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Z. Carter Berry
Chapman University, zcberry@gmail.com

Gregory R. Goldsmith
Chapman University, goldsmit@chapman.edu

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DR Z. CARTER BERRY (Orcid ID : 0000-0001-7227-819X)
DR GREGORY R GOLDSMITH (Orcid ID : 0000-0003-3567-8949)

Diffuse light and wetting differentially affect tropical tree leaf photosynthesis

Z. Carter Berry & Gregory R. Goldsmith

 Schmid College of Science and Technology, Chapman University, Orange, CA, 92866, USA

ORCID IDs:
Z. Carter Berry: https://orcid.org/0000-0001-7227-819X
Gregory R. Goldsmith: https://orcid.org/0000-0003-3567-8949

Corresponding Author Contact:
Z. Carter Berry
One University Drive
Schmid College of Science and Technology
Chapman University
Orange, California 92866
336-769-6743
zcberry@gmail.com

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Summary

-Most ecosystems experience frequent cloud cover resulting in light that is predominantly diffuse

rather than direct. Moreover, these cloudy conditions are often accompanied by rain that results in wet

leaf surfaces. Despite this, our understanding of photosynthesis is built upon measurements made on

dry leaves experiencing direct light.

-Using a modified gas exchange setup, we measured the effects of diffuse light and leaf wetting on

photosynthesis in canopy species from a tropical montane cloud forest.

-We demonstrate significant variation in species-level response to light quality independent of light intensity. Some species demonstrated 100% higher rates of photosynthesis in diffuse light while others had 15% greater photosynthesis in direct light. Even at lower light intensities, diffuse light photosynthesis was equal to that under direct light conditions. Leaf wetting generally led to decreased photosynthesis, particularly when the leaf surface with stomata became wet, however, there was significant variation across species.

-Ultimately, we demonstrate that ecosystem photosynthesis is significant altered in response to environmental conditions that are ubiquitous. Our results help explain the observation that net ecosystem exchange can increase in cloudy conditions and can improve the representation of these processes in earth systems models under projected scenarios of global climate change.

Introduction

Our understanding of photosynthesis is predominantly based on measurements made on dry leaves receiving direct light. But nearly all ecosystems spend considerable time in cloudy conditions, which results in diffuse light. When these clouds are accompanied by precipitation events, leaves and canopies become wet. Understanding the relationship between photosynthesis and environmental conditions is critical for modeling ecosystem primary productivity and research to date has considered many of these variables such as temperature (Way & Oren, 2010), light intensity (Ruimy et al., 1995), CO_2 concentration (Norby & Zak, 2011) and soil moisture (Meir & Woodward, 2010). Explicit tests of the effects of diffuse light or leaf wetting on leaf or canopy photosynthesis are exceedingly limited with only 11 studies in the last 10 years (diffuse light: Brodersen et al., 2008; Mercado et al., 2009; Brodersen & Vogelmann, 2010; Urban et al., 2012; Kanniah et al., 2013; Urban et al., 2014; Cheng et al., 2015; Earles et al., 2017; leaf wetting: Letts et al., 2010; Aparecido et al., 2017; Gerlein-Safdi et al., 2018). In addition, many of these are conducted in highly controlled lab and greenhouse settings which may not reflect the complex environmental conditions and physiological responses that occur in the field.

Light generally arrives to the canopy in direct, parallel beams but is scattered as it encounters particles in the air. If enough radiation is scattered, then the apparent radiation at the plant canopy is no longer direct, but rather predominantly diffuse light. For plant canopies, this most commonly occurs when clouds and aerosols scatter radiation (Mercado et al., 2009). Here, we define diffuse or direct light as conditions where the majority of light arrives in one or the other form, but note that any environmental condition will have some proportion of both forms. At ecosystem scales, diffuse light can increase primary productivity (Roderick et al., 2001; Gu et al., 2003; Urban et al., 2007; Mercado et al., 2009). This increase has largely been ascribed to light penetrating deeper into the canopy and reaching more leaf surface area (Gu et al., 2002; Alton et al., 2007; Urban et al., 2007, 2012; Alton, 2008; Kanniah et al., 2013; Williams et al., 2014; Cheng et al. 2015). Only a few studies have explored how diffuse light might alter photosynthesis at the leaf level. These studies have concluded

that, at the same total light, diffuse light inhibits photosynthesis by 10 to 20% (Brodersen et al., 2008; Urban et al., 2014; Earles et al., 2017). Thus, leaf-level data suggest that diffuse light decreases photosynthesis, while ecosystem studies find that it increases productivity. Understanding the effects of diffuse light on primary productivity is critical for constraining carbon cycling, particularly given that climate change models project an increase to cloud cover and aerosols, which will lead to an increase in diffuse light conditions (Warren et al., 2007; Kanniah et al., 2012).

