Can light- saturated photosynthesis in lowland tropical forests be estimated by one light level?

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Abstract :

Leaf-level net photosynthesis (A_n) estimates and associated photosynthetic parameters are crucial for accurately parameterizing photosynthesis models. For tropical forests, such data are poorly available and collected at variable light conditions. To avoid over- or underestimation of modeled photosynthesis, it is critical to know at which photosynthetic photon flux density (PPFD) photosynthesis becomes light-saturated. We studied the dependence of A_n on PPFD in two tropical forests in French Guiana. We estimated the light saturation range, including the lowest PPFD level at which A_{sat} (A_n at light saturation) is reached, as well as the PPFD range at which A_{sat} remained unaltered. The light saturation range was derived from photosynthetic light-response curves, and within-canopy and interspecific differences were studied. We observed wide light saturation ranges of A_n. Light saturation ranges differed among canopy heights, but a PPFD level of 1,000 µmol m−2 s−1 was common across all heights, except for pioneer trees species that did not reach light saturation below 2,000 µmol m−2 s−1. A light intensity of 1,000 µmol m−2 s−1 sufficed for measuring A_{sat} of climax species at our study sites, independent of the species or the canopy height. Because of the wide light saturation ranges, results from studies measuring A_{sat} at higher PPFD levels (for upper canopy leaves up to 1,600 µmol m−2 s−1) are comparable with studies measuring at 1,000 µmol m−2 s−1.

1. INTRODUCTION

Tropical forests are among the most productive ecosystems on earth, accounting for more than one third of global terrestrial gross primary productivity (GPP), and thereby playing an important role in the global carbon (C) cycle (Beer et al., 2010; Malhi, 2010). Global land surface models are used to quantitatively assess how tropical forest GPP will evolve under climate change. These models require a mechanistic understanding of photosynthesis and accurate estimates of regional photosynthetic parameters: A_{sat} (the light-saturated leaf-level net photosynthetic rate; in µmol/m²/s), V_{cmax} (the maximum carboxylation rate; in µmol/m²/s) and J_{max} (the electron transport rate supporting ribulose 1,5-phosphate (RuBP) regeneration; in µmol/m²/s). Tropical leaf-level photosynthesis data are much sparser than data gathered in temperate ecosystems (Cavaleri, Reed, Smith, & Wood, 2015; Goldstein & Santiago, 2016; Kattge, Knorr, Raddatz, & Wirth, 2009; Niinemets, Keenan, & Hallik, 2015; Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011). The knowledge gap in this biome leads to uncertainties and impedes our ability to predict the photosynthetic response of tropical forests to a changing environment.

There are several reasons why photosynthesis in the tropical biome is understudied, often related to the complications associated with measuring photosynthetic capacity. First, due to high species richness and functional group diversity(Fine, Ree, & Burnham, 2008; Gentry, 1982) large variation in the photosynthetic capacity of tropical tree species occurs, requiring greater sample sizes than in other biomes (Kattge et al., 2011; Reich, Walters, & Ellsworth, 1997). Second, photosynthesis measurement protocols have not been standardized. Leaf-level photosynthesis has, for example, been measured at different light levels and at different temperatures. Therefore, the leaf-level photosynthesis data required to parameterize land surface models are scarce and not always comparable, hampering accurate projections of tropical forest

GPP, as well as global syntheses aimed at comparing photosynthesis among tropical forests or between tropical forests and other biomes. Finally, strong light gradients throughout the canopy exist in forests, resulting in a great variability of light conditions within the canopy (Niinemets, 2007). This effect is especially pronounced in tropical forests because of high leaf layering(Tianxiang et al., 2002; Zhu et al., 2016), and exacerbated by the spatial variation induced by canopy gaps, creating sharp gradients in light intensity (Iida et al., 2014). High variability in photosynthetic photon flux density (PPFD in µmol of photons/m²/s), and variability in how plants adjust to light intensity complicate determining A_{sat} and estimating V_{cmax} and J_{max}, all key parameters of photosynthetic activity and critical for upscaling and modelling (Rogers et al., 2017).

Most land surface models simulate photosynthesis using the leaf biochemical model of Farquhar *et al.* (1980) (Fisher, Huntzinger, Schwalm, & Sitch, 2014). Two key parameters in this model are V_{cmax} and J_{max} and they are typically derived from A_n-C_i curves measured at light saturation. A reasonably accurate alternative way to derive V_{cmax} is through A_{sat} measurements (De Kauwe et al., 2016). To avoid over- or underestimation of these parameters, and hence of photosynthesis, it is critical to know at which PPFD photosynthesis becomes light saturated, and above which PPFD photoinhibition causes reduced A_n. The PPFD levels at which light saturation is reached varies among tree species (Denslow, 1987) and with light acclimation of the leaves (Markesteijn, Poorter, & Bongers, 2007; Rijkers, Pons, & Bongers, 2000; Urban, Holub, & Klem, 2017). The reported PPFD levels for A_{sat} vary highly among studies, with reported values for upper canopy foliage of tropical rainforest ranging from 1000 µmol/m²/s (Doughty, 2011; Doughty et al., 2015; Slot & Winter, 2017) over 1200 µmol/m²/s (Stahl et al., 2013; van de Weg, Meir, Grace, & Ramos, 2012) and 1800 µmol/m²/s (Bahar et al., 2016; Domingues, Martinelli, &

Ehleringer, 2014; Weerasinghe et al., 2014) to 2000 µmol/m²/s (Rowland et al., 2015; Rowland et al., 2016; Santos et al., 2018). Leaves situated in the upper canopy are often in direct sunlight while leaves situated in the lower canopy are often shaded and thus acclimated to lower PPFD levels (Urban et al., 2017). Many studies have, therefore, used different PPFD settings when measuring A_{sat} on sunlit upper or shaded lower canopy leaves (e.g. Domingues et al. (2014); Rowland et al. (2015); van de Weg et al. (2012)). The PPFD levels chosen in these studies were, however, not consistent and ranged between 1200 and 2000 µmol/m²/s for sunlit upper canopy leaves and between 500 and 1000 µmol/m²/s for shaded lower canopy and understory leaves (e.g. Domingues et al. (2014); Santos et al. (2018); van de Weg et al. (2012); Weerasinghe et al. (2014)). Although these light levels may be appropriate for the specific trees/leaves studied, it is usually unclear if light saturation was reached and photoinhibition avoided, hence obscuring inter-study comparisons.

