus*

productivity under environmental change (Barry et al., 2019; Cabal et al., 2021; Wright et al., 2017).

Here, we tested whether the shade created by tree crowns can facilitate the carbon assimilation and growth of neighbouring trees in the Forests and Biodiversity (FAB) experiment at Cedar Creek Ecosystem Science Reserve (East Bethel, MN). We asked the following question: Do some species aid others by shielding them from stress caused by intense sunlight? In particular, we sought to test whether slow-growing, shade-tolerant broadleaf trees might be facilitated by adjacent fast-growing conifers (Table 1). We addressed this question by measuring the physiology and woody growth of broadleaf species across plots that vary in species composition. If certain species do benefit from the shade of their neighbours, we would expect individuals with larger neighbours to have higher growth and carbon assimilation rates. We also posed the hypothesis that trees exposed to high light would use structural and biochemical photoprotective mechanisms more than trees shaded by their neighbours. If true, this finding would imply that trees growing in high light must invest in photoprotection to avoid damage, reinforcing the claim that light stress influences the interactions within these communities.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The FAB experiment was planted in 2013 at Cedar Creek Ecosystem Science Reserve in central Minnesota, USA. Cedar Creek has a continental climate with cold winters and warm summers; the mean annual temperature is about 7°C and the mean annual precipitation is about 660 mm. The site lies on the Anoka Sand Plain, where upland regions tend to have well-drained, sandy soils (Johnston et al., 1996).

FAB comprises 142 4 × 4 m plots, each planted with 64 trees in a 0.5 × 0.5 m grid. The experiment has three blocks, each with 49 plots arranged in a 7 × 7 square. Neighbouring plots within a block share a boundary. Each plot was planted with 1- or 2-year-old seedlings of 1, 2, 5 or 12 species from a pool of 12 species total, including four evergreen conifers with needle-like leaves and eight winter-deciduous angiosperms with broad leaves (Table 1). Except for five-species plots, each distinct species composition is replicated in each block. All species in a plot had nearly equal initial frequency and were placed at random. Grossman et al., (2017) described the experimental design in detail and showed that diversity had positive effects on productivity during the first 3 years. The initial mean relative growth rate in monoculture varied dramatically among species—it was highest in conifers and *Betula papyrifera*, and lowest in *Acer negundo* (Table 1).

2.2 | Tree growth

Within each species, we sought to determine how an individual's stem growth rates were influenced by the size of its neighbours. We assumed that neighbour size affects the focal individual's growth rates, but not vice versa. This assumption of exogeneity was warranted because species varied markedly in their growth rates, so the size of a focal individual's neighbours is explained much more by their species identity than by their interactions with the focal individual.

We surveyed tree growth in late fall of each year. For all living trees, we measured diameter and height to the tallest leader. We measured basal diameter (5 cm from the ground) for trees less than 1.37 m tall and diameter at breast height for trees at least 1.37 m.

For the first year that a tree crossed the threshold, we measured both diameters. To predict a tree's basal diameter when it was not measured, we used species-specific linear relationships ($R^2 = 0.634$–0.784) predicting basal diameter additively from height in the same year and the basal diameter in 2016, which was the last year that the basal diameter of all trees was measured. For the conifer *Pinus banksiana*, basal diameter was measured on few enough trees in 2018 that we could not apply this approach; we instead estimated stem volume under the assumption that relative growth rate (RGR) was the same from 2017 to 2018 as from 2016 to 2017. Because we did not consider *Pinus banksiana* growth as a response variable, this approach avoided circularity and allowed us to get reasonable estimates of size in 2018.

In all other cases, we estimated woody volume as $V = \pi r^2 h$, where h is the height and r is the basal radius. This equation assumes each tree's woody volume can be approximated as a cylinder, an assumption that has been used and justified in other tree diversity studies in the absence of system-specific allometric equations (Tobner et al., 2016; Williams et al., 2017). We then calculated the RGR (per year) between 2016 and 2018 as $(\ln V_{2018} - \ln V_{2016})/2$ (Hoffmann & Poorter, 2002). We chose 2016 as a starting point because no replanting of dead trees occurred after that point. Volume loss could cause RGR to be negative (Mahmoud & Grime, 1974), which often occurred when stems or branches broke, or occasionally when plants lost all above-ground tissue and resprouted the following year.

For each tree, we calculated the average woody volume of its eight neighbours (in cardinal and intercardinal directions) in 2018 as a proxy for the intensity of above-ground interactions. Neighbours were sometimes missing because of mortality or because the focal tree was on the experiment's edge. In such cases, we assigned the neighbour a volume of zero. For each broadleaf species, we tested how individual growth changed as average neighbour size increased using a mixed-effects regression model with plot as a random intercept, implemented in *R v. 3.6.1* (R Core Team, 2019) using package *lme4 v. 1.1.2* (Bates et al., 2015). We calculated the marginal R^2 (R_m^2) of the fixed effect using the method of Nakagawa et al., (2017) as implemented in *MuMIn v. 1.43.17* (Bartoń, 2020), and p values using Satterthwaite's degrees of freedom method as implemented in *lmerTest v. 3.1.2* (Kuznetsova et al., 2017), noting that such values should be interpreted conservatively. We also tested whether any species showed non-monotonic responses to neighbour size using the two-lines test (Simonsohn, 2018) without random effects.

Some species showed a positive response in stem growth to neighbour size. Besides facilitation, such a response could also be caused by shade avoidance, which may lead plants to increase shoot biomass at the expense of root biomass to compete for light (Shipley & Meziane, 2002). We aimed to discern whether such a shade avoidance syndrome could contribute to the positive stem growth response. Lacking root biomass sorted by species, we could not test this idea directly, but we could test another symptom of a typical shade avoidance syndrome: stem elongation, which prioritises vertical growth over lateral growth (Henry & Aarssen, 1999). We considered height and basal diameter in 2016, the last year in which basal diameter was measured directly on all trees. For all species that showed a positive stem growth response, these two variables were linearly correlated. We used mixed-effects linear models with plot as a random intercept to predict diameter from height in each species, then tested whether the residuals—the observed diameters' deviations from the predictions for a tree of equal height—were associated with average neighbour size. If trees with larger neighbours show a shade avoidance syndrome, we would expect them to have smaller diameters for a given height. We obtained similar conclusions when considering the log-transformed diameter-to-height ratio as the response variable rather than the residuals of the linear diameter–height relationship.

2.3 | Photosynthetic physiology

We measured chlorophyll fluorescence and leaf reflectance spectra among all eight broadleaf species, and photosynthetic light–response curves among four focal species (*A. rubrum*, *B. papyrifera*, *Q. ellipsoidalis* and *T. americana*). For physiological measurements, we focused on plots belonging to one of three treatments: (a) relatively open monocultures of broadleaf species ('monoculture'); (b) bicultures comprising one broadleaf and one conifer species ('shaded biculture') and (c) 12-species plots (see Figure S1 for sample images). For each species in each treatment, we measured physiological parameters on six individuals—two in each of three plots. Neither *A. negundo* nor *Q. macrocarpa* was planted with a conifer in any biculture. We used *B. papyrifera* as a shaded biculture partner for *Q. macrocarpa* because it is a fast-growing species and creates shade. We omitted the shaded biculture treatment for *A. negundo*. We performed all leaf-level physiological measurements on fully expanded upper leaves with no visible sign of disease or herbivory. When possible, we chose the same trees within a plot for each kind of measurement so that we could compare these aspects of physiology within individuals.

2.4 | Photosynthetic light–response curves

We measured photosynthetic light–response curves from the four focal species ($n = 72$ total) during July 2018 using an LI-6400 gas exchange system (LI-COR BioSciences, Lincoln, NE, USA) with a 6400-40 Leaf Chamber Fluorometer head. We noted the angle of each leaf relative to horizontal (to the nearest 15°) before beginning measurements. Each curve had nine steps in descending order of brightness: 2,000, 1,500, 1,000, 500, 200, 100, 50, 20 and 0 $\mu mol\ m^{-2}\ s^{-1}$. We also measured the relative electron transport rate (ETR) using chlorophyll fluorescence at each light level. We maintained favourable conditions inside the chamber during each measurement. Following each curve, we removed the leaf to measure leaf mass per area (LMA) using a flatbed scanner and a balance. Further details about light–response curve procedures and ETR calculations are shown in Appendix S1. Finally, we estimated parameters like

the light-saturated carbon assimilation rate (A_{sat}) by fitting a non-rectangular hyperbolic model (Johnson & Thornley, 1984) to each light–response curve using *R* code written by Nick Tomeo, available at: https://github.com/Tomeopaste/AQ_curves.