In addition to changing the quality of light, clouds often bring precipitation leading to wet canopies. Plants in tropical forest ecosystems experience leaf wetting an average of 174 days every year; however, it is assumed that limited carbon exchange occurs when the canopy is wet (Dawson & Goldsmith, 2018). The presumed mechanism for this reduction is that water on leaf surfaces creates a physical barrier for the uptake of CO_2 and therefore limits photosynthesis (Ishibashi & Terashima, 1995; Hanba et al., 2004; Letts et al., 2010). However, this assumes that a film of water entirely covers most stomata during a wetting event. Thus, at the leaf scale, whether there is a reduction in photosynthesis due to this physical barrier will be species- and context-dependent based on wettability of leaf surfaces and spatial distribution of stomata (Aparecido et al., 2017). At the ecosystem scale, leaf wetness has been shown to reduce primary productivity and net ecosystem exchange (Misson et al., 2005; Mildenberger et al., 2009). However, it is challenging to isolate the effect of leaf wetness relative to changes in the intensity and quality of light. In addition, eddy covariance, the primary methodology for measuring net ecosystem exchange, does not work under wet conditions and this limits our understanding of ecosystem primary productivity during leaf wetting events.

Nowhere on Earth does our limited understanding of the effects of cloudy and wet environmental conditions on photosynthesis and ecosystem primary productivity pose more of a problem than in tropical forests. Tropical forests account for 50% of the 2.4 ± 0.4 Pg of carbon stored by terrestrial vegetation, despite experiencing frequent cloud cover and wetting (Pan et al., 2011; Wilson & Yetz, 2016; Dawson & Goldsmith, 2018). Thus, our limited mechanistic understanding of photosynthetic carbon uptake during these periods challenges our ability to estimate both current and future global carbon budgets.

We address the simple yet fundamental question, how do photosynthetic rates change when the angle of light changes and leaves are wet? Understanding the effects of these common environmental conditions on carbon assimilation could improve our estimations of ecosystem primary productivity and reveal new insights into how species maximize photosynthesis given different environmental conditions. Using a tropical rainforest system that commonly experiences these climate conditions, we had three objectives: (1) determine if there are species-specific responses to diffuse light conditions and canopy wetting, (2) test if these responses are driven by morphological and physiological characteristics that influence light penetration, leaf wetting patterns, and carbon uptake, and (3) place the results in the context of common environmental conditions to understand the implications for ecosystem primary productivity. Research to date would lead us to hypothesize that

diffuse light and leaf wetting both lead to a consistent and demonstrable decrease in photosynthesis; however, our results clearly demonstrate that photosynthetic responses to cloudy and wet conditions are species-specific. Moreover, we show that increases in photosynthesis under diffuse light can help explain ecosystem studies showing similar patterns and contribute to improving the representation of these processes in earth systems models.

Materials and Methods

Study Site and Sampling

The study was conducted in a tropical montane cloud forest on the Pacific slope of the Cordillera de Tilarán mountains in Monteverde, Costa Rica (10°17'43" N, 84°47'37" W, 1532 m a.s.l.). Trees were sampled from within a 4 ha long-term forest dynamics plot in the Monteverde Cloud Forest Reserve (Nadkarni et al., 1995). The plot is described by Haber et al. (2000) as old growth lower montane wet forest. The mean annual temperature is 18.8°C, the mean annual rainfall 2519 mm, and average annual relative humidity of 97% (Clark et al., 2000, S. Gotsch unpublished data). Climate is relatively aseasonal, although there is a dry season extending from February to May. Rainfall during the dry season decreases, but fog and wind-driven horizontal precipitation persists and leads to frequent leaf wetting (Goldsmith et al., 2013).

Previous studies in tropical montane cloud forests suggest that solar radiation can be reduced by 10% to 66% during fog and wind-driven precipitation events (Clark et al., 2000; S. Gotsch pers. comm.). At our study site, we find that midday photosynthetically active radiation (1200 to 1400 solar time) is above 410 μmol m^{-2} s^{-1} 81% of the time (Figure S1; *S. Gotsch* unpublished data). The interquartile range of the distribution spans from 496 μmol m^{-2} s^{-1} to 1381 μmol m^{-2} s^{-1}. While we do not have precise data on the fraction of time in direct and diffuse light, we do know the frequency of clouds from remote sensing products. Goldsmith et al. (2013) used a remote sensing product to demonstrate that clouds were frequently observed in daytime images during both the wet (89 $\pm$ 9 %) and dry (52 $\pm$ 11 %) seasons. Urban et al. (2012) found that cloudy periods typically increased the diffuse index greater than 0.7 compared to less than 0.3 during sunny conditions. From these data, we can conclude that (1) diffuse light conditions are a predominant feature in this ecosystem and (2) light intensity is at or above the light compensation points of species 81% of midday hours.

We selected eight common canopy tree species using plot census data on basal area and number of stems collected in 2011 on all individuals >30 cm DBH (Table S1). The species were *Cecropia polyphlebia* Donn. Sm., *Conostegia rufescens* Naudin, *Elaeagia auriculata* Hemsl., *Ficus spp.*, *Heliocarpus americanus* L., *Meliosma vernicosa* (Liebm.) Griseb., *Ocotea meziana* C.K. Allen, and *Ocotea tonduzii* Standl.. All species are considered canopy emergent (although they have different successional patterns) and were only sampled if the tree was mature and sun-exposed. We were unable to locate sufficient individuals from a single species of the genus *Ficus*, which accounts

for a high proportion of the plot basal area, but is low in abundance. Branch samples were collected from 5 – 7 canopy emergent individuals of each species by using a slingshot to secure a branch at least 1 m in length. Once collected, the cut portion of each branch was immediately placed in water and the end of the branch recut. The branch remained in the field in the water during all gas exchange measurements and measurements were begun within 1 hr of collection.