Light levels that exceed the light saturation point may induce photoinhibition, defined as the slow, reversible decline of photosynthetic efficiency when absorbed light is in excess of that required for C assimilation (Demmig-Adams & Adams III, 1992; Long, Humphries, & Falkowski, 1994; Powles, 1984). Because of photoinhibition, measurements of A_{sat} should not be conducted at excessive light conditions, and failure to do so would result in an underestimation of the maximal C uptake by the leaf, and hence by the ecosystem, significantly impacting the estimates of tropical forest C uptake (Clark et al., 2017).

We here studied the PPFD-dependence of leaf-level net photosynthesis (A_n) and how this varies vertically within the canopy. We also identified the light saturation range, *i.e.* the PPFD levels across which A_{sat} is maintained. Different tropical tree species were studied at two lowland tropical rainforests in French Guiana, contrasting climax versus pioneer trees. Climax species are

slow-growing and shade-tolerant and form the great majority of tree species in a tropical

rainforest, whereas pioneer trees are expected to live at high light levels, are shade-intolerant,

and have high growth rates (Kitajima, 1994; Martinez-Camilo, Gonzalez-Espinosa, Ramirez-

Marcial, Cayuela, & Perez-Farrera, 2017; Raaimakers, Boot, & Dijkstra, 1995; Swaine &

Whitmore, 1988). Identifying a common PPFD level at which A_n saturates for lowland tropical

trees would facilitate the comparisons between different tree species and height levels within the

canopy. We hypothesize that the PPFD at which A_n becomes light-saturated, the light saturation

point, decreases vertically within the canopy due to shade acclimation, as has been observed for

temperate forest species (Lewis, McKane, Tingey, & Beedlow, 2000; Parra et al., 2015); and that

it is higher for pioneer species than for shade-tolerant species since pioneers have higher growth

rates and are less adapted to low light conditions (Martinez-Camilo et al., 2017; Raaimakers et

al., 1995). We also hypothesize that at very high PPFD (much above the light saturation point),

photoinhibition occurs irrespective of canopy position, but that this reduction in A_n occurs at

lower PPFD levels and is more pronounced for lower-canopy leaves that are more shade-

adapted.

2. METHODS

2.1 Study sites

This study was conducted at two mature lowland tropical rainforest sites in French Guiana,

South America. The climate at both sites is tropical humid, with a dry season lasting from

August to November and a short dry spell in March. Mean daily temperature is 25.7°C in the dry

season and 26.7°C in the rainy season.

The first study site was located at the Paracou Research Station (5°16' N, 52°16' W), characterized by an average annual rainfall of 3150 mm/y (2015 - 2017). The density of trees with a DBH > 10 cm averaged ca. 620 trees/ha and average tree species richness is ca. 160 species/ha (Bonal et al., 2008). The mean canopy height is 35 m, with emergent trees exceeding 40 m. The second study site was situated at the Pararé site of the Nouragues Research Station (4°02' N, 52°41' W), located 120 km south of Cayenne. This forest receives approximately 3000 mm rain/y (Bongers, Charles-Dominique, Forget, & Théry, 2001). Tree species richness varies between 180 and 200 species/ha. The canopy height ranges between 30–40 m, with emergent trees reaching 60 m (Van Der Meer, Sterck, & Bongers, 1998). The soils at both sites are characterized as nutrient-poor Acrisols (FAO, 1998)(FAO-ISRIC-ISSS 1998), with the soils at Paracou ranging from loamy sand to sandy loam and at Nouragues from sandy loam to silty clay according to the USDA texture classification chart (Van Langenhove et al., 2019). Both forest stands are equipped with an instrumentation tower. Meteorological measurements and measurements of ecosystem net CO_2 exchange with the eddy covariance technique have been conducted on a continuous basis since 2003 in Paracou and since 2014 at Nouragues.

2.2 Leaf gas exchange

Leaf gas exchange measurements were carried out with a set of infrared gas analyzers (IRGAs) incorporated into a portable photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, U.S.A.). During measurements, a leaf was clamped within a chamber with controlled microenvironmental conditions and concentration changes of dihydrogen oxide (H_2O) and carbon dioxide (CO_2) between incoming and outgoing air were measured. During the measurements, the relative humidity inside the leaf chamber was kept as close to ambient ($70 \pm 8\%$) as possible and the air

flow rate was 500 µmol/s. The chamber block temperature was controlled to minimize variation

in leaf temperature and was set at 30 ± 0.15°C.

All leaf gas exchange measurements were performed on newly formed mature leaves

from 2 m-long excised and rehydrated branches, except for those measured on saplings (diameter

0.4-3.4 cm), which were carried out on leaves still attached to the trees. The trunk diameter of

the sampled forest trees ranged from 10.2 to 101.9 cm (diameter at breast height, or 130 cm

aboveground, DBH; Table S3). Excised branches were cut by a tree climber, and immediately

recut under water to restore hydraulic conductivity (Domingues et al., 2010; Dusenge et al.,

2015; Rowland et al., 2015).

