

# Amazon Forest Structure Generates Diurnal and Seasonal Variability in Light Utilization

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## Abstract

The complex three-dimensional (3D) structure of tropical forests generates a diversity of light environments for canopy and understory trees. Understanding diurnal and seasonal changes in light availability is critical for interpreting measurements of net ecosystem exchange and improving ecosystem models. Here, we used the Discrete Anisotropic Radiative Transfer (DART) model to simulate leaf absorption of photosynthetically active radiation (*I*APAR) for an Amazon forest. The 3D model scene was developed from airborne lidar data, and local measurements of leaf reflectance, aerosols, and PAR were used to model *I*APAR under direct and diffuse illumination conditions. Simulated *I*APAR under clear sky and cloudy conditions was corrected for light saturation effects to estimate light utilization, the fraction of *I*APAR available for photosynthesis. Although the fraction of incoming PAR absorbed by leaves was consistent throughout the year (0.80-0.82), light utilization varied seasonally (0.67-0.74), with minimum values during the Amazon dry season. Shadowing and light saturation effects

1 moderated potential gains in forest productivity from increasing PAR during dry season  
2 months when the diffuse fraction from clouds and aerosols was low. Comparisons between  
3 DART and other models highlighted the role of 3D forest structure to account for seasonal  
4 changes in light utilization. Our findings highlight how directional illumination and forest 3D  
5 structure combine to influence diurnal and seasonal variability in light utilization, independent  
6 of further changes in leaf area, leaf age, or environmental controls on canopy photosynthesis.  
7 Changing illumination geometry constitutes an alternative biophysical explanation for  
8 observed seasonality in Amazon forest productivity without changes in canopy phenology.

## 10 **1 Introduction**

11 Seasonal and interannual variability in vegetation productivity has profound impacts  
12 on the global carbon cycle (e.g., Poulter et al., 2014; Zeng et al., 2014; Keppel-Aleks et al.,  
13 2014; Le Quéré et al., 2013; Gatti et al., 2014; Schimel et al., 2015; Cleveland et al., 2015).  
14 Understanding the mechanisms that link environmental variability and vegetation productivity  
15 is particularly important to constrain projections of Earth system feedbacks under future  
16 climate (e.g., Keppel-Aleks et al., 2014; Cox et al., 2013; Randerson, 2013; Boisier et al.,  
17 2015). Under current climate conditions, few tropical forest regions experience temperature  
18 limitations on biologic activity (Nemani et al., 2003), yet to the degree to which water and  
19 light limit forest productivity remains controversial (e.g., Gatti et al., 2014; Morton et al.,  
20 2014; Phillips et al., 2009; Restrepo-Coupe et al., 2013; Samanta et al., 2012; Doughty et al.,  
21 2015; Guan et al., 2015). A detailed understanding of vegetation productivity over large  
22 spatial scales has proven elusive, even using remote sensing data and ecosystem models (e.g.,  
23 Cleveland et al., 2015), given limited data on how species diversity (ter Steege et al., 2013),  
24 strategies for resource competition (e.g., Chave et al., 2010), and interactions between human  
25 and natural systems contribute to spatial and temporal dynamics of tropical forest productivity  
26 (e.g., Chen et al., 2010; Morton et al., 2013; Oliveira et al., 2007; Rap et al., 2015).

27 A more detailed investigation of the underlying mechanisms of Amazon forest  
28 productivity may offer new insights into the spatial and temporal variability in Amazon forest  
29 functioning. Previous studies have collected detailed data on forest growth or net carbon  
30 uptake to estimate seasonal (e.g., Saleska et al., 2003; Hutyyra et al., 2007; Restrepo-Coupe et  
31 al., 2013; Malhi et al., 2015) or interannual variability in Amazon forest productivity  
32 (Nepstad et al., 2007; Gatti et al., 2010; Gatti et al., 2014; Phillips et al., 2009; Doughty et al.,

1 2015). A separate line of analysis has analyzed satellite data on vegetation structure and  
2 reflectance (e.g., Morton et al., 2014), solar-induced fluorescence (e.g., Joiner et al., 2011;  
3 Parazoo et al., 2013; Lee et al., 2013; Guan et al., 2015), canopy moisture (Frolking et al.,  
4 2011; Saatchi et al., 2013), rainfall (Lewis et al., 2011), terrestrial water storage (Chen et al.,  
5 2013b), and fire (Chen et al., 2013a) to characterize Amazon forest responses to large-scale  
6 environmental variability. Most previous studies directly compared environmental inputs and  
7 forest carbon dynamics without a mechanistic approach to translate environmental variability  
8 into differences in plant-available water or light (e.g., Huete et al., 2006; Lewis et al., 2011;  
9 Brando et al., 2010; Doughty et al., 2015; Guan et al., 2015). In addition, few studies have  
10 jointly considered seasonal dynamics in resource availability and forest responses beyond the  
11 scale of forest inventory plots or tower footprints (e.g., Oliveira et al., 2007; Nepstad et al.,  
12 2007; Doughty et al., 2015; da Costa et al., 2010; Asner et al., 2004; Stark et al., 2012),  
13 highlighting the important role of ecosystem models for regional carbon flux estimates.

14 Improving the representation of complex forest canopies in ecosystem models is  
15 essential to understand how variability in canopy illumination contributes to changes in  
16 Amazon forest productivity. Many ecosystem models are structured to partition light and  
17 water vertically, with only local consideration of horizontal resource competition (e.g.,  
18 Moorcroft et al., 2001; Sitch et al., 2003; Krinner et al., 2005; Clark et al., 2011). The  
19 influence of vertical structure on light availability is widely recognized (e.g., Moorcroft et al.,  
20 2001; Clark et al., 2011; van der Tol et al., 2009; Gibelin et al., 2008; Sellers et al., 1992), yet  
21 the influence of horizontal variability in forest structure on light availability is rarely directly  
22 considered in dynamic global vegetation models (except see Scheiter et al., 2013). Horizontal  
23 variability in forest 3D structure results from fine-scale processes of canopy turnover and gap  
24 formation (e.g., Hunter et al., 2015; Asner et al., 2013); within-biome variability in tropical  
25 forest structure may also reflect large-scale environmental, climatic, and disturbance gradients  
26 (e.g., Morton et al., 2014; Saatchi et al., 2011; Baccini et al., 2012; Malhi et al., 2006;  
27 Espírito-Santo et al., 2014). Models of intermediate complexity may not fully account for  
28 shadowing and light saturation effects that alter light utilization—the degree to which leaf  
29 absorbed photosynthetically active radiation (*JAPAR*) can be used for photosynthesis.