Photosynthesis Data

We performed light response curves on dry leaves followed by instantaneous measurements on wet leaves using a portable infrared gas analyzer (LiCor 6800, LiCor Inc. Lincoln, Nebraska, USA) between 20 June and 5 July 2018. For wet leaf measurements, only a single instantaneous value was taken to minimize the amount of time high concentrations of water vapor were entering the LiCor 6800 system. Measurements were made on one fully expanded, mature and healthy leaf between 09:00 and 14:00. If stomatal conductance showed signs of decreasing compared to measurements from other individuals as the day progressed, then measurements were stopped and the individual resampled the following day. Light response curves were only measured on dry leaves under direct light and diffuse light separately. Leaves were placed in the 6 x 6 cm large leaf chamber (Model 6800-13) with the accompanying red (65%), green (10%), blue (20%) and white (5%) LED light source and allowed to acclimate at a PAR of 1400 μmol m^{-2} s^{-1} until photosynthesis was stable. The light response curves began at the highest PAR value and subsequently decreased. When transitioning through each measurement, the leaf was allowed to acclimate under new conditions for at least 2 minutes. Temperature was held at 22°C, CO_2 concentration at 400 ppm, and relative humidity at 70% when leaves were dry.

Light response curves under direct and diffuse conditions required a modification to the traditional gas exchange system. To allow for quick changes between direct and diffuse light, we constructed an integrating sphere with ports for mounting a light source both on the top and side of the sphere (Brodersen et al., 2008). When the light source was mounted to the top of the sphere, light was predominantly direct, while mounting on the side port produced largely diffuse light at the leaf surface. When the light is in each position, some proportion of the light will always be direct and some proportion diffuse. While we did not measure the direct and diffuse fractions of light in each position, we followed the protocol of Brodersen et al. (2008) who quantified the angle of light in each environmental condition (22° for direct light, 105° for diffuse light). Each port was 6 cm^2 to accommodate the large light source and reflective covers were installed on ports not in use. To determine the amount of light that reached the leaf surface with this modified system, calibration curves were conducted in the lab to establish the intensity of light leaving the light source and the intensity arriving to the leaf surface (Figure S2). We also confirmed that the visible light spectra was not altered by diffusion (Figure S3). Curves under direct light had photosynthetically active radiation

(PAR) values that corresponded to 1370, 927, 566, 381, 275, 172, 105, and 39 μmol m^{-2} s^{-1}. Diffuse light curves had PAR values of 1210, 858, 634, 397, 286, 206, 128, and 53 μmol m^{-2} s^{-1}.

Following light response curves on a dry leaf, the leaf was removed from the chamber, misted thoroughly on the adaxial surface, lightly shaken to remove any excess water, and placed back in the chamber in the same position as before. Instantaneous measurements (not light response curves) were then made with wet leaves under direct and diffuse light at 1200 μmol m^{-2} s^{-1}. Dry measurements were always conducted before wet measurements because of concerns about our ability to completely dry a leaf again following wetting. Leaves were allowed to stabilize with wet surfaces, which took as long as 20 to 30 minutes in some cases. Humidity control was turned off. If areas of the leaf became noticeably dry, the chamber was opened and the leaf sprayed again. Single instantaneous measurements at a PAR of 1210 μmol m^{-2} s^{-1} were taken with the adaxial leaf surface saturated with water under direct and diffuse light. To explore the effects of wetting on photosynthesis as a function of which leaf surface was wet, we conducted a follow-up experiment with *O. tonduzii* leaves from 5 individuals in the subcanopy. These leaves were wetted on both the ad- and abaxial side following the procedure above.

Measurements on wet leaves inhibited us from reporting stomatal conductance or transpiration values. Wet surfaces will increase the concentration of water vapor exiting the chamber due to the combination of both transpiration and evaporation of free water from the leaf surface. This results in erroneous values for transpiration rates, as the two components cannot be partitioned. In addition, the calculation of stomatal conductance also utilizes the concentration of water vapor out of the chamber. The calculation of photosynthesis does not require knowing stomatal conductance, but instead simply utilizes the flow rate and CO_2 concentration into and out of the leaf chamber (Jason Hupp, LiCor Biosciences, *pers. comm.*; Aparecido et al. 2017). Therefore, we report leaf photosynthetic rates, but exclude stomatal conductance and transpiration.

Leaf traits

The leaf used for the gas exchange measurements was harvested, placed in a sealed plastic bag with a damp paper towel and transported back to the lab for measurement of traits including leaf wetting capacity, leaf thickness, leaf area, specific leaf area (SLA), and stomatal density.

Leaf wetting capacity was measured as the difference between the mass of a leaf with a dry surface and the mass of the same leaf with water on the adaxial surface. To do this, a fresh mass was measured immediately upon removal from the plastic bag. Then, with the leaf held flat, the leaf was misted using a spray bottle until water was dripping off the leaf. The leaf was then tipped vertically to remove any excess water and the mass immediately measured. This process was repeated three times for each leaf and the three measurements averaged before determining the intensity of water on the leaf surface. The mass (g) of water on the leaf surface was standardized by the leaf area (cm^2).