We aimed to determine how realised carbon assimilation rates vary with the photosynthetic photon flux density (PPFD) at the top of the canopy, a measure of light availability in the absence of shading. While all trees received the same range of light intensities inside the instrument chamber, some trees received much less light than others in situ because their neighbours shaded them more. At any moment, trees that are more shaded are farther to the left on their light–response curve than trees that are less. For example, consider a tree crown whose topmost leaves only receive 50% of the light reaching the top of the canopy. For this tree crown, the realised assimilation rate we estimate at a top of the canopy PPFD of 2,000 μmol photons m^{-2} s^{-1} would be the assimilation rate at a leaf-level PPFD of 1,000 μmol m^{-2} s^{-1}. To visualise the impacts of shading by neighbours, we followed the approach of Howell et al. (2002): we estimated how much light each leaf receives as a constant fraction of light at the top of the canopy, and rescaled each leaf's fitted light–response curve along the *x*-axis by this fraction's reciprocal. We estimated the constant rescaling factor for each individual as $RLA \times \cos(\theta)$, where *RLA* is the relative light availability (see *Light availability*) and θ is the leaf angle from horizontal. (Taking the cosine of θ approximately corrects for the reduction in horizontally projected leaf area in steeply inclined leaves when the sun is directly overhead, as simplified from Ehleringer & Werk, 1986). We used this procedure on each fitted curve to compare across treatments in a way that accounts for the varying fractions of light that trees receive due to differences in relative height and vertical light transmission.

Finally, we used the rescaled light–response curves to estimate carbon assimilation by top leaves throughout July. We used an hourly averaged time series of solar radiation from Carlos Avery Wildlife Management Area in Columbus, MN, 13.6 km away from the study site. Following Udo and Aro (1999), we assumed a conversion rate of 2.08 μmol photons m^{-2} s^{-1} of PAR per Watt m^{-2} of solar radiation. Using these data as inputs to the rescaled light–response curves, we estimated carbon assimilation over the month of July. This procedure assumes that the photosynthetic response to light remains constant and unaffected by factors like leaf temperature and stomatal closure. While this assumption is never quite true, we consider it a useful way of estimating the consequences of realistic fluctuations in light.

We mainly express assimilation per unit of leaf dry mass because we aim to determine the plants' return on the carbon invested in leaf construction. As expected, leaves growing in low light tended to have lower LMA in most species (Figure S2; Poorter et al., 2019; Williams et al., 2020). More carbon is spent on constructing a leaf with high LMA, which means that the leaf has to assimilate more carbon in about the same amount of time to recoup its construction cost. Expressing data on a mass basis accounts for these large differences in construction cost, although we also discuss area-based assimilation rates when they provide additional physiological insight. We also express stomatal conductance (g_s) and electron transport rate (ETR) on a mass basis to compare them with mass-based assimilation rates.

2.5 | Instantaneous chlorophyll fluorescence and spectral reflectance

In all eight broadleaf species, we measured chlorophyll fluorescence parameters using an FMS2 pulse-modulated fluorometer (Hansatech Instruments Ltd., Norfolk, UK) over 2 days in late July 2018 (n = 138 total). We measured dark- and light-acclimated parameters at the same spot on the same leaves. We attached opaque clips to leaves in the evening before measuring dark-acclimated F_v/F_m within 2 hr after sunrise. This parameter describes the maximum quantum yield of PSII and is a general index of photoinhibition (Murchie & Lawson, 2013). We then took light-acclimated measurements between 12:00 and 14:00 h each day. The protocol involved the following steps: actinic light at 1,000 μmol m^{-2} s^{-1} for 15 s, a saturating pulse and 2 s of far-red light. We exposed all leaves to the same actinic light because we aimed to assess photoprotective capacity under comparable light conditions, even though each tree had a different light environment.

From these data, we estimated qN, a parameter that indicates how much a plant relies on photoprotective dissipation (non-photochemical quenching) under the imposed actinic light. This parameter is correlated with the de-epoxidation state of xanthophyll cycle pigments (Cavender-Bares & Bazzaz, 2004; Watling et al., 1997). Following Kramer et al., (2004), we also calculated the quantum yields ϕ_{PSII}, ϕ_{NPQ} and ϕ_{NO}, which sum to 1. These three parameters are the proportions of light energy dissipated by photosynthetic chemistry, non-photochemical quenching and non-regulated dissipation. The last is a crucial parameter because it represents light that a plant cannot dissipate safely; this portion of the absorbed light may contribute to photodamage. Appendix S1 contains formulas for all parameters and justifications for our choices in data analysis (Supplemental Materials).

On separate leaves of the same trees, we measured reflectance spectra (350–2500 nm) using a PSR+ 3,500 field spectroradiometer (Spectral Evolution, Lawrence, MA, USA). We used these spectra to calculate the photochemical reflectance index (PRI), calculated as $PRI = (R_{531} - R_{570})/(R_{531} + R_{570})$, where R_n is the reflectance at a wavelength of n nm. PRI shows a negative correlation with carotenoid : chlorophyll ratios and, over shorter time-scales, also tracks the xanthophyll de-epoxidation state (Gamon et al., 1992; Gitelson et al., 2017; Wong & Gamon, 2015). We estimated species-specific linear responses of PRI and chlorophyll fluorescence parameters to RLA (see *Light availability*).

To understand how photoinhibition and photoprotective strategies vary with adaptations to shade, we used shade tolerance values that Niinemets and Valladares (2006) compiled on a five-point scale. Higher values along this scale indicate that plants are able to grow in lower light conditions.

2.6 | Phenology

We monitored the timing of leaf abscission for *T. americana* in monoculture and shaded biculture plots to assess whether shade could delay senescence and abscission, extending the period for carbon gain (Cavender-Bares et al., 2000). In early August, we surveyed 120 T. *americana* trees (60 in monoculture, 60 in shaded biculture) to determine the proportion of leaves that had fallen based on how many of the top five axillary buds lacked a leaf. From each of these trees, we marked a single leaf and returned every 1–2 weeks to monitor its senescence. We assessed each leaf on a binary basis (senesced or not) based on whether it had at least 50% remaining green leaf area. We chose this criterion as a simple proxy for the continuous scale used by Cavender-Bares et al. (2000). Based on the initial survey and the repeated surveys of marked leaves, we tracked the proportion of leaves that had senesced over time. To check whether leaves were photosynthetically active until near the point of senescence, we collected a one-time measurement of dark-acclimated F_v/F_m in mid-September among remaining leaves.

We also performed a one-time measurement of 60 (30 per treatment) *A. rubrum* plants on October 1, using the same protocol we used to do our initial early August survey of *T. americana*. We intended this survey to help test whether our results hold across species.

2.7 | Light availability

On a cloudy day with diffuse light conditions, we measured the available light above each tree selected for this study ($n = 138$) using an AccuPAR LP-80 ceptometer (METER Group, Pullman, WA, USA). We took the mean of two PAR measurements directly above the topmost leaf of each tree and the mean of two to four measurements in the open. By calculating a ratio of these values, we could estimate the fraction of light transmitted to the top of each tree. We called this value *relative light availability*. This value usually correlates well with the percentage of light a tree can access over much longer time-scales (Parent & Messier, 1996).

2.8 | Additional measurements

We also measured other plant- and microclimate-related factors for insight into the potential role of excess light and other abiotic stressors. Full methods and results for these measurements are presented in Appendix S2, but here we lay them out in brief. In each focal species except *B. papyrifera*, we measured the angles of top leaves in monoculture and shaded biculture plots to assess how plants use structural photoprotection across light environments. We measured pre-dawn water potential for all eight broadleaf species and midday water potential for the four focal species to test how the treatments affect water stress. Finally, we collected some microclimatic data on air temperature and soil moisture to better describe the environmental conditions across treatments.