30 Three-dimensional radiative transfer models offer the ability to quantify light  
31 interactions in complex forest canopies at the scale of individual leaves. A range of  
32 sensitivity studies highlight the importance of 3D structure for the representation of visible  
33 and near-infrared scattering and absorption in forest canopies (Widlowski et al., 2011;

1 Romanczyk et al., 2013; Gastellu-Etchegorry and Trichon, 1998). Several previous studies  
2 have used radiative transfer models to evaluate light absorption in tropical forest canopies and  
3 the impact of structure on forest productivity (e.g., Guillevic and Gastellu-Etchegorry, 1999;  
4 Alton et al., 2007a). There is broad interest in evidence for enhanced tropical forest  
5 productivity under diffuse light conditions (Oliveira et al., 2007; Rap et al., 2015; Mercado et  
6 al., 2009; Cirino et al., 2014; Alton et al., 2007b; Kanniah et al., 2012), but 3D radiative  
7 transfer models have not been specifically used to evaluate the potential for seasonal changes  
8 in tropical forest productivity based on the interactions between illumination geometry (direct  
9 and diffuse) and tropical forest structure.

10 Here, we developed a detailed Amazon forest scene in the DART model (Gastellu-  
11 Etchegorry et al., 2015) using airborne lidar data and in situ measurements of forest structure  
12 and reflectance properties, PAR, and aerosols. The goal of this work was to evaluate the  
13 influence of Amazon forest structure on leaf absorption and light utilization by explicitly  
14 accounting for shadowing and light saturation under diurnal and seasonal variability in  
15 illumination conditions. By targeting the mechanisms that link PAR availability, absorption,  
16 and light utilization in a 3D forest canopy, this study evaluated the potential responses of  
17 tropical forests to changing light conditions on seasonal or interannual time scales. This  
18 detailed investigation of light absorption, including the distribution of sunlit and shaded  
19 leaves, is also an important precursor for efforts to interpret global measurements of solar-  
20 induced fluorescence (SIF, e.g., Joiner et al., 2011; Guan et al., 2015).

21

## 22 **2 Methods**

### 23 2.1 DART Model Simulations

24 Diurnal and seasonal changes in the 3D light environment of an Amazon forest were  
25 simulated using the DART model (Gastellu-Etchegorry et al., 2012; Gastellu-Etchegorry et  
26 al., 2015). The 3D forest scene (50 m  $\times$  50 m) was developed using high-density airborne  
27 lidar data (>20 returns per m<sup>2</sup>) from the Tapajos National Forest near Santarém, Pará, Brazil,  
28 and local measurements of leaf reflectance, litter reflectance, and leaf area (see Extended Data  
29 Figure 1 in *Morton et al.* [2014]). Discrete return airborne scanning lidar data were thinned to  
30 a consistent point density following methods described in (Leitold et al., 2015), and leaf area  
31 (6 m<sup>2</sup>/m<sup>2</sup>, Asner et al., 2004) was allocated to 1 m<sup>3</sup> voxels based on the distribution of

1 multistop lidar returns, with LAI distributed equally among lidar returns (Figure 1). The lidar  
2 digital terrain model was used to represent surface topography in the 3D scene.

3 Tree objects representing stems and branches were added for canopy trees to estimate  
4 PAR absorption by non-photosynthetic canopy elements. Lidar-based estimates of tree height  
5 and crown dimensions were used to scale a generic tree object to represent the stem and  
6 branches for each canopy tree (Figure 1). Woody structures were represented in DART using  
7 facets (triangles), so that light interception by branches and stems could be tracked separately  
8 from absorption by leaves or the ground surface. The geometry of facets is independent of  
9 voxel dimensions, allowing stems and woody branches to be represented at finer scales than  
10 leaf voxels. Previous studies have documented the importance of large branches for  
11 scattering and absorption of near-infrared energy in the forest canopy (Romanczyk et al.,  
12 2013). The use of tree objects in this study builds on the sensitivity study by Romanczyk et  
13 al. (2013) to investigate the impact of PAR absorption by woody branches within the canopy.  
14 Branches are rarely studied in tropical forests (except see Higuchi et al., 1998), and many  
15 radiative transfer and ecosystem models exclude light interactions with branches altogether.

16 DART simulations for cloudy and clear-sky conditions were run for five hours per day  
17 and one day per month to produce 3D estimates of daily, monthly and annual leaf-absorbed  
18 photosynthetically active radiation (*l*APAR). DART simulations were configured to simulate a  
19 repeating (infinite) scene. Illumination geometry, aerosol optical depth, and incident PAR  
20 varied for each hourly simulation, but forest structure and reflectance properties were held  
21 constant. Hourly estimates of incident PAR and cloud cover were based on PAR  
22 measurements from the KM67 eddy flux tower within the Tapajos National Forest (8:00-9:00,  
23 10:00-11:00, 12:00-1:00, 14:00-15:00, and 16:00-17:00 local time, (Hutyra et al., 2008),  
24 Table S1). Cloud cover is highest during the wet season (December-June), with higher  
25 average incident PAR during dry season months (July-November). At 3°S latitude, midday  
26 illumination conditions are near nadir in both March and September. Mean PAR values for  
27 cloudy and clear-sky conditions were estimated based on the distribution of hourly  
28 observations, with clear-sky conditions defined as hourly PAR values between 70-100% of  
29 maximum PAR for each hour and month (Table S1). Mean incident PAR for cloudy  
30 conditions was derived from observations <70% of maximum PAR. These thresholds are  
31 similar to the approaches used in previous studies to interpret in situ measurements of incident  
32 radiation when no diffuse PAR sensor was available (Oliveira et al., 2007). A monthly  
33 climatology of aerosol optical depth was developed using data from the Belterra AERONET

1 station (Holben et al., 1998) to simulate diffuse light from aerosol scattering under clear-sky  
2 DART simulations based on an updated atmospheric radiative transfer scheme in DART  
3 (Grau and Gastellu-Etchegorry, 2013). Cloudy conditions were simulated as 100% diffuse  
4 light. The treatment of illumination conditions as 0% or 100% cloudy is a convenient  
5 simplification that avoids the need to resolve cloud properties (e.g., optical thickness, size,  
6 altitude) and atmospheric transport—attributes that could be the basis for a further study  
7 where more detailed ground measurements are available, or using an Earth system model that  
8 simultaneously considers the impact of dynamic atmospheric processes on surface energy  
9 budgets. Combined hourly simulations were constructed using a weighted average of clear  
10 and cloudy DART model simulations for each hour and month.

11 Model simulations tracked light interactions with leaves, woody elements, and the  
12 ground surface (Table S2). Estimates of  $lAPAR$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for each  $1 \text{ m}^3$  voxel were post-  
13 processed to account for light saturation effects based on a photosynthetic light response  
14 curve from leaf-level measurements of tropical forest trees (*Anacardium*, Kitajima et al.,  
15 1997). Light utilization is therefore a unitless measure of “effective  $lAPAR$ ,” based on the  
16 fraction of light absorbed by leaves that can be used for photosynthesis in the absence of  
17 constraints based on leaf temperature or moisture stress (e.g., Doughty and Goulden, 2008).  
18 Fractional light utilization per unit leaf area decreased for light absorption  $>225 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  
19 declining to approximately 0.8, 0.6, and 0.4 for  $lAPAR$  values of 360, 450, and  $825 \mu\text{mol m}^{-2}$   
20  $\text{s}^{-1}$ , respectively (Figure 2). Throughout the manuscript, light saturation effects were  
21 calculated at the voxel scale and summed for the model scene based on the difference between  
22 absorbed and utilized light. Average light absorption by leaf material (turbid) in each voxel  
23 provided a conservative estimate of light saturation, since absorbed light was distributed  
24 across all leaf area in the voxel. Light saturation effects lead to lower light utilization based  
25 on the reduction in fractional light utilization above  $225 \mu\text{mol m}^{-2} \text{s}^{-1}$ , consistent with a shift  
26 from light to rubisco limitation of photosynthesis.