Leaf thickness was measured at three locations on each leaf and averaged using digital calipers (resolution of 0.001 mm; Mitutoyo Corporation, Kawasaki, Japan). Leaf area was measured by scanning the leaf with a digital scanner and analyzed using ImageJ (version 1.51S, National Institute of Health, USA). Following all of these measurements, leaves were dried in a drying oven at 50°C for approximately 1 week and the dry mass measured to determine specific leaf area and leaf dry matter content. Stomatal density was measured by making stomatal impressions using either clear nail varnish or dental putty (Thermoclone VPS, Fast Set – Superlight Body). A thin layer of nail varnish was applied at three locations on each side of each leaf, allowed to dry, removed and mounted onto a glass slide. For species with waxy cuticles or trichomes, dental putty was first applied to the leaf surface and then nail varnish applied to the imprint of the dried dental putty to obtain a transparent impression of the leaf surface. Images were obtained from three locations on each impression using a compound microscope at either 20x or 40x. Guard cell length was measured on five stomata per image and the total number of stomata per image was counted.

Data analysis

We calculated the effects of diffuse light and wet leaf conditions on photosynthesis by calculating the paired difference in photosynthesis measurements for each individual leaf and then determining a species-level mean. We calculated the percent change in the same manner, by first determining percent change for each individual. To determine if the response to diffuse light or leaf wetting differed among species we conducted a one-way analysis of variance (ANOVA) and compared means using Tukey's HSD. For light response curves, we fit a non-rectangular hyperbola equation through each individual (Prioul & Chartier, 1977) as

$$A_{net} = \frac{\phi PAR + A_{max} - \sqrt{(\phi PAR + A_{max})^2 - 4k\phi A_{max}PAR}}{2k} - R_d \tag{1}$$

where A_{net} = net photosynthetic rate, ϕ = quantum yield, PAR = photosynthetically active radiation, R_d = dark respiration, and k = convexity factor. The light compensation point was calculated by setting A_{net} to 0 and the light saturation point was calculated as when A_{net} was 85% of A_{max}. To compare differences in light response curve parameters (including light compensation point, light saturation point, and quantum yield) for leaves of a given species experiencing direct vs. diffuse light, we conducted a two-tailed paired samples t-test. To determine how the response to diffuse light and leaf wetting varied as a function of morphological or physiological traits, we used a linear mixed-effects model with species as a random effect. All data analysis was conducted in R (version 3.4.2) or JMP (version 13.2, SAS Institute, North Carolina, USA).

Results

Photosynthesis under direct and diffuse light

Species demonstrated diverse leaf photosynthetic responses to light quality ($\Delta A_{DIRECT-DIFFUSE}$), with some species having greater photosynthesis under direct conditions and others under diffuse conditions (Figure 1). Three species had higher A_{net} under diffuse light conditions, 2 species had higher A_{net} under direct light conditions, and 3 species showed no significant differences between treatments (Figure 2a; $F_{7, 31} = 5.58$, p < 0.001). For species demonstrating greater photosynthesis in diffuse light, we observed as much as a 3.4 ± 1.0 μmol m^{-2} s^{-1} difference between measurements (*O. tonduzii*, n=5), which corresponded to a 100% increase in photosynthetic rates. For species with greater photosynthesis under direct light conditions, values tended to be greater by 10 to 20%. When leaves were wet, photosynthesis in direct light was reduced, which resulted in diffuse light A_{net} being higher for most species when wet (Figure 2b).

Diffuse light also resulted in higher light compensation points ($t_{38} = 1.76$, p = 0.04) and light saturation points ($t_{38} = 2.62$, p = 0.006), but did not alter the quantum yield of photosynthesis (Table 1; $t_{38} = 0.74$, p = 0.23). While there was an overall effect of diffuse light on light compensation points, there were pairwise differences for only two species. *Heliocarpus americanus* had a greater light compensation point under direct light while *C. rufescens* had a greater light compensation point under diffuse light. Four species (*C. rufescens*, *E. auriculata*, *H. americanus*, and *O. tonduzii*) had greater diffuse light saturation points, while the other four species showed no significant differences in the post hoc pairwise comparisons. The shifts in light saturation point were large, ranging from 153 μmol m^{-2} s^{-1} to 391 μmol m^{-2} s^{-1}. The four species with significant differences in light saturation points included two with significantly greater photosynthesis under diffuse light conditions and two with equal direct and diffuse light photosynthesis. Thus, it is not universally true that it requires more photosynthetically active radiation to reach light compensation and saturation under diffuse light conditions.

We then explored if leaf traits were related to $\Delta A_{DIRECT-DIFFUSE}$. Neither specific leaf area, leaf dry matter content, nor leaf thickness explained $\Delta A_{DIRECT-DIFFUSE}$ (Figure S4a, S4b, and S4c). However, there was a significant negative relationship between $\Delta A_{DIRECT-DIFFUSE}$ and increasing leaf thickness ($F_{1,37} = 14.62$; p < 0.001, $r^2 = 0.31$) when *Ficus spp.* was removed. Because of the response of the light saturation points to diffuse light, we also considered the relationship between the light saturation point and $\Delta A_{DIRECT-DIFFUSE}$ and found a significant positive relationship (p = 0.002, $r^2 = 0.60$; Figure S4d). Trait values for all species can be found in Table S2.