2.3 Photosynthetic light-response curves

Photosynthetic light-response curves were measured on a total of 74 leaves from 23 different

species, corresponding to 17 mature trees (13 species) and 12 saplings (4 species) at Paracou,

and 4 pioneer trees (3 species) and 10 mature trees (8 species) at Nouragues (Table S1; Table

S3). The trees were classified as climax or pioneer species based on local species knowledge

(Bongers et al., 2001; Laurance et al., 2004; Molino & Sabatier, 2001; Raaimakers et al., 1995).

Measurements were performed at four different canopy heights, estimated relative to the top of

the canopy: upper sunlit foliage, middle canopy foliage, lower canopy foliage, and branches of

saplings ranging between 1 and 2 m height. For each species, sampling at two canopy heights

was required to determine the height effect, and additional measurements on more canopy

heights were carried out whenever possible to further strengthen the data analyses. Due to

logistical constraints the measurements at Paracou were carried out at the end of the wet season

and at Nouragues at the onset of the dry season, except for four pioneer trees that were measured during the wet season.

Light-response curves were established by measuring A_n at different PPFD levels, while maintaining a relatively constant chamber temperature. Leaves were first acclimated to 2000 µmol/m²/s by exposing them to this PPFD level and waiting until A_n was stabilized. We subsequently decreased the PPFD in steps of 50-300 µmol/m²/s down to 0 µmol/m²/s to obtain a total of 14 and 11 measurements of A_n per leaf respectively for Nouragues and Paracou (PPFD levels in Nouragues: 2000-1800-1600-1400-1200-1000-800-600-400-200-100-50-25-0 µmol/m²/s, PPFD levels in Paracou: 2000-1800-1500-1000-800-600-400-200-100-50-0 µmol/m²/s). We considered the respiration measured at 0 µmol/m²/s to be an estimate of mitochondrial respiration in the light because there had not been sufficient time to completely relax respiration (Crous et al., 2012), but this is appropriate for light response curves. The CO_2 concentration was kept constant at 400 ppm using an integrated gas mixing system and miniature CO_2 cylinders.

2.4 Photosynthetic CO_2-response curves

To obtain photosynthetic CO_2-responses, we measured A_n at different CO_2 concentrations by controlling the reference CO_2 concentrations, starting at the ambient CO_2 concentration of 400 ppm, but we maintained a constant temperature and PPFD level. The CO_2 concentration was then first reduced stepwise to 50 ppm (in steps of 50-100 ppm), then returned to 400 ppm and thereafter increased to 2000 ppm in steps of 200-300 ppm to obtain a total of 14 measurements per leaf (reference CO_2 concentrations: 400-300-200-100-50-400-400-600-800-1000-1200-1500-1700-2000). These A_n-C_i curves (based on C_i, the CO_2 concentration of the leaf intercellular

spaces) were measured on the upper sunlit foliage and lower canopy foliage for three trees (Table S2). Additional measurements were carried out on the middle canopy foliage for one of these trees and on four additional trees, resulting in a total of 14 curves on seven trees (six species) (Table S2). Response curves were made at a constant PPFD of 1300 and 1800 μmol/m²/s consecutively, to study the effect of light intensity on the photosynthetic parameters V_{cmax} (μmol/m²/s) and J_{max} (μmol/m²/s) (Table S4). These parameters were derived by fitting the A_n-C_i curves using the biochemical photosynthesis model of Farquhar, Von Caemmerer and Berry (Farquhar, Caemmerer, & Berry, 1980) after temperature-correction (to 25°C) using the equations and generalized kinetic coefficients from Sharkey, Bernacchi, Farquhar, and Singsaas (2007), without including the limitation by triose phosphate utilization. We assumed that mesophyll conductance was infinite.

2.5 Data analysis

Since maximum A_n varied widely across species and canopy height classes, all individual light response curves were normalized by scaling the A_n values between zero and one (Eq. 1) to examine relative declines in A_n with PPFD in all species.

$$A_{n,norm} = \frac{A_n - \min(A_n)}{\max(A_n) - \min(A_n)} \tag{1}$$

where $A_{n,norm}$ is the normalized value of A_n, A_n is the measured A_n, and min and max are the minimum and maximum values of the measured A_n for each curve, respectively.

To test whether a common saturating PPFD level could be found over all canopy height levels, these normalized curves were averaged across species for each canopy height level, separating shade-tolerant climax species from light-demanding pioneer species (Bongers et al.,

2001). For each canopy height level, we determined the light saturation range, i.e. the PPFD range at which maximum A_n occurred. Starting from the highest observed $A_{n,norm}$, we employed two criteria that both needed to be met for adjacent PPFD levels to be included into this light saturation range. First, neighboring PPFD levels that did not significantly differ in $A_{n,norm}$, based on their 95% confidence intervals, were also considered as light saturated. Second, the regression slope between the measured $A_{n,norm}$ values considered at light saturation could not differ from zero.