27

### 28 3.2 Model Comparisons

29 DART model simulations of  $lAPAR$  and light utilization were compared with two  
30 additional modeling approaches. *Stark et al.* (2012) used a light extinction model to estimate  
31 the vertical profile of light interception in Amazon forests. We used the vertical distribution  
32 of LAI across the DART scene and identical inputs for incident radiation (Table S1) to  
33 estimate the profile of light absorption following the methods described in *Stark et al.* (2012).

1 We also used the Ecosystem Demography (ED) model (Version 2.2, Longo, 2014) to simulate  
2 the vertical profile of light absorption and light utilization. The vertical profile of LAI was  
3 used to initialize an ED patch. Tower measurements of PAR (Hutyra et al., 2008) and the site  
4 coordinates were used to simulate incident radiation. ED model simulations also evaluated  
5 light absorption and utilization without moisture stress. Separate simulations considered the  
6 influence of dividing the DART scene into 1, 25, and 2500 patches in ED to evaluate the role  
7 of horizontal heterogeneity in forest structure on light absorption. Representing the DART  
8 scene as a single ED patch simulates the influence of the average forest structure. ED  
9 simulations with 25 patches (100 m<sup>2</sup>) is a typical representation of forest structure in the  
10 model (Moorcroft et al., 2001), while simulations with 2500 patches (1 m<sup>2</sup>) examined the  
11 potential to represent horizontal heterogeneity in vertical structure using the ED modeling  
12 approach.

13

### 14 **3 Results**

15 Light availability in tropical forests is dynamic on diurnal and seasonal time scales.  
16 Hourly distributions of *l*APAR at the voxel scale highlighted diurnal variability in leaf  
17 absorption, including the fraction of leaves experiencing light-saturated conditions (Figure 3,  
18 Table S2). Shadowing effects were pronounced in early morning (09:00) and late afternoon  
19 (17:00) DART simulations, with most leaf voxels experiencing low *l*APAR. The degree of  
20 shadowing changed seasonally, such that early morning overpass satellites (e.g., Terra  
21 MODIS, GOME-2) observe large seasonal changes in shadowing and illumination of tropical  
22 forests, altering the overall distribution of light absorption at the leaf level and the reflectance  
23 from sunlit and shaded leaves.

24 Seasonal variability in total *l*APAR at the canopy scale was driven by a combination  
25 of changes in solar zenith angle and the fraction of diffuse light from clouds and aerosols  
26 (Figure 4). Combined cloudy and clear-sky simulations showed highest total *l*APAR in  
27 March and September, consistent with more even distribution of light under near-nadir  
28 midday illumination conditions in these months. March simulations were characterized by a  
29 more even distribution of *l*APAR but lower incident radiation under cloudy conditions.  
30 Lower light utilization in September, based on light saturation effects under clear-sky  
31 simulations, led to similar estimates of total utilized *l*APAR in both months (Figure 4). These

1 cases illustrate how different mechanisms interact with forest structure to alter light  
2 availability for photosynthesis.

3         Shadowing, light saturation, and light absorption by woody branches reduced the  
4 fraction of absorbed PAR available for photosynthesis. At the scene scale, DART estimates of  
5 monthly fractional *l*APAR varied between 0.8 and 0.85, depending on illumination conditions  
6 (Figure 5b). Fractional losses of 0.15 – 0.20 of incoming PAR resulted from the combined  
7 influence of leaf reflectance ( $0.036 \pm 0.014$ ), wood absorption ( $0.094 \pm 0.024$ ) and light  
8 reaching the ground surface ( $0.065 \pm 0.029$ ) (Table S2). Light saturation effects at the leaf  
9 level, calculated as the difference between leaf absorption and light utilization, further  
10 reduced effective *l*APAR. Mean saturation effects were lowest for simulations at 09:00  
11 ( $0.0428 \pm 0.0237$ ) and highest in midday simulations (13:00,  $0.121 \pm 0.027$ ), with a maximum  
12 of 0.17 in September (Table S2, see Figure 2). At the monthly time scale, saturation effects  
13 varied from 0.05-0.13, such that only 67% - 74% of incoming PAR was estimated to be  
14 available for photosynthesis.

15         Light saturation effects moderated the apparent benefit of increasing PAR during dry-  
16 season months (Figure 4, Figure 5). During July-November, saturation effects under midday  
17 conditions were similar in magnitude to combined APAR losses from absorption by woody  
18 elements and the ground (Table S2). Together, midday light saturation effects and non-leaf  
19 absorption led to the lowest light utilization during July-November (Figure 5). Canopy 3D  
20 structure generated a decrease in light utilization during the dry season based on two  
21 competing processes. Lower cloud cover in the early dry season increased PAR at the top of  
22 canopy (Table S1, Figure 5b), but lower sun angles and more direct radiation altered the  
23 distribution of light at the leaf level. Thus, monthly increases in PAR were not distributed  
24 across all leaves, as some canopy leaves were light saturated while shading other parts of the  
25 same crown or shorter neighboring trees.

26         This decrease in canopy light utilization can be described in terms of efficiency.  
27 Increased incident PAR between June and July ( $+40.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) only resulted in a 50%  
28 relative increase in light utilization ( $+20.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Figure 4, Table S2), with the  
29 remaining *l*APAR lost to light saturation. Even under near-nadir illumination conditions in  
30 September, light saturation effects moderated the change in effective *l*APAR to 65% of the  
31 relative increase in PAR between August and September. These cases highlight the need to  
32 consider how forest 3D structure alters the distribution of *l*APAR at the leaf level in order to  
33 estimate light utilization in tropical forests.



1 Horizontal variability in forest 3D structure generated clear spatial and temporal  
2 differences in light absorption profiles and the vertical distribution of light saturation effects  
3 (Figure 6). DART model results differed substantially from the depiction of diurnal  
4 variability in light interception from the exponential model (non-spatial) or the pseudo-spatial  
5 representation of forest structure in ED. The exponential model of light extinction  
6 overestimated total absorption by leaves compared to DART or ED under midday and  
7 afternoon illumination conditions (Figure 6b, 6d). Adding more patches in ED model  
8 simulations generated light absorption profiles that were more similar to DART results, with  
9 horizontal differences in forest structure lowering cumulative light absorption from  
10 simulations with a single patch to a hyper-parameterization of forest structure with 2500  
11 patches. However, estimates of light utilization in ED exhibited different vertical profiles and  
12 cumulative *l*APAR than in DART (Figure 5b, 5d). ED model estimates of light utilization  
13 were more strongly influenced by total incident PAR than the diversity of patch  
14 environments, since each patch receives the same incident PAR at the top of canopy.  
15 Differences between models also reflect a more complete characterization of light interactions  
16 in DART, including 3D representation of shading from neighboring trees and absorption by  
17 woody elements.