Photosynthesis of wet and dry leaves

Photosynthesis was reduced for six of the species when leaves were wet as compared to when leaves were dry under direct light (Figure 3a; $F_{6,28} = 3.49$, p = 0.011). Of the remaining species, photosynthesis was greater under wet conditions in *C. rufescens* and showed no change in *O. meziana*. The difference in dry and wet photosynthesis ($\Delta A_{DRY-WET}$) under diffuse light conditions was more consistent across species; all species except one had significantly higher A_{net} under dry conditions (all p-values were < 0.025).

Across all species, we found a significant positive relationship between $\Delta A_{DIRECT-DIFFUSE}$ and $\Delta A_{DRY-WET}$ (Figure S5a; $F_{1,37} = 19.41$, p < 0.0001). Thus, species that had greater A_{net} under diffuse light also had greater A_{net} under wet conditions. There were also positive relationships between A_{net} under diffuse (Figure S5b; $F_{1,37} = 18.56$, p = 0.0001) or wet (Figure S5c; $F_{1,37} = 17.85$, p = 0.0002) conditions and the A_{net} (instantaneous) under dry and direct light conditions. Thus, species with a lower A_{net} in dry, direct conditions tended to have greater A_{net} in diffuse conditions.

We then explored if leaf water storage capacity and stomatal density were related to the $\Delta A_{DRY-WET}$. The $\Delta A_{DRY-WET}$ demonstrated a significant positive relationship with leaf water storage capacity (Figure S6a; $F_{1,37} = 3.95$, p = 0.05, $r^2 = 0.50$) and a significant negative relationship with abaxial stomatal density (Figure S6b; $F_{1,37} = 6.77$. p = 0.01, $r^2 = 0.15$). None of the species possessed adaxial stomata. Thus, leaves that retained more water per unit area and had fewer stomata had a greater positive difference between dry and wet A_{net} values. Surprisingly, the presence of trichomes and leaf thickness did not explain the response of A_{net} to leaf wetting.

To further explore the photosynthetic response to leaf wetting, we compared photosynthetic rates for subcanopy leaves of *Ocotea tonduzii* when leaves were dry, wet on the adaxial side, and wet on the abaxial side (Figure 4). Photosynthesis rates were 68 - 71% lower when the abaxial side of the leaf was wet compared to dry leaves ($F_{5,24} = 6.78$, p = 0.0005). In post-hoc tests, there were no differences between diffuse and direct light photosynthesis within each treatment.

Comparing photosynthesis in common environmental conditions

Because clouds commonly reduce total available photosynthetically active radiation (PAR), we compared mean species' photosynthesis for dry leaves given saturating direct light (1200 μmol m^{-2} s^{-1}) to both wet and dry leaf diffuse light photosynthesis under low light (400 μmol m^{-2} s^{-1}) (Figure 5). The value of 400 μmol m^{-2} s^{-1} was used by analyzing local climate data, which found that fog typically reduces total solar radiation to 30 to 40% of maximum values (Haber et al., 2000; S. Gotsch pers. comm.). There were significant differences among the three scenarios, driven by significant reductions in photosynthesis under low diffuse light and wetting ($F_{2,116} = 12.06$, p < 0.001). The photosynthesis of wet leaves in low diffuse light was 33% (5.56 μmol m^{-2} s^{-1}) lower than dry and saturating direct light conditions (8.49 μmol m^{-2} s^{-1}). However, the mean rates of light-saturated

photosynthesis under saturating direct light and diffuse, low light (7.61 μmol m^{-2} s^{-1}) did not differ among species in post hoc comparisons.

Discussion

Our results demonstrate species-specific differences in photosynthesis depending on the angle of light and wetness of leaves. Despite expectations that diffuse light would consistently reduce photosynthesis, species ranged from 100% greater photosynthetic rates under diffuse light conditions to 15% greater photosynthetic rates under direct light conditions at the same light intensity. We also demonstrate that even when diffuse light environments have lower light intensities, photosynthesis is equal to that under direct light with high intensities, indicating greater light use efficiency (Figure 5). Leaf wetting primarily decreased photosynthesis, particularly when the leaf surface with stomata became wet. Interestingly, there was no consistent effect of species successional status on the response to diffuse light or wetting (e.g. *C. rufescens*, *H. americanus,* and *C. polyphlebia* are considered canopy emergent primary successional species). Ultimately, we demonstrate that photosynthetic rates vary significantly across species in response to environmental conditions that are prevalent, yet, rarely considered in understanding net primary productivity of ecosystems (but see Mercado et al., 2009). Below, we expand on the mechanisms that might explain these differences and explore the implications for ecosystem primary productivity.