3 | RESULTS

3.1 | Tree growth

Species varied in their relationship between neighbour stem volume and focal individual relative growth rate (RGR; mixed-effects ANCOVA, neighbour volume × species interaction; $p < 10^{-15}$; $F_{11,7680} = 14.988$). For individual species, relationships between RGR and neighbour volume were noisy but often highly significant (Figure 2). In most species, individuals with larger neighbours had lower RGR, including in *A. rubrum* ($R_m^2 = 0.027$, $p < 0.005$, $t(366) = -3.257$), *Q. alba* ($R_m^2 = 0.030$, $p < 10^{-4}$, $t(486) = -3.932$), *Q. ellipsoidalis* ($R_m^2 = 0.051$, $p < 10^{-7}$, $t(341) = -5.485$), *Q. macrocarpa* ($R_m^2 = 0.006$, $p = 0.0380$, $t(697) = -2.079$) and *Q. rubra* ($R_m^2 = 0.053$, $p < 10^{-7}$, $t(444) = -5.785$). But *B. papyrifera* had a weakly positive response to neighbour size ($R_m^2 = 0.010$, $p = 0.049$, $t(124) = 1.993$), and two more species grew faster with larger neighbours, but only when average neighbour size was log-transformed: *A. negundo* ($R_m^2 = 0.014$, $p = 0.019$, $t(380) = 2.361$) and *T. americana* ($R_m^2 = 0.018$, $p < 0.005$, $t(405) = 3.073$). These results were qualitatively unchanged by removing trees on a block edge or including focal plant volume in 2016 as a covariate, although the effect of neighbour size in *B. papyrifera* or *Q. macrocarpa* sometimes became statistically insignificant under these alternate model specifications (Appendix S3). No species had a non-monotonic response to neighbour size.

Trees that died between 2016 and 2018 dropped out of our individual-level analyses of RGR because their stem volume was 0 in 2018, making it impossible to calculate RGR. To see whether mortality could alter our conclusions, we also performed statistical analyses on absolute change in stem volume from 2017 to 2018, in which we alternately (a) treated mortality as a decline in volume to 0, or (b) removed trees that died from analyses. The rate of mortality was low between 2016 and 2018 (~7.5%), and accounting for mortality made little qualitative difference when considering absolute growth rate as the response variable (Figure S3). In general, trends in the absolute growth rate across the gradient of neighbour size mirrored those in the relative growth rate (Figure S3; Appendix S3).

We also aggregated these observations to the plot scale by considering the RGR of summed stem volume of each species in each plot from 2016 to 2018 (Figure 2). (This approach is distinct from an average of individual RGRs, which would assign equal weight to small and large individuals.) Although aggregation left less statistical power to detect relationships, it also reduced noise, so the relationships we did find explained much more of the variation in growth across plots. As average neighbour size increased, plot RGR declined in *Q. alba* ($R^2 = 0.297$, $p < 0.005$, $t(28) = -3.642$) and *Q. macrocarpa*

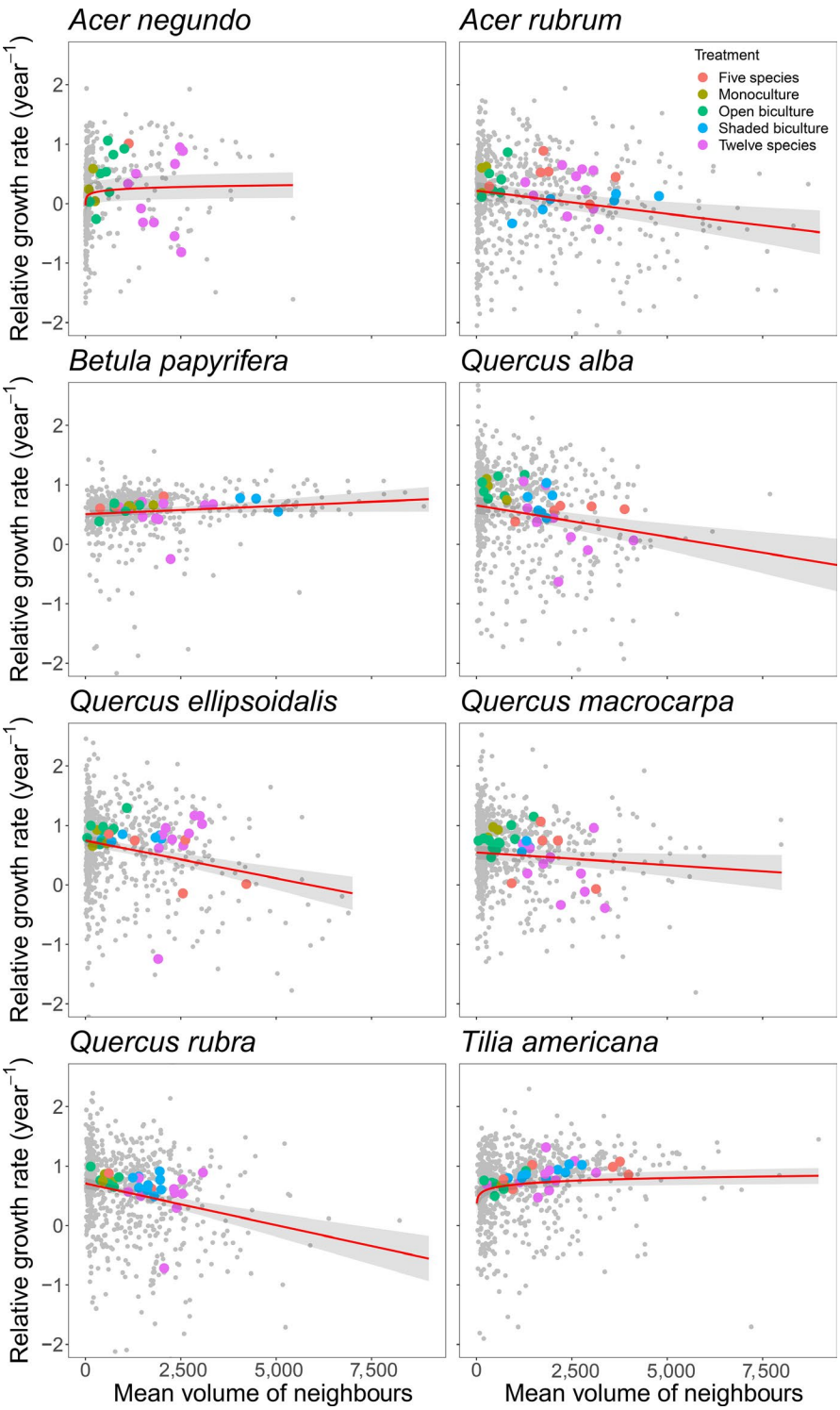

FIGURE 2 Relative growth rate (RGR) of woody stem volume in individuals of each species between fall 2016 and 2018 as a function of the average stem volume of all neighbours. Grey dots represent individuals, and the regression is fit based on a mixed-effects model with plot as a random intercept. For *Tilia americana* and *Acer negundo*, the relationship with neighbour volume is modelled as logarithmic rather than linear. The large coloured dots aggregate data to the plot scale, as described in the main text, and are colour coded by treatment. A shaded biculture is a plot where the focal broadleaf species grows with either a conifer or *Betula papyrifera* (unless *B. papyrifera* is the focal broadleaf species). An open biculture is a plot where the focal broadleaf grows with a broadleaf species other than *B. papyrifera*. About 1.1% of trees fall outside the plot bounds

($R^2 = 0.265$, $p < 0.005$, $t(31) = -3.540$), but increased in *T. americana* ($R^2 = 0.312$, $p < 0.001$, $t(32) = 3.995$).

Finally, for the three species that showed positive individual-level stem growth responses to neighbour size (*T. americana*, *A. negundo* and *B. papyrifera*), we performed a follow-up analysis to test whether they showed a shade avoidance response. We found that trees with larger neighbours had smaller diameters than expected based on their height in *B. papyrifera* ($R^2 = 0.009$, $p = 0.008$, $t(795) = -2.645$), but not *T. americana* and *A. negundo* ($p > 0.05$).