18 Light-saturated leaves were distributed throughout the vertical canopy profile under  
19 midday or diffuse illumination conditions in the DART simulations (Figure 6a, Movie S1).  
20 Greater light penetration in DART, with light saturation effects below mean canopy height,  
21 further distorted the vertical profile of DART light utilization relative to more simplified  
22 representations of forest structure (Figure 6b). Evidence for greater light absorption by  
23 shorter canopy trees than taller canopy trees underscores the need for a full 3D representation  
24 of the tropical forest light environment to accurately estimate tropical forest responses to  
25 changing light conditions. Horizontal variability in 3D structure also generated a diversity of  
26 light environments at the forest floor (Movie S2). The frequency, intensity, and duration of  
27 sun flecks offers a promising avenue for studies of forest regeneration and the role of gap  
28 dynamics for the heterogeneity of light environments in the forest understory.

29

#### 30 **4 Discussion**

31 Incident PAR at the top of a tropical forest canopy is an imperfect measure of light  
32 availability for photosynthesis. The 3D structure of tropical forests, combined with diurnal

1 and seasonal variability in direct and diffuse illumination, alters *l*APAR and light saturation  
2 effects. Together, shadowing and saturation may reduce the amount of light available for  
3 photosynthesis by 11% - 23%, given estimates of mean monthly light utilization in this study  
4 (0.67-0.74) and biome-wide estimates of Amazon FAPAR from satellite data (0.85-0.9;  
5 (Senna et al., 2005). An accurate representation of light saturation effects in ecosystem  
6 models is critical to constrain potential gains in gross primary productivity from changing  
7 light levels under scenarios of future climate, including the influence of clouds and biomass  
8 burning aerosols on diffuse light conditions (Rap et al., 2015; Mercado et al., 2009; Oliveira  
9 et al., 2007; Cirino et al., 2014; Kanniah et al., 2012). Ecosystem models of intermediate  
10 complexity may not fully account for shadowing and light saturation effects in tropical  
11 forests, including illumination differences among canopy trees and light penetration to lower  
12 canopy layers. For these models, it may be possible to leverage information on forest  
13 structure from satellite data to account for these processes. Forest types with greater vertical  
14 and horizontal heterogeneity generate stronger bidirectional reflectance effects in passive  
15 optical remote sensing data (Morton et al., 2014; Nagol et al., 2015), providing a proxy for  
16 fine-scale spatial variability in canopy structure.

17 Changing illumination geometry influences the distribution of light within the forest  
18 canopy, and this physical mechanism may partially explain patterns of seasonal carbon uptake  
19 in Amazon forests. Evidence for seasonal variability in light utilization in this study  
20 constitutes an alternate biophysical explanation for Amazon forest seasonality without  
21 concurrent changes in canopy phenology. Previous studies have estimated changes in  
22 photosynthetic capacity ( $P_c$ ) of Amazon forests based on the ratio of net ecosystem exchange  
23 (NEE) to incident PAR (e.g., Hutyra et al., 2007; Restrepo-Coupe et al., 2013). One suggested  
24 mechanism for seasonal variability in  $P_c$  is forest phenology. New leaves photosynthesize  
25 more efficiently than old leaves, and evidence for seasonal flushing of new leaves has  
26 therefore been hypothesized to promote greater  $P_c$  from leaf demographics (Huete et al.,  
27 2006; Brando et al., 2010; Restrepo-Coupe et al., 2013; Wu et al., 2016). However,  $P_c$  does  
28 not account for the influence of forest 3D structure on light utilization from shadowing or  
29 light saturation effects. The impact of changes in leaf age or leaf characteristics (e.g.,  
30 Kitajima et al., 1997) must therefore be evaluated based on the distribution of *l*APAR at the  
31 leaf level. At present, is unclear whether seasonal changes in illumination are simply aliased  
32 to other seasonal phenomena in studies of  $P_c$ , including phenology (Restrepo-Coupe et al.,  
33 2013; Medvigy et al., 2013; Wu et al., 2016), since these studies do not specifically separate

1 leaf demography from other mechanisms for upregulation of  $P_c$ . The results of this study  
2 highlight how directional illumination and forest 3D structure combine to influence diurnal  
3 and seasonal variability in light utilization, independent of further changes in leaf area, leaf  
4 age, or environmental controls on canopy photosynthesis. DART model results emphasize  
5 the importance of light utilization (rather than PAR, FAPAR, or even  $lAPAR$ ) to attribute  
6 changes in light availability to seasonal dynamics of Amazon forest productivity.

7 Whether the differences between DART and other models represent an offset or a bias  
8 depends on whether forest structure influences PAR absorption and utilization in consistent  
9 ways across seasons, latitudes, and forest types. In this study,  $lAPAR$  varied diurnally, but  
10 midday simulations (11:00 and 13:00) were more consistent across months, suggesting that  
11 shadowing may be less important than light saturation effects for estimates of midday  
12 photosynthesis in tropical forests. Saturation losses of 13-17% in midday simulations with  
13 DART underscore the need for leaf-level information to convert leaf absorption to light  
14 utilization. ED model simulations overestimated midday light saturation losses compared to  
15 DART, and underestimated light saturation effects at lower sun angles, likely because all  
16 patches receive the same incident PAR at the top of canopy (no shadowing from neighboring  
17 patches). Tropical forests present particular challenges for ecosystem models; regional  
18 differences in Amazon forest structure (Morton et al., 2014) interact with seasonal and  
19 interannual differences in diffuse illumination cloud cover and biomass burning aerosols.  
20 These challenges point to the potential benefits of developing more robust, 3D ecosystem  
21 models to estimate forest productivity under direct and diffuse illumination conditions.

22 Illumination conditions differ dramatically between the tropics and higher latitudes;  
23 temperate and boreal forests may never experience near-nadir illumination conditions  
24 approximated using one-dimensional light extinction profiles (Guillevic and Gastellu-  
25 Etchegorry, 1999), except under full diffuse illumination conditions. Seasonal variability in  
26 shadowing and light interception by woody elements may therefore be more important for  
27 understanding photosynthesis in these systems. Importantly, radiative transfer models such as  
28 DART must be coupled with ecosystem models to estimate how temperature and moisture  
29 stress reduce the utilization of  $lAPAR$  for midday, clear-sky simulations.

30 Light interactions at the leaf level are the basis for remote sensing approaches to  
31 monitor vegetation productivity. This study highlighted how horizontal variability in forest  
32 3D structure altered  $lAPAR$  and light absorption by woody elements and the ground surface.  
33 The influence of diurnal and seasonal variability in illumination is one factor that contributes

1 to variability in surface reflectance estimates over Amazon forests (Morton et al., 2014; Nagol  
2 et al., 2015). Changes in the fraction of sunlit and shaded leaves, along with differences in  
3 the degree of light saturation, likely contributes to seasonal variability in SIF measurements  
4 from satellite platforms (e.g., Joiner et al., 2011; Guan et al., 2015), especially given the early  
5 morning overpass time of satellites such as GOME-2 (09:30, see Figure 5a). To date, models  
6 and remote sensing approaches do not account for the role of local heterogeneity in forest  
7 structure as a mechanism for SIF variability (Joiner et al., 2011; Guan et al., 2015; Zhang et  
8 al., 2014).