Photosynthesis under diffuse light

Our results indicate that some species have greater photosynthesis under diffuse light while others have greater photosynthesis under direct light. Previous research has suggested that diffuse light results in higher absorption of light in the upper palisade layer, resulting in less light penetrating deeper into leaves and leading to a 10 -15 % reduction in the photosynthetic rates of two herbaceous species (Brodersen et al., 2007; Brodersen and Vogelmann, 2010; Earles et al., 2017). These studies also propose that sun-grown leaves have greater direct light photosynthesis relative to diffuse light due to a thicker palisade mesophyll (and greater overall thickness) that facilitates light penetration deeper into the leaf (Smith et al., 1997). Limited light penetration may be true in some species, but our results suggest that this is not universal. While all leaves were sun-exposed, species with greater photosynthesis under diffuse light were thicker, a characteristic of sun leaves, but also had low light saturation points, a characteristic of shade leaves (Figure S4c & S4d). This suggests that photosynthesis under diffuse conditions is driven by more than just leaf thickness. Leaf biochemistry could explain these responses. Enhanced diffuse light photosynthesis could be driven by greater chloroplast concentration in the upper layers of palisade mesophyll cells or by improved efficiency through greater electron transport rates (J_{max}), the maximum rates of carboxylation (V_{cmax}), or the quantum yield of photosystem II (ϕ_{PSII}) (Hogewoning et al., 2012; Oguchi et al., 2011; Earles et al.,

2017). Understanding the mechanisms driving differences in photosynthesis in diffuse light would add to our ability to predict the response of primary productivity to changing cloud cover conditions (Karmalkar et al., 2011)

In natural conditions, diffuse light is often accompanied by changes to light intensity. Diffuse light is the result of scattering due to aerosols and clouds which typically results in less total light arriving at the canopy (Oliphant et al., 2011; Kanniah et al., 2012). But this reduction in light intensity may not lead to reduced photosynthesis. In our study site, midday light levels are above 400 μmol m^{-2} s^{-1} 81% of the time, meaning that all study species spend the majority of the time above their light saturation point (Figure S1). The average response across species demonstrate that the increase in diffuse light photosynthesis can compensate for reduced light intensity, ultimately increasing the light use efficiency of forest canopies (Figure 5). The improved light use efficiency of leaves of certain species in diffuse light adds an additional explanation to studies that demonstrate greater ecosystem productivity under these conditions.

The spectral quality of light also changes in diffuse conditions with increased percentage of blue wavelengths and red to far-red ratios (Navratil et al., 2007; Grant, 1997; Reinhardt et al., 2010). These spectral changes are known to increase stomatal aperture and total photosynthetic rate (Shinazaki et al., 2007; Dengel and Grace, 2010) and lead to greater canopy productivity (Urban et al., 2007). While this study did not test spectral quality (direct and diffuse light had similar spectra), these potential changes would only further increase photosynthesis under diffuse light. Thus, the reduction in diffuse light photosynthesis for some species in this study may be compensated for by increased stomatal conductance. The total photosynthetic rate of a canopy will be dependent on species-level responses to directionality, intensity, and spectral quality, with the net effect largely increasing photosynthesis in diffuse light.

Photosynthesis during leaf wetting

Wetting of the adaxial surface of the leaf resulted in reduced photosynthetic rates in six of eight species. This is similar to Aparecido et al. (2017), who found reductions in photosynthesis in nine out of ten species from a temperate savanna and tropical rainforest. However, both studies demonstrate notable variation across species. The proposed mechanism of water creating a CO_2 diffusion barrier (Ishibashi & Terashima, 1995; Hanba et al., 2004; Letts et al., 2010) misses a key point; in many tree species (and this study) wetting mostly occurs on the adaxial side of a horizontally oriented leaf, while most species have stomata predominantly on abaxial sides of leaves. Leaf wetting should also change the water status of the leaf through foliar water uptake (e.g. Berry et al., 2018), create a more humid boundary layer on the bottom of the leaf, and scatter light. However, all of these effects should increase stomatal conductance and photosynthesis, which would explain the increased photosynthesis during wetting in *C. rufescens*. It is possible that *C. rufescens* has greater stomatal conductance or foliar water uptake under wet conditions, driving the increased photosynthesis. But for

species with reduced photosynthesis in wet conditions, this leaves us with the lack of a clear mechanism. Despite this, we find that species capable of storing greater quantities of water on their leaf surfaces and those that have fewer stomata show the greatest reductions in photosynthesis when wet (Figure S6). While these relationships cannot resolve the mechanism(s), they suggest that traits that confer water retention and carbon uptake are linked to photosynthesis under wet conditions.

The results from this study demonstrate at least three different ways for maximizing photosynthesis given wet conditions. The first way, which has long been presumed to be the most common, is that species in wet ecosystems need to avoid being wet for extended periods; i.e. these species have leaf surface properties (cuticle structures or waxy layers) that make them very hydrophobic (Smith and McClean, 1989; Fernandez et al., 2017). However, Goldsmith et al. (2017) demonstrates that tropical rainforest leaves are largely hydrophilic, so many species must be able to maximize photosynthesis despite having leaves where water spreads across the surface. Secondly, species can have suites of leaf traits that maximize daily carbon gain through higher photosynthetic rates during dry conditions, thus compensating for low photosynthesis during wet conditions. Finally, other species may have stomata on abaxial surfaces where wetting is less likely to occur, thus minimizing the inhibition of photosynthesis during wetting events (Aparecido et al., 2017). With recent estimates demonstrating that tropical rainforest canopies experience wetting on more than half the days of the year (Dawson and Goldsmith, 2018), it is logical that multiple functional strategies have evolved to maximize photosynthesis.