We compared the obtained light saturation ranges for all measured leaves at all canopy heights and searched for a PPFD level that occurred in all light saturation ranges, which we coined the common saturating PPFD level. To test whether A_n at this common saturating PPFD level differed from an estimated A_n at 2000 µmol/m²/s under the assumption that no photoinhibition occurred, we then fitted a nonrectangular hyperbola based model (Eq. 2; (Lobo et al., 2013)) to the measured A_n-PPFD curves and calculated A_n at this common saturating PPFD level. We tested whether this value was within five percent of $A_{sat,mod}$, defined as the modelled A_n value at a PPFD of 2000 µmol/m²/s. Hence, if for example A_n at the common saturating PPFD is greater than $A_{sat,mod}$ (±5%), this is taken to suggest photoinhibition at a PPFD of 2000 µmol/m²/s. To test for interspecific differences and differences among canopy heights in the PPFD level at which A_n becomes saturated, we tested the effects of species and canopy height level on the residuals of A_{sat}, measured at the common saturating PPFD, and $A_{sat,mod}$, using a linear mixed model (nlme package (Pinheiro, Bates, Debroy, Sarkar, & R Core Team, 2020)) with canopy height level as fixed factor and species as random factor. Note that these analyses were done only for the climax species, not for the pioneer species, because for the latter A_n did not saturate within the light range used in this study.

$$A_n = \frac{\phi*PPFD+A_{gmax}-\sqrt{(\phi*PPFD+A_{gmax})^2-4*\phi*\theta*A_{gmax}*PPFD}}{2*\theta} - R_d \qquad (2)$$

where A_n is the net photosynthetic rate (µmol (CO_2)/m²/s); φ is the apparent quantum yield at

PPFD = 0 (µmol (CO_2)/µmol (photon)); PPFD is the photosynthetic photon flux density (µmol

(photon)/m²/s); A_{gmax} is the asymptotic estimate of the maximum gross photosynthetic rate (µmol

(CO_2)/m²/s); θ (dimensionless) indicates the convexity.

Stomatal closure induced by water limitation could have occurred at the highest PPFD levels and

could therefore contribute to the observed decline in A_n above light saturation. We therefore

tested whether the stomatal conductance measured at a PPFD of 2000 µmol/m²/s differed from

the stomatal conductance measured at the common saturating PPFD level obtained in this study.

Since normality assumptions were not met, a paired Wilcoxon signed-rank test was performed to

test if the stomatal conductance at and above light saturation was significantly different.

We calculated the ratio of $J_{max,1300}$: $J_{max,1800}$ and $V_{cmax,1300}$: $V_{cmax,1800}$, measured at a PPFD

of 1300 µmol/m²/s and 1800 µmol/m²/s respectively, to test for an effect of PPFD on J_{max} and

V_{cmax}. These ratios were calculated as the slope estimates of the linear regression by 10,000

bootstrap replicates. Both PPFD levels were assumed to be at light saturation if the ratio did not

differ significantly from 1, based on the 95% confidence intervals corresponding to 2.5 and

97.5% quantiles after bootstrapping. Bootstrapping involves resampling with replacement from

the original data to simulate multiple samples from a population (Chernick & LaBudde, 2011).

Additionally, we performed a paired t-test to test whether J_{max} and V_{cmax} differed between a

PPFD of 1300 µmol/m²/s and 1800 µmol/m²/s. We tested if the J_{max}:V_{cmax} ratio differed between

1300 and 1800 µmol/m²/s with a linear regression with the ratio as the dependent variable and

the PPFD level as fixed factor. All analyses were performed in R 3.3.3 (R Core Team, 2017) using the ggplot2 package (Wickham, 2009) for visualization of the data.

3. RESULTS

For upper canopy sunlit leaves, the light saturation point was reached at ca. 1000 µmol/m²/s (Figure 1a,d). In Nouragues, $A_{n,norm}$ did not change between 1000 and 1600 µmol/m²/s, but decreased statistically significantly ($F_{1,91}$ = 4.69; P = 0.03) at higher PPFD (2.4% decrease from 1600 to 2000 µmol/m²/s, Figure 1a). This decrease in $A_{n,norm}$ at 2000 µmol/m²/s was not apparent at the Paracou site (Figure 1d), where $A_{n,norm}$ did not significantly differ between 1000 and 2000 µmol/m²/s.

Compared to the upper canopy sunlit leaves, leaves within the canopy (e.g. 'lower' and 'middle' canopy) saturated at lower PPFD. At Nouragues, the light saturation point of these mid-canopy leaves was reached at 800 µmol/m²/s and $A_{n,norm}$ did not change between 800 and 1400 µmol/m²/s (Figure 1e). This light-saturating PPFD range was similar for both the middle and lower canopy foliage (Figure 1b,c). At Paracou, in the lower canopy stratum, the light saturation point was reached at 800 µmol/m²/s, and $A_{n,norm}$ did not vary significantly between 800 and 1800 µmol/m²/s (Figure 1e). For saplings, the light saturation range was smaller and light saturation occurred between 800 and 1000 µmol/m²/s (Figure 1f). In strong contrast with the leaves of shade-tolerant tree species, the $A_{n,norm}$-PPFD curves for sunlit leaves of pioneer trees showed no signs of saturation of $A_{n,norm}$ within the investigated PPFD range (0 to 2000 µmol/m²/s, Figure 2).

Aside from the pioneer species, light saturation was reached within a PPFD range that varied per canopy height, with 1000 µmol/m²/s as common saturating PPFD level. 73 percent of

the $A_{sat,1000}$ (n = 50), the A_{sat} measured at 1000 µmol/m²/s, was within five percent of $A_{sat,2000}$, defined as the modelled A_{sat} value at a PPFD of 2000 µmol/m²/s (Figure 3), while ten percent of $A_{sat,1000}$ (n = 7) was above $A_{sat,2000}$ + 5% and 17 percent (n = 12) below $A_{sat,2000}$ - 5%. Canopy height level (likelihood ratio = 3.33; P = 0.19) had no significant effect on deviations of the residuals of $A_{sat,1000}$ and $A_{sat,2000}$ for climax species. The variance of the tree species only accounted for less than one percent of the total variance, with a random intercept of 3.96E-06.

The stomatal conductance at a PPFD of 2000 µmol/m²/s differed significantly from the stomatal conductance measured at the common saturating PPFD level of 1000 µmol/m²/s (Wilcoxon paired test, V = 533; P < 0.001; Figure 4). The stomatal conductance at a PPFD of 2000 µmol/m²/s was higher than at a PPFD of 1000 µmol/m²/s.