9         The growing availability of lidar-based measurements of forest structure opens several  
10 important avenues for ecosystem model development. One under-represented element of  
11 forest structure in ecosystem models is branches. In tropical forests, branches may account  
12 for 1/3 of the total aboveground biomass (Higuchi et al., 1998), yet few ecosystem models  
13 realistically account for the roles of branches and stem material for light interception or  
14 canopy turnover from branch falls. New measurement capabilities from terrestrial lidar  
15 scanning (TLS) systems, including multispectral instruments, offer new insights into the  
16 contribution of branches to 3D structure and canopy reflectance in visible and near-infrared  
17 wavelengths. TLS data also provide a detailed depiction of the vertical distribution of leaf  
18 area and the forest understory environment that could improve model parameterization.  
19 Finally, model simulation studies offer the potential to run simple or complex scenarios; in a  
20 future study, the single light saturation curve, leaf angle distribution, and leaf reflectance  
21 properties in this analysis could be modified based on new regional measurements to evaluate  
22 the influence of plant trait diversity on light responses in tropical forests.

23         In addition to data on branch structure, new field data are needed to constrain the  
24 influence of plant trait variability on canopy reflectance and light utilization. Recent studies  
25 highlight the potential for leaf demography to alter leaf reflectance on a seasonal basis  
26 (Chavana-Bryant et al., 2016; Wu et al., 2016; Brando et al., 2010). Without a broader  
27 sample of Amazon tree species, and additional data on transmittance and absorptance, it is  
28 unclear whether subtle and short-term changes in leaf reflectance properties (Chavana-Bryant  
29 et al., 2016) are sufficient to alter PAR availability for canopy and understory trees. New data  
30 are also needed to model differences in light saturation among species, canopy positions, and  
31 leaf ages. Subsequent studies that combine forest 3D structure (including branches) with leaf-  
32 level variability in light saturation could extend the work in this paper on the contributions

1 from shadowing and light saturation to seasonal variability in light utilization in tropical  
2 forests.

3 This study illustrates the importance of realistic, 3D representations of the forest  
4 canopy for accurate simulations of light availability in tropical forests. DART model results  
5 have important implications for both modeling and remote sensing of tropical forest  
6 ecosystems, including how the vertical and horizontal distributions of light saturation effects  
7 influence remote sensing measurements and model estimates of forest productivity. Radiative  
8 transfer models provide an important link between top-down estimates from remote sensing  
9 platforms and bottom-up estimates of forest structure and carbon fluxes from field and tower-  
10 based instruments. The growing availability of airborne lidar data offers the potential to  
11 investigate complex ecosystem interactions using DART or similar models to improve the  
12 representation of light utilization in ecosystem models.

13

#### 14 **Acknowledgements**

15 This research was funded by NASA's Terrestrial Ecology and Carbon Monitoring System  
16 programs and Brazil's National Council on Scientific Development & Technology (CNPq)  
17 Science Without Borders Fellowship Program. Funding for lidar data collection was provided  
18 by the U.S. Department of State, USAID, and the US SilvaCarbon Program. Lidar data are  
19 available from the Sustainable Landscapes Project:

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32

## 1 **Figure Legends**

2 Figure 1. DART model scene of an Amazon forest (50 m × 50 m): a) nadir view of canopy  
3 height, b) oblique view of 1 m<sup>3</sup> leaf voxels and woody architecture, and c) tree objects for  
4 canopy tree crowns and stems.

5

6 Figure 2. Probability distribution of average leaf absorbed PAR (*l*APAR, red) and absolute  
7 light utilization (dashed black) for the September 13:00 DART simulation. Fractional light  
8 utilization (blue) for different *l*APAR values is plotted on the right y-axis, based on leaf  
9 measurements of light saturation from *Kitajima et al.* [1997]. Absolute light utilization  
10 (dashed black) is the product of *l*APAR (red) and fractional light utilization (blue). Light  
11 saturation reduces the effective leaf absorption for voxels with average *l*APAR >225 μmol m<sup>-3</sup>  
12 s<sup>-1</sup> LAI<sup>-1</sup>.

13

14 Figure 3. Illumination geometry alters the distribution of light absorption by leaves on a  
15 diurnal and seasonal basis. Simulation results for June, September, and December illustrate  
16 the distribution of fractional *l*APAR across the model scene under direct illumination  
17 conditions, where diffuse light is modeled using observations of aerosol optical depth from  
18 Aeronet. Fractional *l*APAR exceeds 1 for some voxel columns with high interception of  
19 incoming PAR, especially with low sun angles in the morning (09:00 LT) and late afternoon  
20 (17:00 LT).

21

22 Figure 4. Cloudy (blue) and clear-sky DART simulations (red) were corrected for light  
23 saturations effects. Combined results (black line) are a weighted average of light utilization  
24 estimates from clear and cloudy simulations for five hours per day and one day per month.

25

26 Figure 5. PAR (solid black) and modeled light utilization (dashed black) for DART  
27 simulations at 09:00 (a, top) and monthly average values (b, bottom), based on a weighted  
28 average of hourly DART simulations. Simulated monthly values of *l*APAR (solid red) and  
29 fractional light utilization (dashed red) are plotted on the right-hand axis. Gray shading  
30 indicates dry season months (July-November).

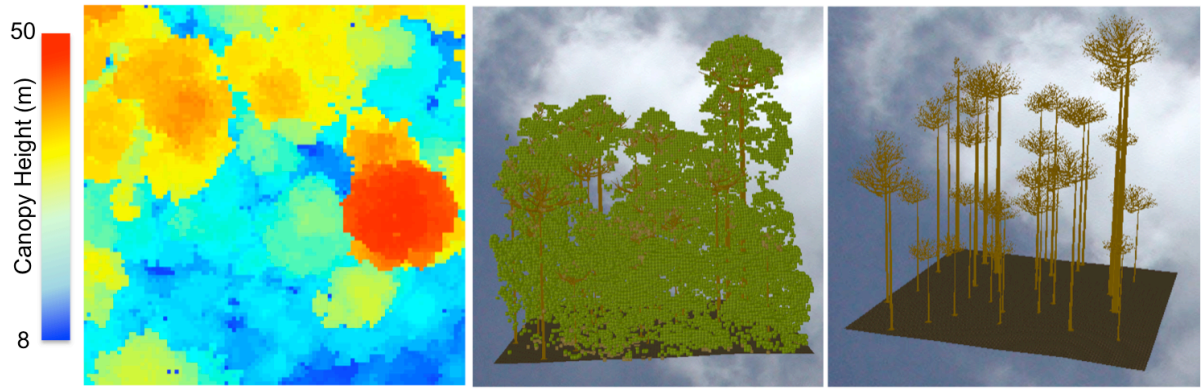
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32 Figure 6. Forest 3D structure alters total leaf absorption, light utilization, and the vertical  
33 distribution of light saturation effects compared to more simplified representations of the

1 Amazon forest scene. a) Vertical profiles of leaf area density (black) and light saturation  
2 effect (red, difference between absorbed and utilized light) for September 13:00 DART  
3 simulations. b) DART cumulative *l*APAR (black) and light utilization (dashed black);  
4 differences between light absorption and light utilization in DART simulations are plotted as  
5 the red curve in panel “a” to illustrate the vertical distribution of light saturation effects  
6 through the profile of canopy leaf area. DART results were compared to an exponential  
7 model of light extinction (blue, following *Stark et al.*, [2012]) and ED2 model simulations  
8 (green). Solid and dashed green lines depict cumulative leaf absorption and cumulative light  
9 utilization, respectively, for ED2 simulations with 1, 25, and 2500 patches. c, d) Same as ‘a’  
10 and ‘b’ for September 17:00 illumination conditions.