Ecosystem implications

Changes in light intensity, light quality and leaf wetting often occur in tandem, such as when clouds bring rainfall and diffuse light simultaneously. We find that when leaves are wet, photosynthetic rates are greater or equal under diffuse versus direct light conditions (Figure 2b). The fact that species with greater direct light photosynthesis had lower values under wet conditions while those with greater diffuse light photosynthesis were relatively unaffected reinforces a critical point: that the response to diffuse light and wet conditions varied similarly across species. In other words, species with greater photosynthesis under diffuse light tended to have greater photosynthesis in wet conditions. It is possible that the structural and functional traits that maximize photosynthesis in diffuse light might also serve similar functions for leaf wetness. Additionally, it is likely that films of water on leaf surfaces cause some additional scattering functionally resulting in diffuse conditions even if incoming light is predominantly direct (Egri et al., 2010).

These results provide an additional explanation for ecosystem studies demonstrating that diffuse light conditions can increase the light use efficiency and total carbon stored (Gu et al., 2002; Urban et al., 2007, 2012; Alton, 2007; Kanniah et al., 2012; Williams et al., 2014; Cheng et al., 2015). This diffuse fertilization effect (Roderick et al., 2001) posits that diffuse light can penetrate deeper into complex canopies and illuminate many understory leaves. Our results find that increased

ecosystem diffuse light photosynthesis could also be explained by a species assemblage that has increased leaf photosynthesis in diffuse light. Ecosystem photosynthesis of wet canopies is less clear, as standard methods (e.g. eddy covariance) do not work in wet conditions and disentangling the effects of canopy wetting from diffuse light remains challenging.

Anthropogenic climate change will alter cloud cover, influencing light intensity and quality as well as the frequency and duration of leaf wetting. While understanding how cloud patterns will change given future climate scenarios remains difficult, ensemble models such as CMIP5 project major changes to precipitation variability (e.g. dry sunny days vs. cloudy and rainy days) in the future (e.g. Polade et al., 2014). At tropical latitudes, models project an increase in cloud cover and higher cloud bases, which may lead to increased diffuse light periods (Norris et al., 2016). Additionally, Mercado et al. (2009) modeled an increase in the diffuse radiation fraction from 1960 to 1999, leading to a 23.7% increase in the net ecosystem exchange (NEE). Similar research on the ecosystem effects of leaf wetting on productivity remains limited (Dawson and Goldsmith, 2018). Linking the integrated effects of changing cloud patterns to empirical data on changes in ecosystem productivity will be a key feature to improving models.

Conclusions

Almost every measurement of leaf-level photosynthesis is made on a dry leaf experiencing direct light. However, this is a vast oversimplification of the complex environmental conditions experienced by most plants. It is easy to assume that diffuse light and leaf wetting are conditions under which we would expect minimal photosynthesis and therefore only nominal contributions to ecosystem primary productivity. However, our results indicate that photosynthesis does not cease under these conditions. In fact, certain species can double their photosynthetic rates under diffuse light conditions. Even at lower light intensities, diffuse light photosynthesis can still equal or be greater than direct light photosynthesis at saturating light intensities. This may help explain the growing number of studies that demonstrate higher net ecosystem exchange when it is cloudy (Roderick et al., 2001; Gu et al., 2003; Urban et al., 2007; Mercado et al., 2009). Rather, the single most detrimental effect on photosynthesis is likely to be when canopies are wet. However, this is not driven by CO_2 limitation as reductions still occur despite wetting only in areas without stomata. Importantly, the directionality and magnitude of these changes are likely to be highly species-specific. Ultimately, understanding the effects of light quality and leaf wetting on photosynthesis, as well as how this varies among plant functional types, will allow us to better constrain estimates of primary productivity in earth systems models.

Author Contributions

ZC Berry and GR Goldsmith both planned and designed the experiment and collected data. ZC Berry analyzed the results and wrote the manuscript with feedback from GR Goldsmith.

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Supplemental Information

Table S1. List of species used in this study.

Table S2. Leaf traits measured of the eight species.

Figure S1. Distribution of light intensity data from the field site.

Figure S2. Integrating sphere calibration curves.

Figure S3. Spectral analysis of direct and diffuse light used in the study.

Figure S4. Relationships between diffuse light photosynthesis and leaf traits.

Figure S5. Relationships between diffuse light photosynthesis and wet leaf photosynthesis.

Figure S6. Relationships between wet leaf photosynthesis and leaf traits.

Tables

Table 1. Light response curve parameters for eight canopy tree species from a tropical montane forest in Monteverde, Costa Rica.