Across all species and heights in the canopy, the photosynthetic parameters J_{max} and V_{cmax} did not significantly differ between the light intensities of 1300 and 1800 µmol/m²/s. When treating the data in a paired way, there is no significant difference for J_{max} (t_{13} = 1.70; P = 0.11) and V_{cmax} (t_{13} = 1.31; P = 0.21) between these parameters measured at a PPFD of 1300 and 1800 µmol/m²/s. After bootstrapping the data, the ratio of $J_{max,1300}$: $J_{max,1800}$ and $V_{cmax,1300}$: $V_{cmax,1800}$ were 1.08 ± 0.07 µmol/m²/s and 0.97 ± 0.30 µmol/m²/s, respectively. The 95% confidence interval for both J_{max} ([0.92; 1.17]) and V_{cmax} ([0.27; 1.32]) included one and thus the ratio did not differ significantly from one. The mean ratio $J_{max,1300}$:$V_{cmax,1300}$ (1.54) was not significantly different from the mean ratio $J_{max,1800}$:$V_{cmax,1800}$ (1.71) ($F_{1,26}$ = 1.03; P = 0.32).

4. DISCUSSION

A common PPFD level at which leaf-level photosynthesis saturates in lowland tropical forests would facilitate the comparison between different tree species and height levels within the

canopy, and between different study sites and studies. Our data suggest that at our study sites in French Guiana, dominated by shade-tolerant tree species growing on infertile soils (Grau et al., 2017; Hammond, 2005; ter Steege et al., 2013), A_{sat} can best be measured within a PPFD range of 1000 to 1400 µmol/m²/s for canopy trees, while saplings showed saturation at lower light conditions, within a range of 800 to 1000 µmol/m²/s, since they are acclimated to a low PPFD regime. Saplings in tropical forests typically receive less than two percent of the incoming light at the top of the canopyv(Montgomery & Chazdon, 2002; Théry, 2001; Yoda, 1974). For climax canopy trees, A_{sat} can thus be measured within a wide PPFD range, with a common PPFD of 1000 µmol/m²/s throughout the whole canopy (Figure 1).

It must, however, be clearly stated that the above does not hold for the pioneer species investigated in this study. None of the seven measured pioneer trees belonging to the Cecropiaceae family included in this study showed signs of saturation up to a PPFD of 2000 µmol/m²/s (Figure 2) – the maximum light intensity that could be reached with our device. Pioneer trees typically have higher light saturation points compared to climax trees (Chazdon, Pearcy, Lee, & Fetcher, 1996; Lüttge, 2008; Silvestrini, Válio, & Mattos, 2007), which is supported by this study. Measuring leaf-level photosynthesis of pioneer trees at the light saturation range established in this study, or even at PPFD of 2000 µmol/m²/s is thus likely to underestimate A_{sat}, and generalization beyond the Cecropiaceae family requires further study. Hence, studies seeking to compare photosynthetic traits in early-successional habitats or pioneer species with late-successional species need to evaluate traits such as A_{sat}, V_{cmax} and J_{max} for different, saturating PPFD levels appropriate to their successional status.

We hypothesized that photosynthesis becomes light saturated at lower PPFD levels when leaves are more shade-adapted. In accordance with this hypothesis, the light saturation range

measured in this study started at lower PPFD levels and became more narrow for leaves positioned deeper in the canopy (i.e. more shade-adapted leaves). Nonetheless, this saturation range of shade-adapted leaves overlapped with the saturation range of sun-adapted leaves at the top of the canopy. At the Nouragues site, the upper boundary of the light saturation range decreased vertically from the top of the canopy (1600 µmol/m²/s) to the forest floor (1400 µmol/m²/s). Opposed to results from previous studies (e.g. Ellsworth and Reich (1993)), we did not find a continuous decrease in light saturation point towards the lower canopy, as the middle and lower canopy foliage at the Nouragues site showed the same light saturation point range (800 to 1400 µmol/m²/s). At Paracou, the light saturation range of the lower canopy foliage (800 – 1800 µmol/m^2/s) was slightly lower than that of the upper canopy sunlit leaves (1000 – 2000 µmol/m^2/s), and the lower boundary overlapped with the range of the saplings in the understory.

We hypothesized that at high PPFD (above saturation for photosynthesis), photoinhibition would occur at all heights in the canopy, but that this reduction in leaf-level photosynthesis would be more pronounced lower in the canopy where leaves are not used to receiving high light intensities. At the Nouragues site, upper sunlit canopy foliage exhibited a statistically significant decline in $A_{n,norm}$ measured at a PPFD of 2000 µmol/m²/s, which was not caused by stomatal closure based on available evidence (Figure 4; Figure S1; Figure S2). However, this decline was only minor in magnitude (2%) and did not occur at the other canopy heights, nor was it found for sunlit leaves at the Paracou site. We thus refute the hypothesis of a pronounced decline in A_n measured at a PPFD of 2000 µmol/m²/s for more shade-adapted leaves, although it is obviously more advisable to measure A_{sat} at lower PPFD for all but pioneer tree leaves.