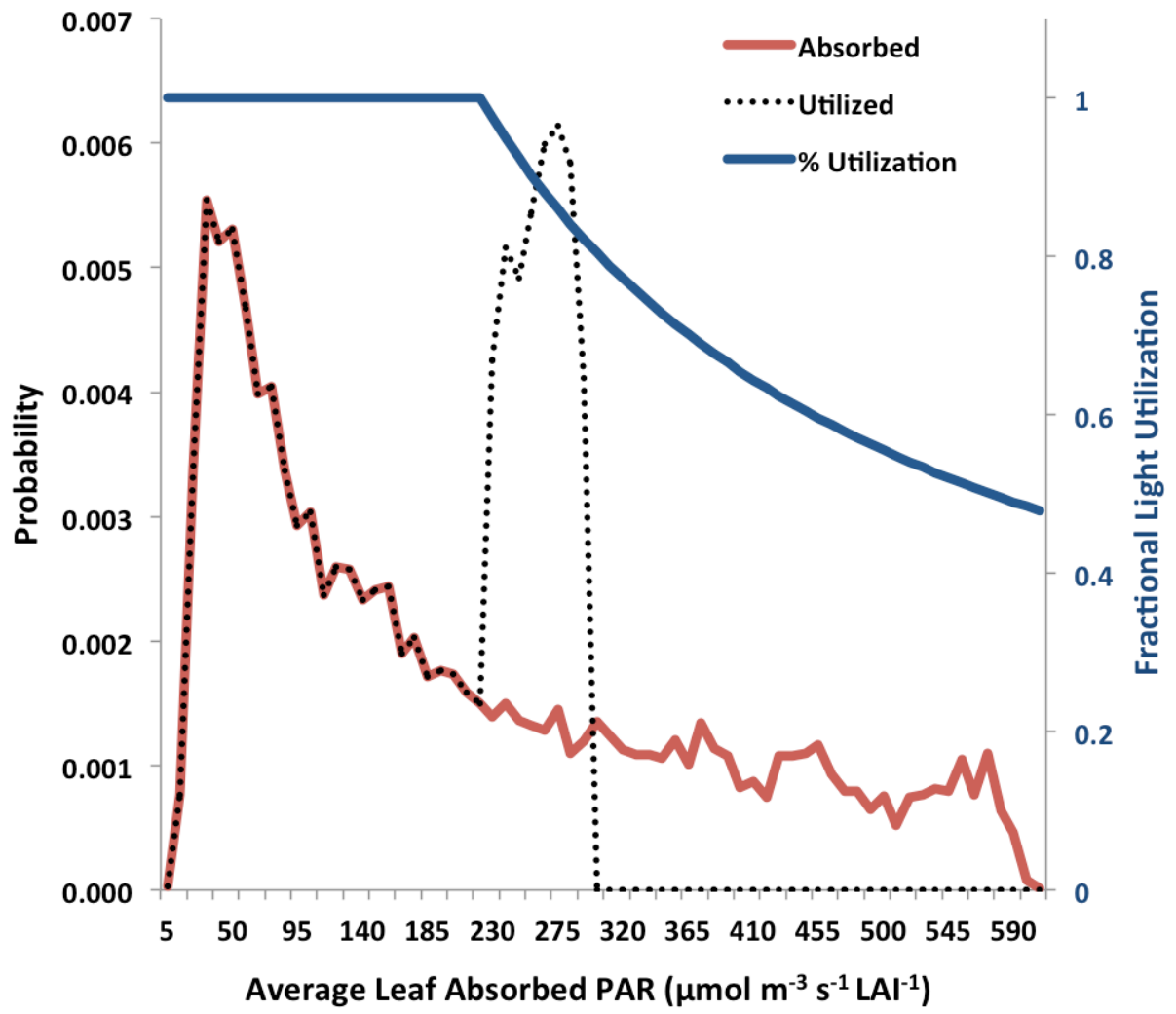
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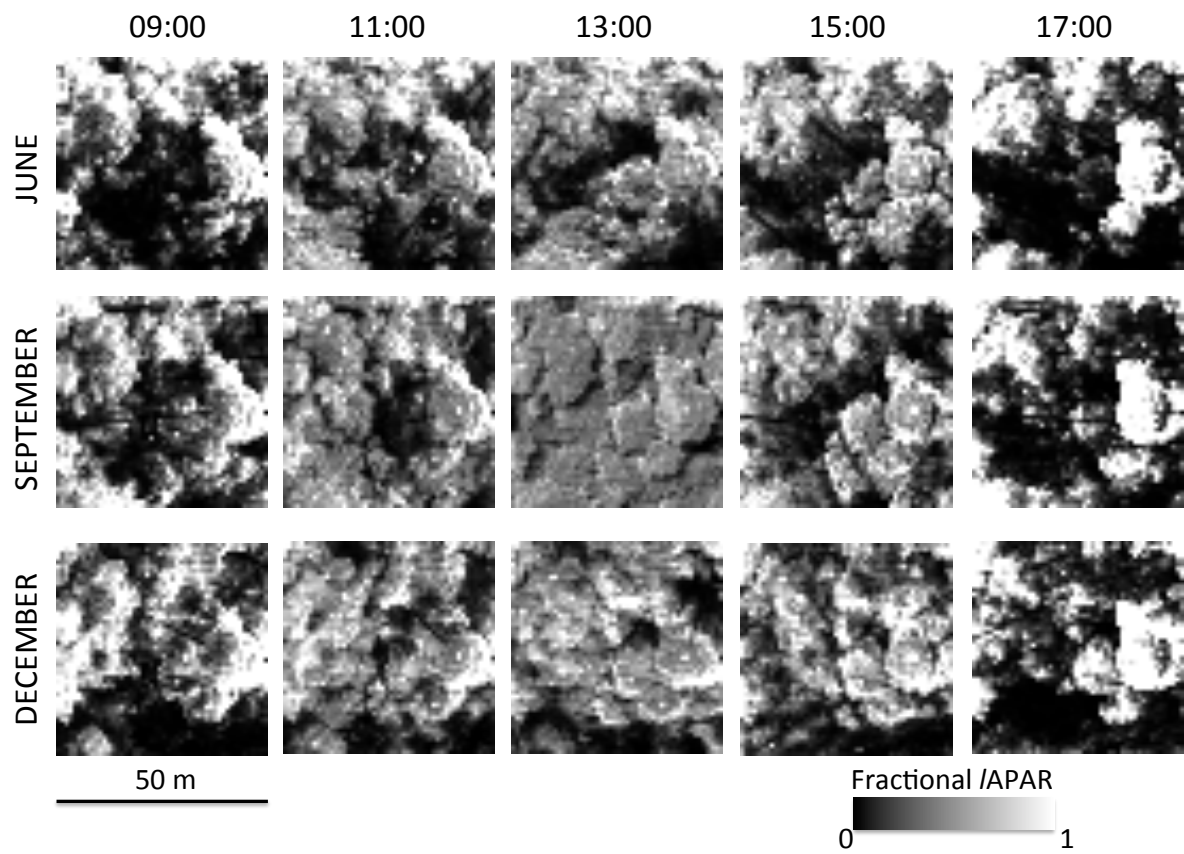