Species	Direct				Diffuse			
	A_{net} ($\mu mol\ m^{-2}\ s^{-1}$)	Φ ($\mu mol\ CO_2\ \mu mol^{-1}$ photon)	Light compensation point ($\mu mol\ m^{-2}\ s^{-1}$)	Light saturation point ($\mu mol\ m^{-2}\ s^{-1}$)	A_{net} ($\mu mol\ m^{-2}\ s^{-1}$)	Φ ($\mu mol\ CO_2\ \mu mol^{-1}$ photon)	Light compensation point ($\mu mol\ m^{-2}\ s^{-1}$)	Light saturation point ($\mu mol\ m^{-2}\ s^{-1}$)
Cecropia polyphlebia	11.00 ± 0.76	0.087 ± 0.013	18.5 ± 1.5	630.8 ± 81.6	10.29 ± 1.21	0.082 ± 0.024	23.3 ± 3.7	672.7 ± 125.4
Conostegia rufescens	4.69 ± 0.42	0.046 ± 0.006	5.0 ± 2.3	221.7 ± 39.2	7.69 ± 0.47	0.042 ± 0.003	10.4 ± 3.0	494.0 ± 105.2
Elaeagia.auriculata	11.42 ± 0.28	0.068 ± 0.010	12.6 ± 2.0	411.8 ± 59.1	10.27 ± 0.42	0.094 ± 0.027	17.6 ± 2.7	586.2 ± 77.0
Ficus spp.	11.71 ± 1.25	0.061 ± 0.013	17.1 ± 4.2	830.7 ± 233.1	9.79 ± 0.79	0.062 ± 0.015	16.8 ± 4.0	734.7 ± 183.5
Heliocarpus americana	12.89 ± 1.42	0.056 ± 0.003	21.8 ± 2.5	649.1 ± 133.2	12.81 ± 1.10	0.047 ± 0.004	19.4 ± 3.2	802.9 ± 110.2
Meliosma vernicosa	6.28 ± 1.01	0.073 ± 0.013	12.5 ± 1.5	342.4 ± 67.4	5.91 ± 1.21	0.090 ± 0.023	14.3 ± 3.2	440.2 ± 125.2
Ocotea meziana	7.73 ± 1.22	0.073 ± 0.015	10.6 ± 2.4	392.9 ± 121.7	8.93 ± 0.89	0.061 ± 0.006	7.8 ± 2.0	352.3 ± 41.1
Ocotea tonduzii	5.73 ± 1.44	0.058 ± 0.005	13.4 ± 3.3	349.2 ± 80.0	9.18 ± 0.79	0.082 ± 0.030	16.4 ± 1.7	740.6 ± 229.8

Leaves were exposed to either direct or diffuse light and the values were derived from curves on 5-7 individuals of each species. Data are means ± standard error. The Φ is the quantum yield of photosynthesis. All parameters were derived by fitting a non-rectangular hyperbola equation through each individual (Prioul & Chartier, 1977) and averaging the parameters for each species.

Figure Captions

Figure 1. Light response curves conducted under direct (closed circles) or diffuse (open circles) light conditions for eight canopy tree species occurring in a tropical forest in Monteverde, Costa Rica (n = 5-7 individuals). The x-axis represents photosynthetically active radiation (PAR). Each panel (a-h) represents a different species. Data was collected using the LiCor LI-6800 modified with an attached integrating sphere to create diffuse light conditions. Temperature was held at 22°C, CO_2 concentration at 400 ppm, and relative humidity at 70%. Data are means ± standard error.

Figure 2. The difference between leaf photosynthesis (*A*) values observed under direct and diffuse light conditions for eight canopy tree species occurring in a tropical forest in Monteverde, Costa Rica. Measurements were taken at a light level of 1210 μmol m^2 s^{-1} when leaves were dry (a) or wet (b) and are reported as the absolute difference in photosynthesis. Values that are above zero had greater photosynthesis under direct light conditions while those below zero had greater photosynthesis under diffuse light conditions. Points represent the average of 5-7 individuals ± standard error with the box plot representing the distribution of all species.

Figure 3. The difference between photosynthesis (*A*) values taken when leaves are dry and wet on the adaxial surface for eight canopy tree species occurring in a tropical forest in Monteverde, Costa Rica. Measurements were taken at a light level of 1210 μmol m^2 s^{-1} when light was direct (a) or diffuse (b) and are reported as the absolute difference in photosynthesis. Values that are above zero had greater photosynthesis when leaves were dry while those below zero had greater photosynthesis when leaves were wet. Points represent the average of 5-7 individuals ± standard error with the box plot representing the distribution of all values.

Figure 4. Photosynthetic rates for subcanopy leaves of *Ocotea tonduzii* when dry, wet on the adaxial surface (top of leaf), and wet on the abaxial surface (bottom of leaf). Leaves were located 5-10 meters off the ground under a closed canopy. Measurements were taken under both direct (circles) and diffuse (triangles) light conditions. Data represent means of 5 individuals per treatment ± standard error.

Figure 5. Boxplot of photosynthetic rates observed under three common environmental conditions; (1) full sun (dry leaf, direct and saturating light), (2) cloudy conditions (dry leaf, diffuse, and low light), or (3) rain or fog conditions (wet leaf, diffuse, and low light). Box plots represent the aggregate of eight different canopy tree species (n = 5-7 per species). High light or low light values were calculated from light response curves and chosen as 1200 μmol m^{-2} s^{-1} (saturating light) or 400 μmol m^{-2} s^{-1} (low light). Significant differences were determined using Tukey's HSD and are denoted on the figure.