Total incoming light at the top of the canopy in tropical forests can exceed 2000 µmol/m²/s (Shuttleworth, 1984), and we therefore expected that the light saturation point of the upper canopy sunlit leaves would be reached at PPFD levels close to 2000 µmol/m²/s for optimal light use efficiency. However, the upper canopy sunlit leaves typically received much less incoming PPFD due to the diel cycle of the solar zenith angle and the leaf angle (Ventre-Lespiaucq, Flanagan, Ospina-Calderon, Delgado, & Escudero, 2018). This is demonstrated by the comparison of light interception by sensors installed on the leaves themselves compared to measurements of incoming light on the flux tower (Figure S3), indicating that the leaves are not frequently exposed to very high PPFD levels. Trees are able to adjust the spatial configuration of their leaves by changing the leaf angle or orientation to control their light interception and energy balance, e.g. reorient a leaf blade parallel to the sun rays to intercept less PPFD and avoid excessive light (Posada, Lechowicz, & Kitajima, 2009). Increasing the frequency of low/medium PPFD incident on leaves can increase photosynthetic light use efficiency (Posada et al., 2012), but can also reduce photoinhibition and stress associated with high irradiance (Posada et al., 2009; Walters & Field, 1987) and warming (Doughty, 2011; Slot & Winter, 2017). This is an important characteristic, especially for sunlit leaves of canopy dominant trees that are frequently exposed to high PPFD levels and risk experiencing high-radiation damage. Due to their leaf angle not being perpendicular to the solar beams, sunlit leaves thus typically intercept less light than is incoming at the top of the canopy and we postulate that this is the reason why the light saturation point occurred at much lower PPFD levels than the typical incoming light intensity at the top of the canopy.

We further tested whether V_{cmax} and J_{max} differed between PPFD levels of 1300 and 1800 µmol/m²/s. Assuming that the PPFD of 1800 µmol/m²/s does not induce photoinhibition , A_n is

light saturated at this PPFD level (as reported in e.g. Weerasinghe et al. (2014) and Bahar et al. (2016)), and thus maximum values for V_{cmax} and J_{max} are reached. Below light saturation, A_n is usually considered to become limited by rates of photosynthetic electron transport (J_{max}) (Farquhar et al., 1980). Hence, measuring A_n-C_i curves below light saturation is more likely to lead to underestimation of J_{max} (Buckley & Diaz-Espejo, 2015), than of V_{cmax}. The lack of difference between $V_{cmax,1300}$ and $V_{cmax,1800}$ was thus expected and was even hypothesized by Buckley and Diaz-Espejo (2015). In contrast, J_{max} is derived from the light limited part of the curve and a higher J_{max} at a PPFD of 1800 µmol/m²/s than at 1300 µmol/m²/s would be expected if light was not saturating at 1300 µmol/m²/s, because this term of the Farquhar-von Caemmerer-Berry (1980) photosynthesis model is light sensitive below light saturation. However, J_{max} did not significantly differ between a PPFD of 1300 and 1800 µmol/m²/s, which is in accordance with the light saturation range established for A_{sat} and confirms that the PPFD of 1300 µmol/m²/s was at light saturation. Although the ratio J_{max}:V_{cmax} in this study was in the lower range of what was found in other studies (e.g. Bahar et al. (2016); Rowland et al. (2015)), the ratio J_{max}:V_{cmax} did not differ significantly between PPFD levels of 1300 and 1800 µmol/m²/s, confirming light saturation at both PPFD levels and no photoinhibition at 1800 µmol/m²/s.

Overall, A_n was light-saturated over a wide range of PPFD levels, but for all tree species and on all heights within the adult tree canopy A_n reached saturation at 1000 µmol/m²/s. The exception to this generalization were the pioneer trees, which did not reach light saturation even at light levels up to 2000 µmol/m²/s. These results suggest that a light intensity of 1000 µmol/m²/s is sufficient for measuring A_{sat} of climax species in the lowland forests of French Guiana, no matter at which canopy height the measurements are taken. Moreover, the negligible magnitude of photoinhibition (if at all present) in our study implies that any value of PPFD

within the range of 1000-2000 µmol/m²/s would have yielded accurate values of A_{sat}. This study thus clearly shows that, with exception of pioneer species belonging to the Cecropiaceae family, tropical tree photosynthesis data reported in previous studies can quite safely be compared even if different PPFD levels were used, given that a minimum of 1000 µmol/m²/s PPFD was provided for canopy leaves. Some caution is warranted since this study took place in the nutrient poor forests of French Guiana, and different light, water and nutrient environments of tropical forests and different species composition might have the potential to change the light saturation range.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.5hqbzkh39.

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FIGURE LEGENDS

FIGURE 1 Normalized leaf net photosynthesis (A_n) in response to light (PPFD; µmol/m²/s), averaged over a set of eight tropical tree species (10 trees in total) and a total of 23 leaves measured at the Nouragues site for (a) top sunlit leaves (n = 15 leaves), (b) middle canopy foliage (n = 3) and (c) lower canopy foliage (n = 5), and a set of 15 tropical tree species (17 trees and 12 saplings) and a total of 44 leaves measured at the Paracou site for (d) top sunlit leaves (n = 13 leaves), (e) lower canopy foliage (n = 19) and (f) saplings (n = 12). The error bars are the standard errors of the mean. The black filled points, underlined with a black line, indicate the light saturation range, which is the range of PPFD levels at which A_n is light saturated and for which the points do not significantly differ from each other ($p > 0.05$). The slope between these data points is not significantly different from zero. The inset is a zoom of the main figure for which normalized A_n ranges between 0.85 and 1.

FIGURE 2 Normalized mean of leaf net photosynthesis (A_n; µmol/m²/s) in response to light (PPFD; µmol/m²/s) for seven pioneer trees (n = 7). The error bars are the standard errors of the

mean. Light-saturated leaf net photosynthesis was not reached according to the criteria for testing light saturation (see Methods).