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2 Figure 1.  
3

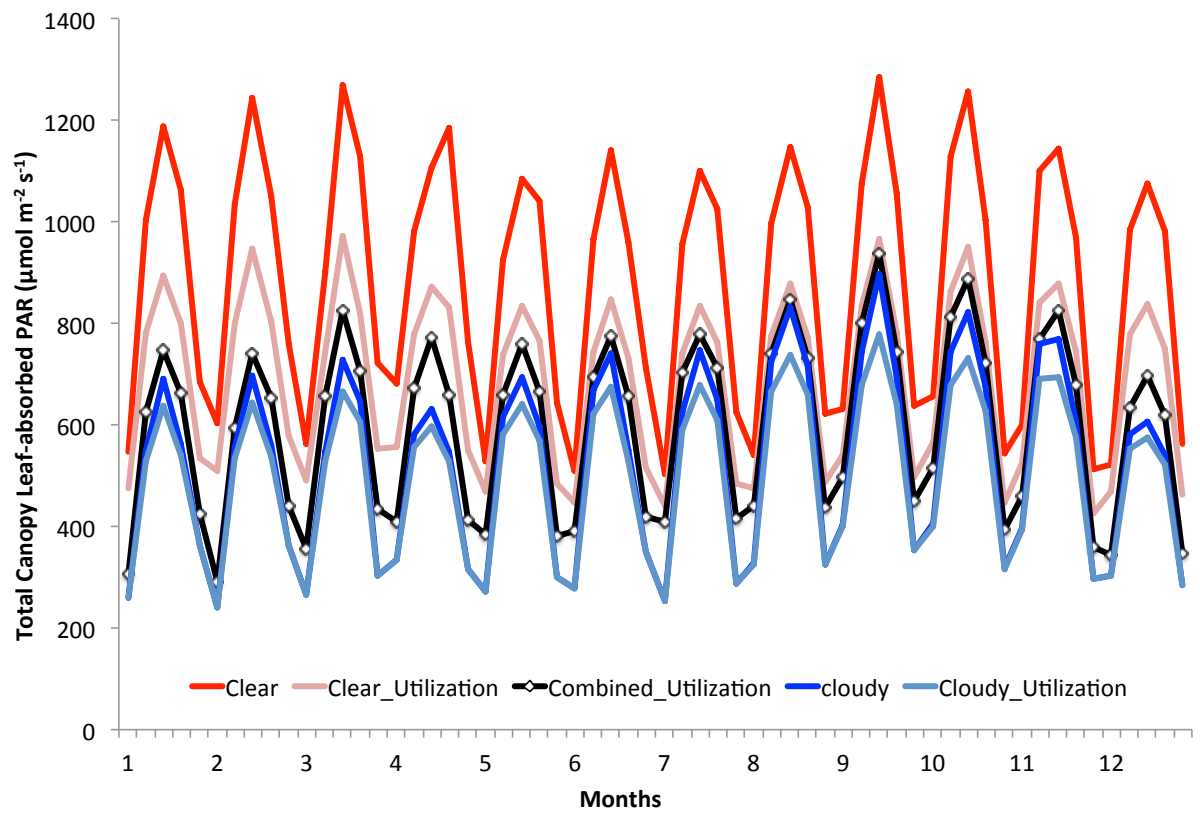




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 2 Figure 2.  
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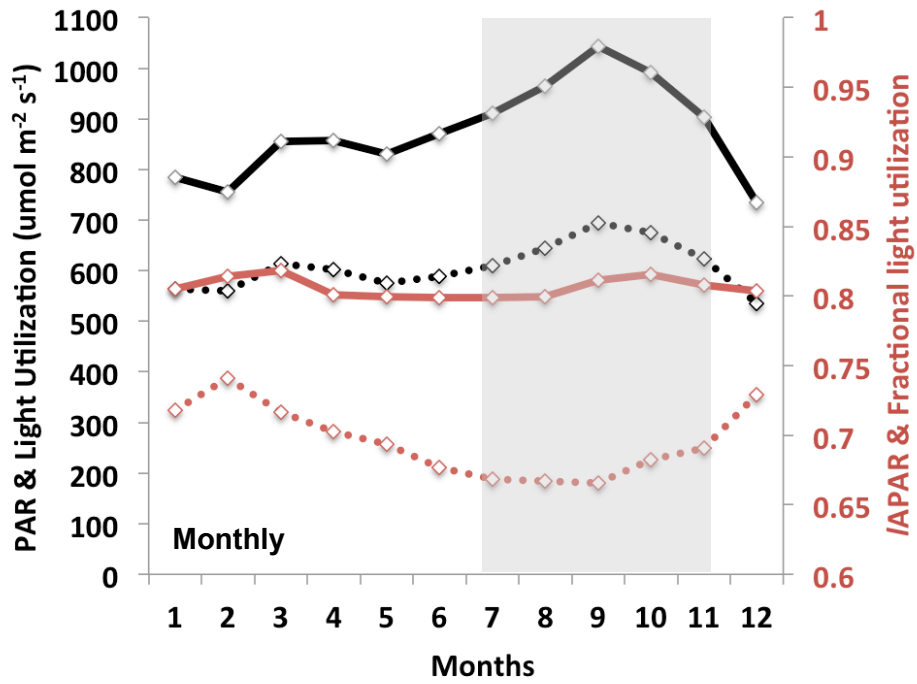
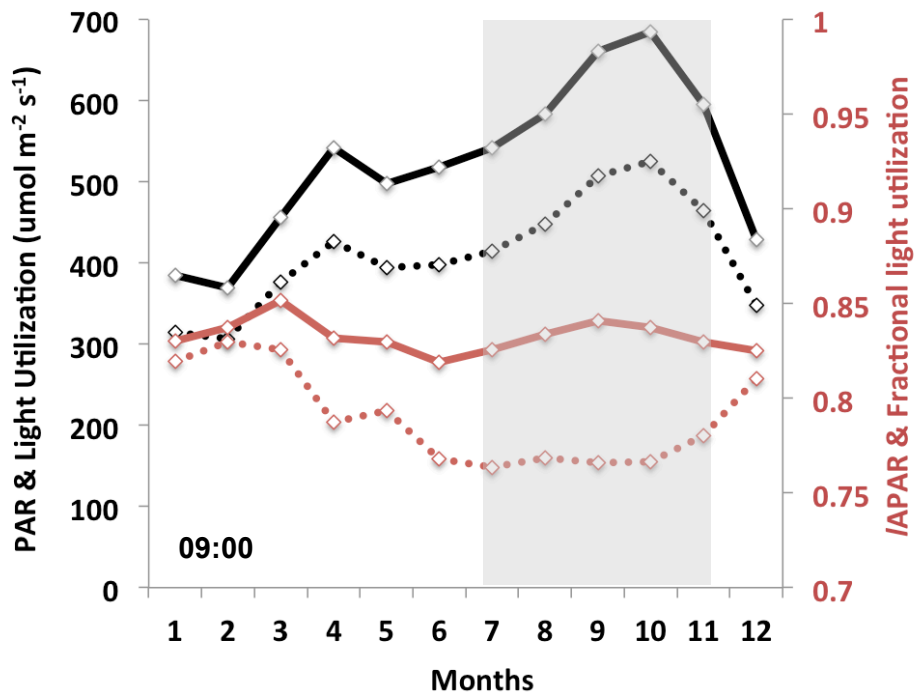