3.2 | Photosynthetic physiology

3.2.1 | Photosynthetic light–response curves

As a function of the chamber light level, mass-based assimilation rates were higher in shaded biculture and 12-species treatments than in monoculture in three out of the four focal species (*Q. ellipsoidalis*, *A. rubrum* and *T. americana*; Figure 3, left). In *B. papyrifera*, mass-based assimilation rates in shaded biculture were lower than

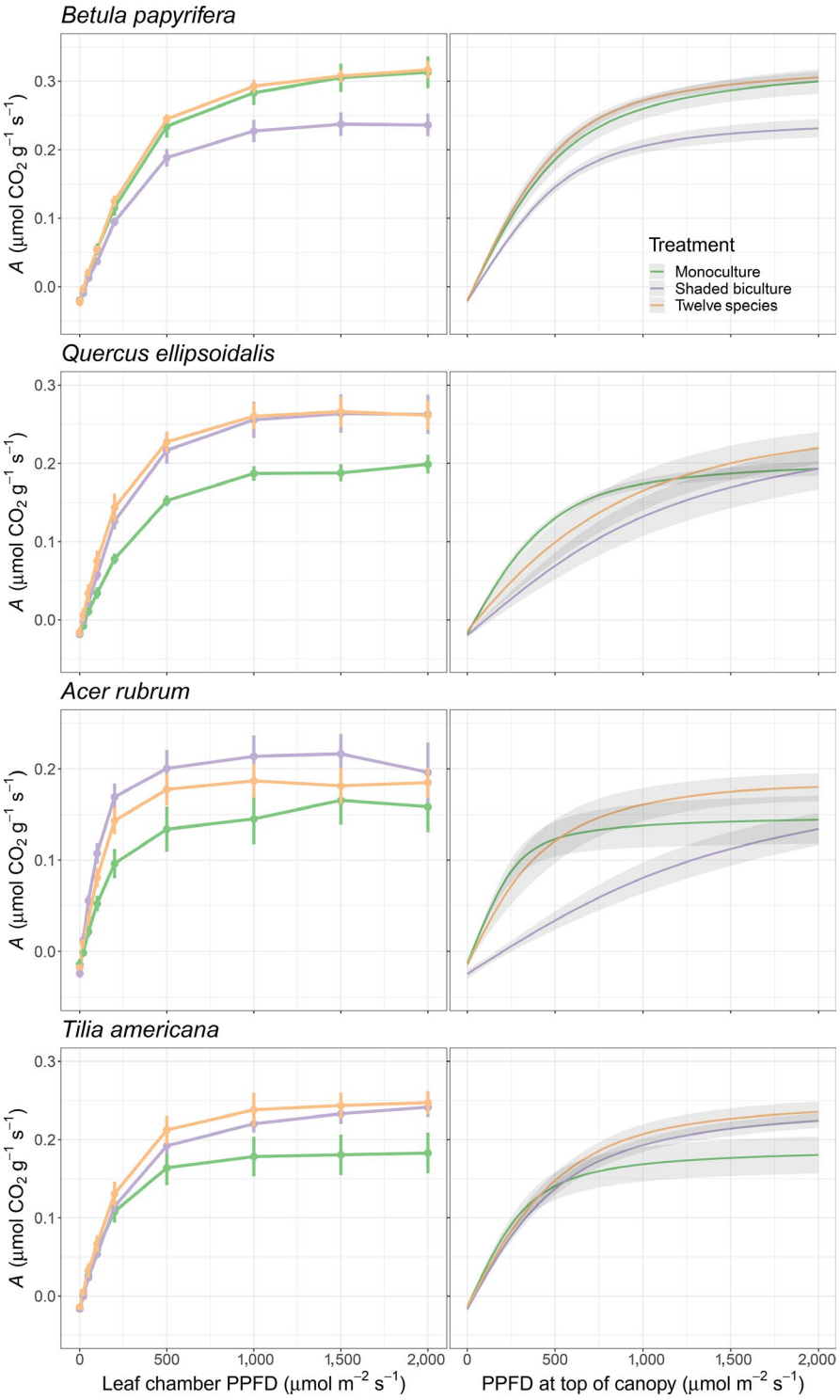

FIGURE 3 Mass-based photosynthetic light–response curves for four broadleaf species. The left panels depict carbon assimilation rates as a function of light intensity in the chamber; the right panels present estimates of realised carbon assimilation rates as a function of light intensity at the top of the canopy. These rates are lower because of shading by neighbours (as in Figure 1, middle column). Species are arranged from the least shade-tolerant (*Betula papyrifera*) to the most (*Tilia americana*). Error bars in left panels and grey ribbons in right panels are ±1 *SE*

in the other two treatments. Area-based assimilation rates showed similar trends in *T. americana*, but varied less among treatments in *B. papyrifera* and *Q. ellipsoidalis*—and in *A. rubrum*, they were lower in shaded biculture than the other treatments (Figure S4) because LMA was much lower in shaded biculture (Figure S2).

In all broadleaf species except *B. papyrifera* and *T. americana*, LMA was higher in monoculture than the other two treatments (Figure S2). Across the four focal species, the light-saturated assimilation rate A_{sat} on an area basis was positively correlated with LMA ($R^2 = 0.431$; $p < 10^{-9}$; $t(69) = 7.349$; Figure S5). Within species, there was no correlation in *B. papyrifera* and *A. rubrum*, but a positive correlation in *Q. ellipsoidalis* ($R^2 = 0.192$; $p = 0.039$; $t(16) = 2.243$) and *T. americana* ($R^2 = 0.436$; $p = 0.002$; $t(16) = 3.759$). In *T. americana*, the intercept was statistically indistinguishable from zero, making the relationship between area-based A_{sat} and LMA close to a direct proportionality.

The rate of photosynthesis is often limited either by ETR or by the RuBP carboxylation rate; the latter may, in turn, be limited by

stomatal diffusion of CO_2 (Farquhar et al., 1980). In our data, both ETR and stomatal conductance (g_s) increased with light availability (Figure S5). (ETR tended to decline at very high light levels, especially in shaded treatments, perhaps because of acute photoinhibition.) Within each species, the rank order of treatments in carbon assimilation rates, ETR, and g_s were broadly congruent. One exception is that *T. americana* in shaded biculture had much higher g_s than in 12-species or monoculture plots, despite having slightly lower assimilation rates than in 12-species plots.

Compared to the unscaled chamber light–response curves, the picture that emerged from rescaled light–response curves was more complex (Figure 3, right). In *B. papyrifera*, the assimilation rate was still lowest across light levels in the shaded biculture treatment. In late-successional *T. americana*, the assimilation rate was higher in shaded biculture and 12-species treatments by up to 25% compared to monoculture across most light levels. In the other two species, the mass-based assimilation rate was highest in monoculture at low light, but 12-species and (in *Q. ellipsoidalis*) shaded biculture plots intersected and surpassed monocultures when enough light was available. *A. rubrum* and *Q. ellipsoidalis* grew less and had lower light availability in shaded bicultures than *T. americana* (Figure S2), so their mass-based assimilation rates dropped considerably more due to rescaling. The area-based assimilation rate in these two species was lower in shaded bicultures (and in *Q. ellipsoidalis*, 12-species plots) than in monocultures across the full domain of light availability (Figure S4), but otherwise, mass-based and area-based rates showed similar patterns across treatments within species.

Using a time series of solar radiation, we estimated total mass-based assimilation rates in July 2018 based on each rescaled light–response curve (Figure S6). We found that trees would have lower total assimilation in shaded biculture than in monoculture in *A. rubrum* (ANOVA; $p = 0.009$; $F_{2,14} = 6.759$) and *B. papyrifera* ($p = 0.002$; $F_{2,15} = 10.267$). In both species, Tukey's HSD test showed that trees in 12-species plots did not significantly differ from those in monoculture. There were no significant differences among treatments in *T. americana* ($p = 0.359$; $F_{2,15} = 1.099$) or *Q. ellipsoidalis* ($p = 0.294$; $F_{2,15} = 1.330$), although the mean assimilation in shaded biculture was higher than monoculture by 10.0% in the former and lower by 30.0% in the latter. Considering area-based assimilation, we see similar results, except that there were no significant differences in *B. papyrifera* ($p = 0.089$; $F_{2,15} = 2.852$), only in *A. rubrum* ($p = 0.001$; $F_{2,14} = 11.556$).