FIGURE 3 Leaf-level net photosynthesis at 2000 µmol/m²/s ($A_{sat,2000}$) derived from a nonrectangular hyperbola based model (Eq. 2) in function of the leaf-level net photosynthesis at 1000 µmol/m²/s ($A_{sat,1000}$) derived from the measured data. 1000 µmol/m²/s is assumed to be at light saturation in this study since it is at the lower PPFD for which A_n saturated here. Grey dots represent $A_{sat,1000}$ data that are within five percent from $A_{sat,2000}$ (n = 50). Yellow dots represent $A_{sat,1000}$ that are above $A_{sat,2000}$ + 5% (n = 7). Blue dots represent $A_{sat,1000}$ below $A_{sat,2000}$ − 5% (n = 12). The error bars show the 5%-derivations from $A_{sat,2000}$. The black line is the 1:1 line.

FIGURE 4 The stomatal conductance (g_s; mol/m²/s) measured at PPFD = 2000 µmol/m²/s compared to the stomatal conductance at the common saturating PPFD level of 1000 µmol/m²/s (n = 68). 56 points are above the 1:1 line (black line), and 12 are below the 1:1 line.
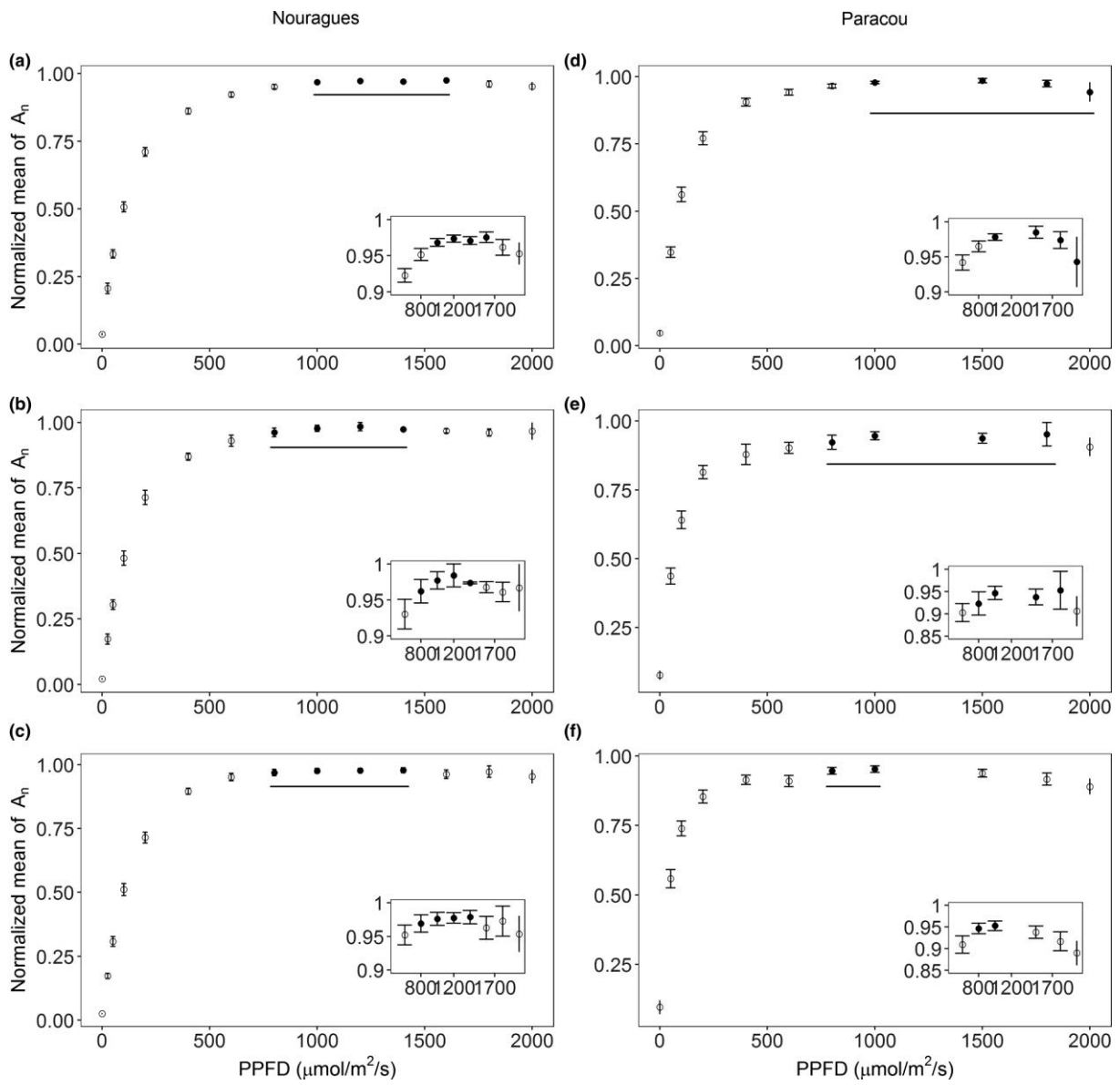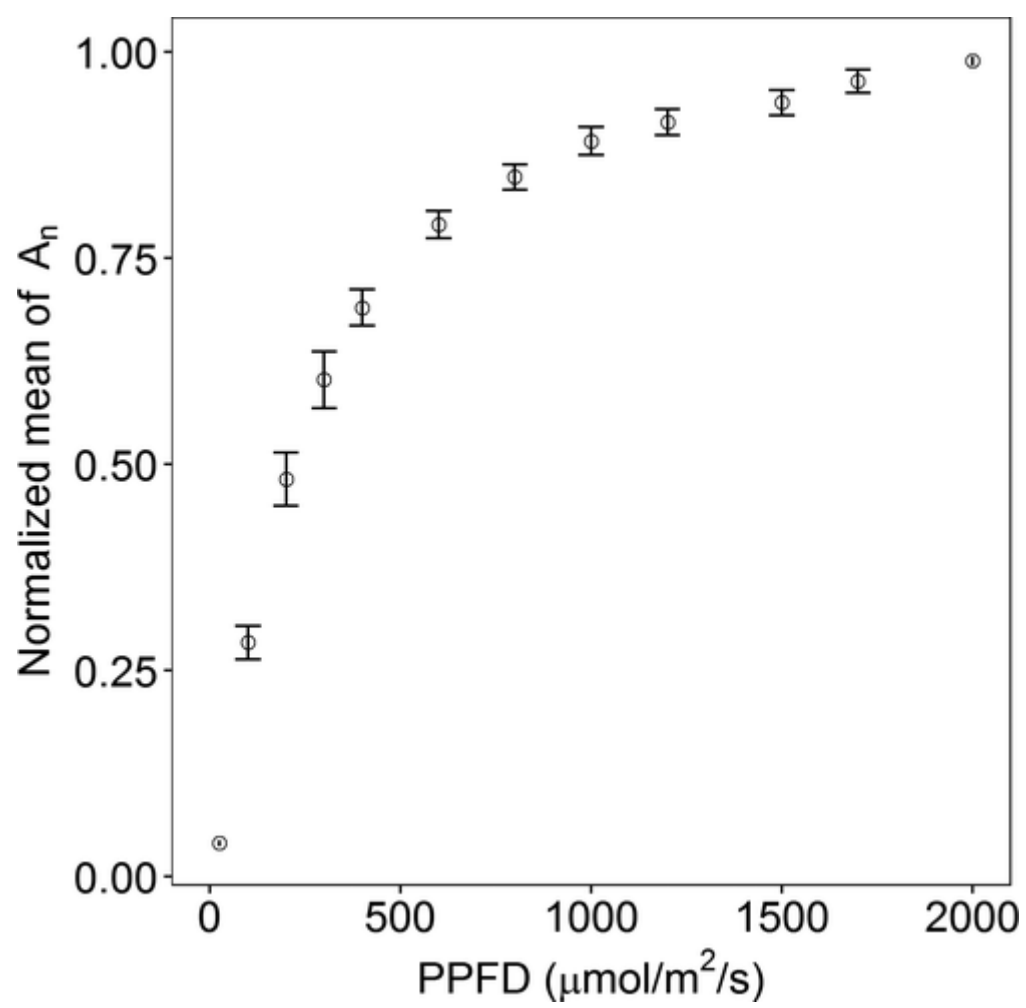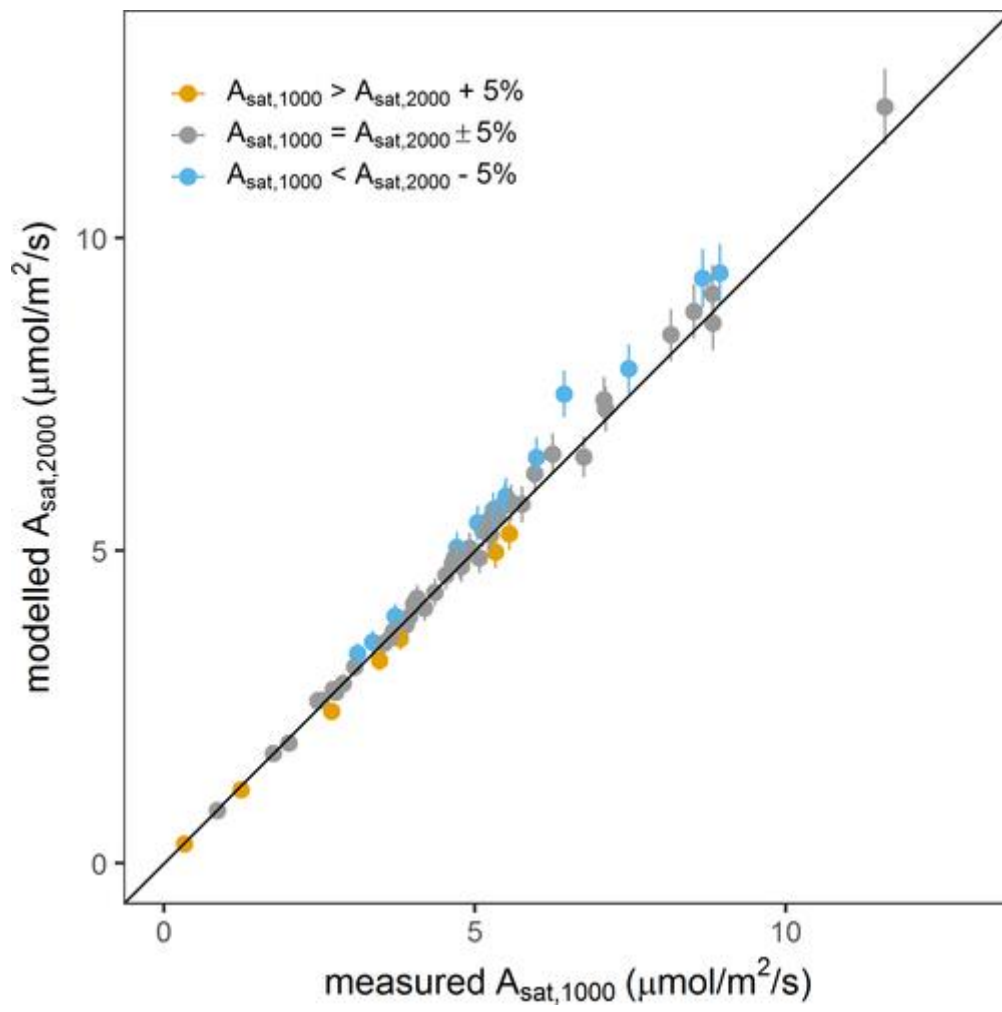
Figure 1

Figure 2

Figure 3

Figure 4