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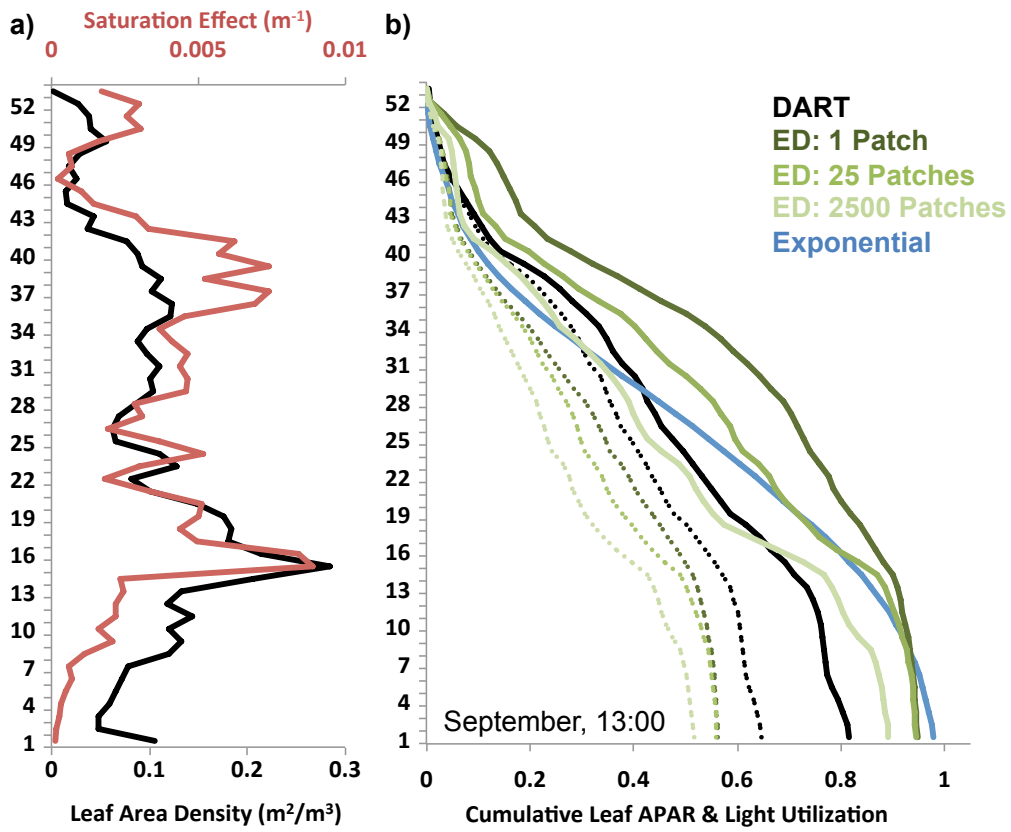
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2 Figure 4.

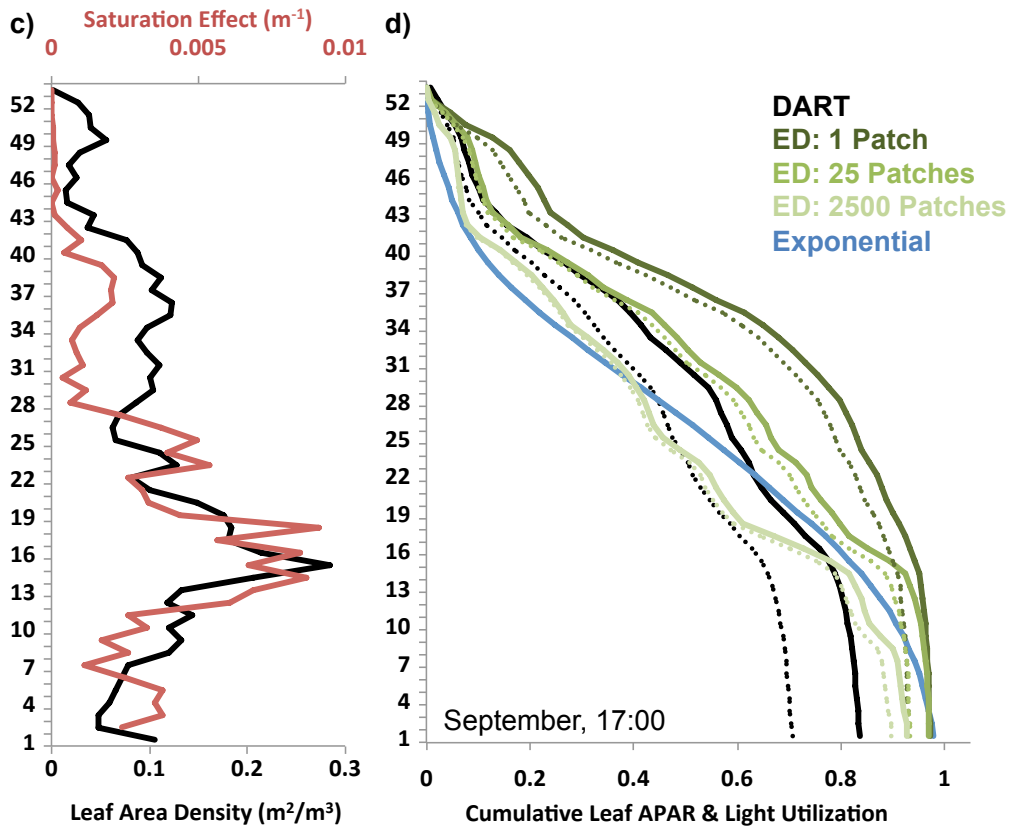
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2 Figure 5.  
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3 Figure 6.