3.2.2 | Instantaneous chlorophyll fluorescence and spectral reflectance

Among all eight species except *B. papyrifera*, dark-acclimated F_v/F_m declined as RLA increased (Figure 4). Extracting the species-specific slopes of this relationship, we found that species with high shade tolerance (as quantified by Niinemets & Valladares, 2006) had the greatest decline in F_v/F_m (Figure 5; $R^2 = 0.601$; $p = 0.025$; $t(5) = -3.167$). In most species, non-photochemical quenching (qN) rose with RLA, but in shade-tolerant *T. americana* and *A. negundo*, qN was nearly constant across light environments (Figure 4). Consequently, we found that shade-tolerant species also had smaller rises in qN with RLA (Figure 5; $R^2 = 0.619$; $p = 0.022$; $t(5) = -3.276$). PRI declined as RLA increased, with statistically indistinguishable slopes among species (Figure 4).

To explain the causes of variation in photoinhibition, we considered ϕ_{PSII}, ϕ_{NPQ} and ϕ_{NO}—the quantum yields of PSII photochemistry, non-photochemical quenching and non-regulated

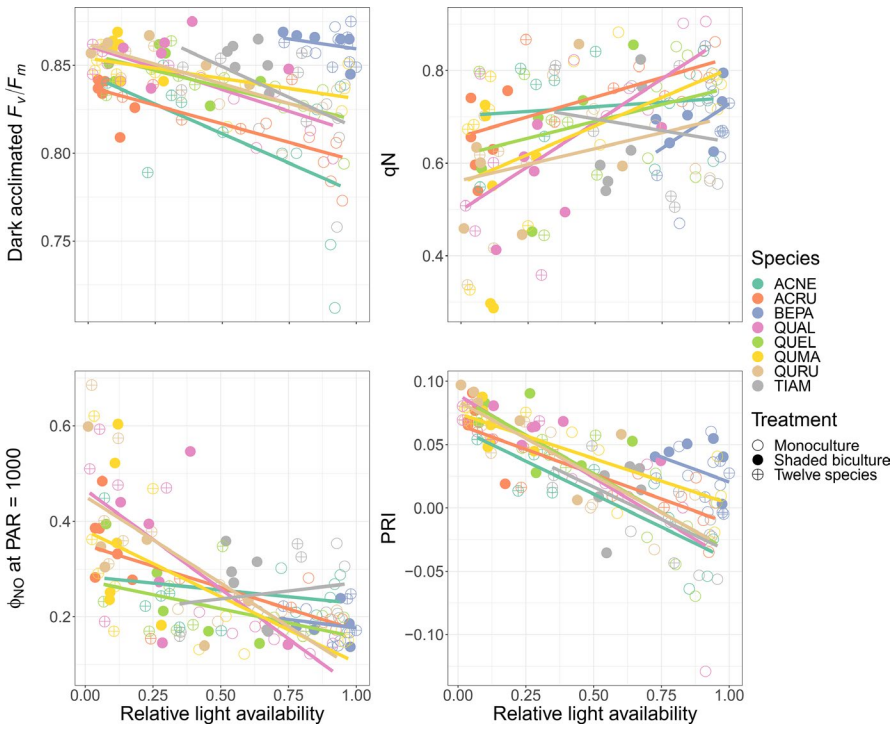

FIGURE 4 Chlorophyll fluorescence parameters and the photochemical reflectance index (PRI) as a function of relative light availability across species and treatments. Best-fit lines come from species-specific OLS regressions. Dark-acclimated F_v/F_m is the maximal quantum efficiency of PSII photochemistry and declines as a plant becomes more photoinhibited. qN describes a plant's capacity to use non-photochemical quenching to dissipate energy. ϕ_{NO} represents the proportion of light dissipated in an unregulated way, which may contribute to photodamage. PRI correlates negatively with carotenoid:chlorophyll ratios

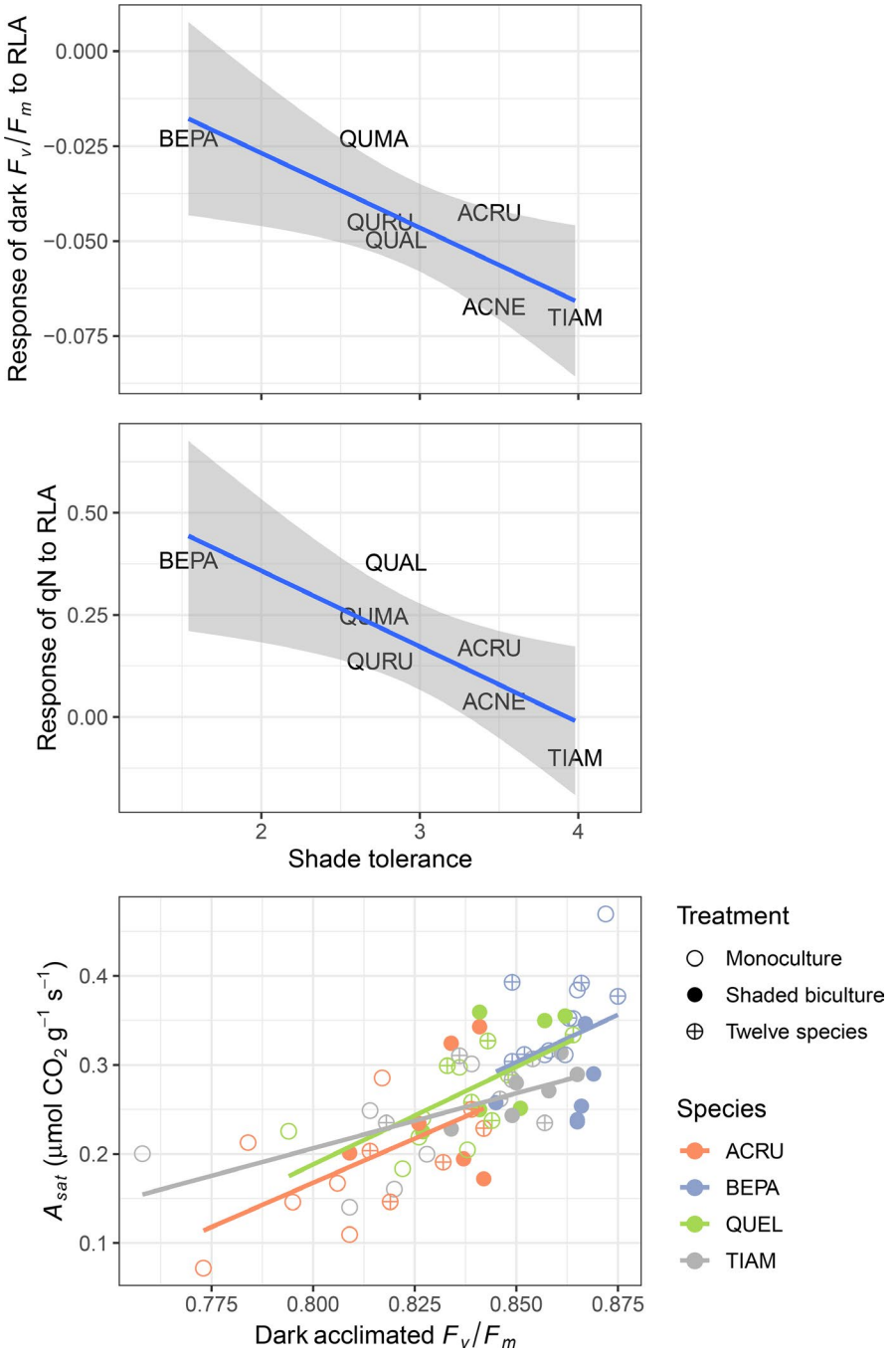

FIGURE 5 Compared to shade-intolerant species, shade-tolerant species show greater declines in dark-acclimated F_v/F_m (top) and smaller increases in qN (middle) as light availability increases. A_{sat} derived from light–response curves correlates positively and strongly with dark-acclimated F_v/F_m; slopes are statistically indistinguishable among species (bottom). Species codes are found in Table 1

dissipation. In most species, ϕ_{NO} decreased with light in the growth environment (Figure 4)—for trees growing in the open (RLA ≈ 1), the sum $\phi_{PSII} + \phi_{NPQ}$ at 1,000 µmol photons m^{-2} s^{-1} was usually above 0.8, keeping ϕ_{NO} close to the oft-cited theoretical minimum of ~0.17 (Björkman & Demmig, 1987; Figure S7). But in *T. americana* and *A. negundo*, ϕ_{NO} was nearly equal across the gradient of light availability.

To illustrate how photoinhibition affected photosynthetic function, we examined the relationship between dark-acclimated F_v/F_m and A_{sat}. Among the four focal species, dark-acclimated F_v/F_m was positively correlated with mass-based A_{sat} (OLS regression; $R^2 = 0.493$; $p < 10^{-11}$; $t(69) = 8.304$; Figure 5), and slopes were not significantly different among species (ANCOVA, species × dark-acclimated F_v/F_m interaction; $p = 0.658$; $F_{3,63} = 0.539$). The same overall relationship held when A_{sat} is expressed on an area basis ($R^2 = 0.447$; $p < 10^{-9}$; $t(69) = 7.588$), although within species, *A. rubrum* and *B. papyrifera* had no significant relationship.

Since photoinhibition and leaf plasticity (in particular, LMA) both influenced assimilation rates, one way to disentangle their roles is to consider the residuals of the species-specific relationships between area-based A_{sat} and LMA. These residuals quantify how much larger or smaller A_{sat} is than predicted based on LMA alone for a given species. Dark-acclimated F_v/F_m had a positive correlation with these residuals in *T. americana* ($R^2 = 0.368$;

$p = 0.004$; $t(16) = 3.304$) and *Q. ellipsoidalis* ($R^2 = 0.351$; $p = 0.006$; $t(16) = 3.189$). These relationships predict that a rise of 0.01 in dark-acclimated F_v/F_m would cause a rise in carbon assimilation of 0.85 μmol m^{-2} s^{-1} or 0.0124 μmol g^{-1} s^{-1} in *T. americana*, and 1.41 μmol m^{-2} s^{-1} or 0.0160 μmol g^{-1} s^{-1} in *Q. ellipsoidalis*. Based on the mean dark-acclimated F_v/F_m in *T. americana* in shaded bicultures (0.853) and monocultures (0.811), we estimate that the alleviation of photoinhibition increased mass-based A_{sat} in shaded bicultures by 0.0516 μmol g^{-1} s^{-1}, which accounts for 82.6% of the difference in mean A_{sat} between these two treatments. The equivalent figure in *Q. ellipsoidalis* is 0.0363 μmol g^{-1} s^{-1}, which accounts for 51.8% of the difference in A_{sat}.

We found no relationship between the residuals of the A_{sat}-LMA relationship and dark-acclimated F_v/F_m in *B. papyrifera* or in *A. rubrum*, although in *A. rubrum* alone, dark F_v/F_m showed a strong negative correlation with LMA ($R^2 = 0.460$; $p = 0.002$; $t(15) = -3.826$). This multicollinearity makes it hard to estimate the true contribution of either variable to area-based A_{sat}, and leaves open the possibility that a potential positive effect of LMA on A_{sat} is offset by photoinhibition as light availability increases.

3.3 | Phenology

In *T. americana*, leaf abscission in monoculture began in early August, and more than half of all leaves had senesced by September 3 (Figure 6). In shaded bicultures, more than 90% of leaves remained by September 3, and no survey found greater than 50% senescence until October 1. We assigned the senescence date of each leaf as the date of the first survey by which it had senesced; using this response variable, leaves in monoculture senesced 22 days earlier than those in shaded bicultures (*t* test; $p < 10^{-11}$; $t(116) = 7.822$). In mid-September, dark-acclimated F_v/F_m averaged 0.745 among remaining leaves in shaded biculture, but only 0.642 in monoculture (*t* test; $p = 0.061$; $t(33) = 1.936$).

Our one-time measurement of *A. rubrum* leaves in early October confirmed that this pattern is not limited to *T. americana*. *A. rubrum* trees in shaded biculture plots retained about 56% of their leaves, while those in monoculture retained only 10% (*t* test; $p < 10^{-4}$; $t(44) = -4.486$).

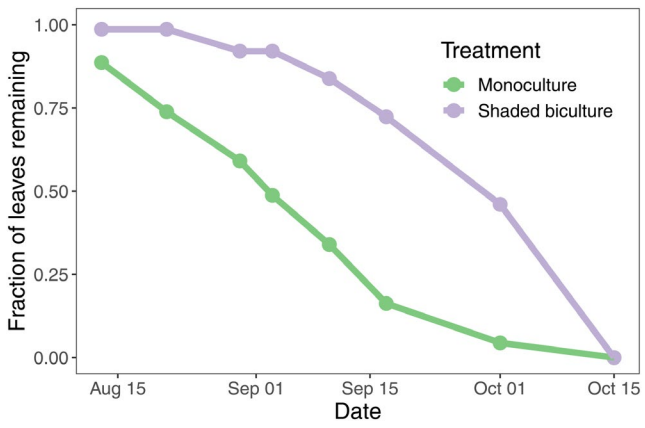

FIGURE 6 In *Tilia americana*, fall leaf abscission occurs later in monoculture than in shaded biculture

4 | DISCUSSION

We investigated how species interactions in a tree diversity experiment might emerge from the physiological responses of trees to the light environment created by their neighbours. We found that as neighbour size increased, five broadleaf species (*A. rubrum*, *Q. alba*, *Q. ellipsoidalis*, *Q. macrocarpa* and *Q. rubra*) had slower stem growth on average while the remaining three (*A. negundo*, *T. americana* and *B. papyrifera*) had faster stem growth. The five species with declining stem growth responses to neighbour size were shade-intolerant, resistant to photoinhibition in high light and tended to have lower carbon assimilation in shaded bicultures. Two of the three species with increasing responses were shade-tolerant and susceptible to photoinhibition. The divergent responses of these two groups of species seem driven in part by their tolerance to excess light. The one remaining species, *B. papyrifera*, had a positive response to neighbour size despite lower photosynthetic rates. Here, we interpret these patterns further.

4.1 | Competition and shade-intolerant species

Individuals of all four *Quercus* species and *A. rubrum* had lower stem growth when surrounded by larger neighbours (Figure 2). Although the individual-level effects were noisy ($R^2 = 0.006$–0.053), they revealed strong tendencies in average stem growth across the full range of neighbour size. For example, in *Q. rubra*, which had the strongest negative response to neighbour size, the median stem grew 32 cm^3 (25–75th percentile: 3.9–124 cm^3) in monoculture between 2017 and 2018, but only 12 cm^3 (−5.2 to 89 cm^3) in shaded biculture with *P. strobus*. This pattern implies that neighbourhood interactions were dominated by competition, potentially both above- and below-ground—and indeed, soil moisture was lowest in shaded bicultures, suggesting a role for below-ground competition (Appendix S2).

The physiological data can help us make sense of these growth patterns. We measured light–response curves of two species in this group: *A. rubrum* and *Q. ellipsoidalis*. In the untransformed chamber light–response curves, both had lower mass-based assimilation rates in monoculture than in the other two treatments (Figure 3, left). On an area basis, *A. rubrum* had its lowest assimilation rates in the shaded biculture treatment, and *Q. ellipsoidalis* was similar across all three treatments. The discrepancy between area- and mass-based results was explained by higher LMA in monocultures (Figure S2). Because chamber light–response curves do not account for the light-limiting effects of shade, it may appear as if shading increased mass-based carbon assimilation in these two species.

Multiple structural and physiological factors help explain variation in chamber light–response curves across treatments among all four focal species. *Q. ellipsoidalis* and *T. americana* had positive

relationships between LMA and area-based A_{sat} (Figure S6), which may imply that much of the variation in LMA is driven by the mass of photosynthetic tissue such as mesophyll cytoplasm (Osnas et al., 2018). In contrast, *B. papyrifera* and *A. rubrum* had no correlation between LMA and area-based A_{sat}, suggesting that much of the variation in LMA is driven by allocation to non-photosynthetic structural tissue such as cell walls, which may improve leaf toughness. However, for *A. rubrum* in particular, there was a strong negative correlation between LMA and dark-acclimated F_v/F_m, two variables jointly affected by light availability (Figure S2; Figure 4). As a result, a potential positive relationship between LMA and A_{sat} in *A. rubrum* could have been masked by photoinhibition. We found clearer evidence that photoinhibition lowers A_{sat} in *Q. ellipsoidalis* and *T. americana*. Since photoinhibition occurs through damage or downregulation of PSII, it is usually thought to depress photosynthesis by lowering ETR. But both ETR and stomatal conductance mirrored assimilation across treatments in chamber light–response curves (Figure S5), so both may have some role in explaining why most species had lower assimilation in monoculture at a given chamber light level.

As an alternative to photoinhibition, one might propose that leaf plasticity explains why mass-based A_{sat} is lowest in monocultures in three out of four focal species. If leaves in monoculture have a larger fraction of non-photosynthetic structural mass, their mass-based photosynthesis rates could be lower. Structural mass can also depress mass- and area-based photosynthesis rates alike by lowering mesophyll conductance (Onoda et al., 2017). Furthermore, sun leaves tend to have slightly less nitrogen per unit mass (Poorter et al., 2019). However, in *B. papyrifera*, whose variation in LMA seemed to be driven by non-photosynthetic mass, monocultures had higher mass-based A_{sat} than shaded bicultures. On the other hand, in *T. americana*, whose variation in LMA seemed to be driven by photosynthetic mass, shaded bicultures had higher A_{sat} than monocultures. Finally, none of these aspects of leaf plasticity should have had a direct influence on dark-acclimated F_v/F_m, but we found that dark F_v/F_m accounts for much of the variation in A_{sat} among treatments in *T. americana* and *Q. ellipsoidalis*, which indicates that photoinhibition did have a strong role. These observations somewhat limit the potential role of leaf construction in explaining why mass-based A_{sat} was often higher in shaded bicultures.

Based on chamber light–response curves, shading may appear to have aided carbon assimilation in *A. rubrum* and *Q. ellipsoidalis*, as well as *T. americana*. But rescaling the light–response curves allowed us to consider the costs of photosynthetic light limitation. Compared to monoculture, *A. rubrum* and *Q. ellipsoidalis* in shaded biculture had lower mass-based carbon assimilation for most values of light at the top of the canopy (Figure 3, right). For these two species, shading was often severe enough to limit growth and photosynthesis, erasing the advantage that trees in shaded biculture would otherwise have. The light-limiting effect of competition explains much of the negative growth response in these species.

Given that light availability fluctuates—diurnally, seasonally and with cloud cover—the treatment that performs best may also vary from moment to moment. We used a time series of solar radiation to estimate total carbon assimilation throughout July. We found that *A. rubrum* and (only on a mass basis) *B. papyrifera* had lower carbon assimilation in shaded biculture than in the other treatments (Figure S6). PPFD was under 500 μmol m^{-2} s^{-1} more than 60% of the time during the month; it is under such dim conditions that trees in monoculture had the greatest photosynthetic advantage over those in shaded biculture, no matter what benefits shading could confer at sunnier times (Figure 3; Figure S4). We also caution that we only measured top leaves, so we cannot directly compare whole-plant carbon gain.

Trees in FAB and elsewhere often vary in size by orders of magnitude, which foregrounds the size-asymmetry of light competition. Research on light competition in biodiversity–ecosystem function research underscores a tension between competitive imbalance caused by size-asymmetry and competitive relaxation caused by light-use complementarity, in which species may partition their exploitation of the light environment (Sapijanskas et al., 2014; Williams et al., 2017; Yachi & Loreau, 2007). We leave the potential for light-use complementarity unaddressed, but we show that competitive imbalance can suppress the photosynthesis and growth of species that are poorly adapted to shade. Such imbalances could promote selection effects (sensu Loreau & Hector, 2001), in which the most productive species become even more dominant in mixtures.

4.2 | Facilitation and shade-tolerant species

In *T. americana*, *A. negundo* and *B. papyrifera*, having larger neighbours increased stem growth (Figure 2; Figure S3). The former two are the most shade-tolerant broadleaf species in the experiment while the last is the most shade-intolerant. Moreover, these three species showed divergent photosynthetic responses to the light environment (Figures 3 and 4), which suggests that different mechanisms may explain the positive stem growth response in *B. papyrifera* than in the other two species.

We first discuss the positive trend in *T. americana* and *A. negundo* before returning to *B. papyrifera* in the following section. In these two species, we interpret this trend mainly as an outcome of facilitation, reinforcing prior results that show that shade-tolerant species often have facilitative responses to being shaded (Montgomery et al., 2010). In particular, these two species' growth trends were best fit by a model where neighbour size is log-transformed (Figure 2, Appendix S2). Increasing neighbour size thus had positive but diminishing marginal benefits, which may result if neighbour size had a nonlinear influence on light availability, or if deep shade had escalating costs that began to offset its benefits. As among less shade-tolerant species, the individual-level effects were noisy but strong. For example, the median *T. americana* stem in monoculture grew 99 cm^3 (25–75th percentile: 21–237 cm^3) between 2017 and 2018, compared to 267 cm^3 (29–633 cm^3) in shaded biculture with *P. strobus* or *J. virginiana*. The result was species-specific overyielding in shaded biculture compared to monoculture.

Here, the physiological data again help us explain the growth patterns. *T. americana* was the only one of the four focal species in which the monoculture treatment had the lowest carbon assimilation rates across most light levels in the rescaled light–response curves (Figure 3). The steep decline in dark-acclimated F_v/F_m with increasing light (Figure 4) suggests that the low A_{sat} in monoculture resulted from photoinhibition (Figure 5). This pattern aligns with *T. americana*'s role as a late-successional dominant species throughout much of its range (Braun, 1950). Our finding that carbon gain in *T. americana* could increase under shade is reinforced by Carter and Cavaleri (2018), who found that its assimilation rates may increase down vertical gradients from the upper canopy to the subcanopy. Nevertheless, we found no significant differences among treatments in estimated assimilation across the whole month of July (Figure S6), mainly because under low light, monocultures still had higher assimilation rates in the rescaled light–response curves. The amelioration of photoinhibition very likely contributed to the positive effect of neighbour size on growth in *T. americana*, but it may not fully explain it.

4.3 | Delayed senescence and microclimatic effects

Next, we discuss mechanisms of facilitation that could also have contributed to positive growth responses to neighbour size in *T. americana* and *A. negundo*, but which analyses based on light–response curves do not account for: delayed senescence and microclimatic effects.

In the fall, *T. americana* dropped its leaves 3 weeks sooner in monoculture than in shaded biculture (Figure 6). Given that leaves remained photosynthetically active until shortly before abscission (as suggested by Mattila et al., 2018), shade could have allowed these trees a longer period of carbon gain. Air temperatures in full sun were higher than in shaded plots (Appendix S2), casting doubt on a potential role for temperature or photoperiodic cues. Instead, we propose that abiotic stress, including light and water stress, accelerated senescence (Brelsford et al., 2019; Cavender-Bares et al., 2000; Estiarte & Peñuelas, 2015), especially as colder weather began to render leaves more susceptible to photodamage (Renner & Zohner, 2019). Without measuring the timing of senescence in other species, we do not yet know how general this effect is.

Although we emphasise the role of light stress, other microclimatic factors could also have contributed to variation in assimilation rates among treatments. For example, we found that pre-dawn leaf water potential (Ψ_{PD}) was slightly more negative in shaded bicultures while midday water potential (Ψ_{MD}) was more negative in monocultures (Figure S8; Appendix S2). These results are consistent with the idea that soil moisture was higher in low biomass plots, as we found, while daytime VPD was lower in high biomass plots, as Wright et al. (2015) found on hot, dry days in a grassland biodiversity experiment. If Ψ_{MD} responded in other tissues as in leaves, highly negative values could have caused stronger physical constraints to tissue growth in monocultures (Tardieu et al., 2014), resulting in carbon sink limitation. In response, plants may have downregulated electron transport and photosynthesis as a photoprotective response, reducing dark-acclimated F_v/F_m (Adams et al., 2013). From this perspective, the high risk of photoinhibition in species like *T. americana* and *A. negundo* would not have limited their growth, but would rather have been caused by limits to growth.

Nevertheless, it is hard to explain why such sink limitation would have particularly mattered in *T. americana* (and perhaps *B. papyrifera*) among the four focal species; for example, *A. rubrum* also had more negative Ψ_{MD} in monoculture (Figure S8). Moreover, trends in ϕ_{NO} suggest that *T. americana* and *A. negundo* in high light were especially vulnerable to photodamage (Figure 4). Photoinhibition due to source–sink imbalance is usually accompanied by compensatory upregulation in protective non-photochemical quenching (Adams et al., 2013), but these two species failed to increase qN under high light (Figure 4). These findings reinforce that damage, not just downregulation, contributed to the steep declines in dark-acclimated F_v/F_m these species show as light increases. Sink limitation may have contributed to lower monoculture growth in these species, but we believe it is not the main explanation.

The microclimate could also have altered photosynthesis directly in ways our light–response measurements did not capture because we controlled the chamber microclimate. Water stress was seldom very severe in any treatment (Figure S8), but even modest differences could have changed the timing of stomatal closure (Brodribb et al., 2003). Greater light exposure may also have raised leaf temperature in monoculture (Schymanski et al., 2013), perhaps pushing leaves above thermal optima for photosynthesis. Such microclimatic factors could have added to the physiological benefits of shading beyond what we measured in light–response curves.

4.4 | Shade avoidance and early-successional species

In the only early-successional broadleaf species, *B. papyrifera*, the positive response of stem RGR to neighbour size was weak and dependent on the model specification (Appendix S3), but it appears to reflect a longer-term trend. Between 2017 and 2018, *B. papyrifera* stems grew faster in shaded bicultures with *P. banksiana* (median: 578 cm^3; 25th–75th percentile: 231–1,168 cm^3) than with other broadleaf species (median: 496 cm^3; 25th–75th percentile: 87–836 cm^3). But there was a striking mismatch between the growth patterns and photosynthetic physiology: In untransformed and rescaled light–response curves alike, *B. papyrifera* had lower photosynthetic rates in the shaded biculture compared to the other treatments. Because it tended to overtop even its largest neighbours, the top leaves received nearly the full amount of available light in all treatments (Figure S2) and showed few signs of photoinhibition (Figure 4). These results suggest that the increase in stem volume was unrelated to photosynthetic physiology.

One possibility is that rather than (or in addition to) representing an increase in total growth due to facilitation, the positive trend in

stem volume in *B. papyrifera* was driven by a competitive shade avoidance response, which could increase allocation to shoot biomass at the expense of root biomass. Such responses tend to be especially strong in shade-intolerant, early-successional species like *B. papyrifera* (Gilbert et al., 2001; Henry & Aarssen, 1997). While we could not test directly for a change in the root-to-shoot ratio, we did find evidence that *B. papyrifera*, but not *A. negundo* or *T. americana*, had another symptom of the shade avoidance syndrome: greater allocation to elongation growth near larger neighbours, which caused trees to have smaller diameters than expected based on their height (Henry & Aarssen, 1999). This finding may suggest that a broader shade avoidance syndrome may contribute to the positive influence of neighbour size on stem volume in *B. papyrifera*. This finding would be in contrast to another tree diversity experiment, where both root-to-shoot ratios and the allometric relationship between basal area and biomass were nearly unaffected by the local neighbourhood (Guillemot et al., 2020).

4.5 | Mechanisms of photoprotection

Plants' strategies to avoid damage from the stress of excess light can be classified broadly into biochemical and structural strategies. We show that trees in monoculture allocated more to biochemical photoprotection, as indicated by lower PRI in all species and higher qN in all species but *T. americana* and *A. negundo* (Figure 4). Our leaf angle survey was also consistent with the idea that trees in monoculture steeply inclined their leaves to reduce light interception per unit area (Figure S9). The dramatic trend in leaf angles suggests that gross structural traits allowed these species use to regulate their light exposure.

Some plants may lack perfect photoprotective mechanisms in part because they are adapted to environments where the costs of high photoprotective investment outweigh the benefits. Delayed relaxation of non-photochemical quenching may hinder photosynthesis even when light declines enough to relieve the imminent threat of damage (Kromdijk et al., 2016; Murchie & Niyogi, 2011; Zhu et al., 2004), and there may also be small direct costs of building photoprotective pigments and proteins. Steep leaf angles may also decrease photosynthesis by reducing light interception even when light is limiting (Valladares & Pugnaire, 1999)—and all plants experience light-limiting conditions at least sometimes, as on cloudy days. All the same, plants in more open environments may need photoprotective mechanisms to avoid even greater costs due to photodamage under brighter conditions. That most species upregulate photoprotection in high light, despite the costs, implies that these species may otherwise incur a risk of damage from excess light, reinforcing the role of light stress in shaping the community.

4.6 | Competition and facilitation in biodiversity–ecosystem function relationships

The finding that shade can increase growth and photosynthesis has precedents. Ball et al. (1991) and Egerton et al. (2000) showed that shade enhances assimilation and growth of evergreen *Eucalyptus* seedlings during the winter, when cold causes photoinhibition. Howell et al. (2002) also found that among evergreen divaricating shrubs of New Zealand, leafless outer branches increase photosynthesis during the winter by reducing photoinhibition. Species can also facilitate each other from light stress in communities of phytoplankton (Gerla et al., 2011), which nearly all face some risk of photoinhibition (Edwards et al., 2016). These studies show that facilitation through shading can occur in many environments, and perhaps more so in otherwise stressful ones.

Much of the work on facilitation in plant communities is guided by the stress-gradient hypothesis (SGH), which proposes that facilitative interactions are more common in stressful environments (Bertness & Callaway, 1994; Maestre et al., 2009). Photoinhibition may contribute to this pattern: stressful conditions limit the use of light for photochemistry, turning high light exposure into an additional stressor. Under such conditions, shade from neighbours can ameliorate stress, resulting in facilitation. Under more benign conditions, where plants can use more of the available light for photochemistry, high light exposure may not cause damage. There, shading by neighbours is more likely to cause light limitation, resulting in an adverse, competitive effect on growth. As we show here, how much a species is stressed by its environment also depends on its own physiological tolerances.

The SGH brought greater attention to facilitation in plant ecology. Within biodiversity–ecosystem function research, a growing literature has since investigated the diverse mechanisms through which plant species can facilitate each other (Temperton et al., 2007; Li et al., 2014; Wright et al., 2015; Grossman et al., 2019; reviewed in Wright et al., 2017). We show that shading can reduce stress induced by the light environment—a specific form of abiotic stress amelioration, in which certain species alter the local environment and make it less stressful to others (Wright et al., 2017). But shading can also cause light limitation, resulting in a net competitive effect. The facilitation of shade-tolerant species by mainly shade-intolerant neighbours may help explain the result that heterogeneity in shade tolerance can drive positive effects of tree diversity on productivity (Searle & Chen, 2020; Toïgo et al., 2017; Zhang et al., 2012).

In the literature on biodiversity and ecosystem function, the attempt to parse out mechanisms—such as niche partitioning and facilitation—often depends on statistical partitions of biomass or productivity data (Fox & Kerr, 2012; Loreau & Hector, 2001) whose interpretation is often debated (Carroll et al., 2011; Pillai & Gouhier, 2019). But because productivity has physiological determinants, we can explain its patterns using physiological measurements. In this study, both survey-based tree growth data and careful physiological measurements show that certain species respond positively and others respond negatively to the size of their neighbours. The physiological measurements let us explain this divergence, showing that these interactions emerge in part from the photosynthetic responses of trees to the light environment created by their neighbours. The insights gained from such physiological techniques may benefit plant ecology more widely as we seek to explain community patterns in terms of basic aspects of plant function.

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AUTHORS' CONTRIBUTIONS

S.K. conceived the project with J.C.-B., conducted the physiological measurements, analysed and interpreted the data with J.C.-B. and R.A.M., and wrote the first draft of the paper; J.C.-B. and R.A.M. designed the FAB experiment, coordinated annual growth surveys and contributed to subsequent revisions of the paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Measurements of chlorophyll fluorescence (Kothari, 2021a; https://doi.org/10.6073/pasta/dbc0d28354b462d7eae9ec6bba7d0863), gas exchange (Kothari, 2021b; https://doi.org/10.6073/pasta/bff0d15bb1afa3f363bc832b2e43aabf), light availability (Kothari, 2021c; https://doi.org/10.6073/pasta/425c337895a1a7d29210508609ff1518) and phenology (Kothari, 2021d; https://doi.org/10.6073/pasta/8c4e6ffcf7de709c780419c8cf4241dc) are archived with the Environmental Data Initiative and available at the Cedar Creek Data Catalog (URL: https://www.cedarcreek.umn.edu/research/data). Spectral data are archived on EcoSIS (Kothari, Montgomery, et al., 2018; https://doi.org/10.21232/FR7US97g). Biomass survey data and an analysis script are archived at Data Repository for University of Minnesota (Kothari et al., 2021; https://doi.org/10.13020/zfkr-6b35).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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