

Interactive comment on “Amazon forest structure generates diurnal and seasonal variability in light utilization” by D. C. Morton et al.

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Referee #1 General comments This paper reports seasonal and diurnal patterns of light utilisation in Amazonian forest, which are independent of total absorption of PAR, and which would expect to significantly affect vegetation productivity. The study is significant in explaining seasonal variability in particular, inclusion of realistic structure from new airborne lidar measurements, and highlights the need to consider light use efficiency and canopy structure in modelling productivity.

The results predict a strong seasonal cycle independent of leaf area changes, and gives a quantitative estimate of 2-3% annual variation due to interception by non-photosynthetic elements, and 7-10% due to light saturation. In dry season we may expect

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higher light levels due to decreased cloudiness, but the effect of aerosols and sun angle also is modelled. While the results are based on model predictions alone, the magnitude agrees broadly with previous estimates combining model and flux tower estimates for Amazonia (Alton et al 2007a). Much previous work has been carried out on understanding and modelling light saturation effects, but many questions remain especially in modelling complex canopies under highly variable light conditions (see review, e.g. by Kanniah et al 2012). This study is novel in considering 3D structure in detail by including state-of-the-art lidar measurements, detailed modelling of interception by non-photosynthetic elements and the focus on explaining seasonal variability of photosynthesis in tropical forests.

The main caveats are reliance on model output alone and interpretation of magnitude of results. DART is a very good model which has been widely used and tested, but inclusion of leaf-level light use efficiency is new to this model, and some approximations are made which are likely to give a reduced sensitivity to light saturation and the impact of diffuse light. In addition, leaf-level light response may be expected to show acclimation to light levels both seasonally and with canopy position (Kitajima et al 1997; Valladares et al. 1997). Neglecting this by contrast is likely to give greater sensitivity to saturation/diffuse light impacts. However no current models can claim to include all effects satisfactorily. The final question raised (including by the title) is how much of the seasonal effect should we attribute to three-dimensional structure, and how closely should this be modelled? We would expect to see some impact of light saturation at high light levels in a one-dimensional model also (e.g. Mercado et al. 2009). Running DART with uniformly distributed foliage could establish the impact of 3D structure.

In summary, this is an important study giving the first estimate of the role of structure and light saturation in seasonal variation of Amazonian photosynthesis, and should be published after revision to address the specific points below.

Response: We appreciate the referee's appreciation of the broader impacts of our results. Our responses to specific comments (see #2 and #3, below) consider the

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strengths and limitations of our modeling approach and the overall impact of 3D structure on our findings.

Specific comments 1. Model structure and instantiation (i) The model is set up using high density lidar point data, with careful processing to create uniform spatial sampling density, and the appearance of the scene shown in Figure 1 is realistic. However the paper would benefit from a clearer explanation of exactly how the canopy structure was set up for the DART model. (Also, presumably the cell represented in figure 1 is repeated in simulation rather than running as an isolated cell, but this should be stated).

Response: The model scene was run in DART as repeated (or infinite). This clarification has been added to our revised description of the model set up and experimental design.

(ii) "leaf area . . . was allocated to 1 m³ voxels based on the distribution of multistop lidar returns" How was this done? In particular how was point density scaled to vertical profile of leaf area density, which should account for interception increases with canopy distance. Probably the results are not too sensitive to the process used here, but it would be good to clarify.

Response: Leaf area was allocated uniformly to all lidar returns. The sentence has been updated accordingly.

(iii) How are branches represented/inserted in relation to the measured leaf area density? This is important as the results of the study depend in part on what fraction of direct light is intercepted by leaf vs non-leaf plant elements. Sun angle changes are expected due to lower sun angles being increasingly intercepted by vertical trunk/branch structures, but this is not typically modelled, so this is an interesting part of the simulation.

Response: Branches and stem material were only inserted for canopy trees, with vis-

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ible crowns in the lidar canopy height model (see Figure 1). Woody structures were represented in DART using geometric objects (triangles), so that light interception by branches and stems could be tracked separately from absorption by leaves or the ground surface. The inclusion of branches and stems for canopy trees is conservative, since no branch elements were added to represent mid-canopy or understory trees. However, branch material is poorly constrained by existing field measurements in Amazon forests. Most studies of leaf area index actually measure plant area index, an integrated measure of light absorption by leaves and woody elements, and it is not possible to isolate the leaf and branch contributions from these measurements.

(iv) If voxels are at 1m³ resolution, how are finer structures than this represented? This includes both branches and leaves, and casting of shadows by elements within the voxel.

Response: Leaves were modeled as turbid material within each 1 m³ voxel, and lidar data were used to allocate leaf material to each voxel. Branch structures and stem material were represented at finer resolution, using triangle facets to define the surfaces of large branches and stems (see response to 1-iii, above).

2. Modelling of interception and light use efficiency. (i) "Estimates of IAPAR for each 1 m³ voxel were post-processed to account for light saturation effects based on a photosynthetic light response curve from leaf-level measurements of tropical forest trees" This seems one of the most major approximations used here, and it would be good comment or quantify the impact. In particular light saturation is estimated based on a model of leaf-level PAR (Kitajima et al 1997), but applied using an absorption level averaged over all leaves within 1m². This is likely to work well if light is diffuse (overcast conditions or deep in canopy), but misses the dispersion of leaf intercepted PAR in full sunlight, where some leaves will experience high light conditions (2000 $\mu\text{mol}/\text{m}^2/\text{s}$) while others much less due to both shadowing by leaves and orientation away from the direct beam. The approximation will likely underestimate the expected impact of diffuse vs direct light, as locally light is already effectively modeled as perfectly diffuse

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at the leaf level. The authors should clarify the approximations used and likely impact on results.

Response: By representing leaves as turbid material within each 1 m³ voxel, our estimate of light saturation effects assumes that all leaves in a voxel receive the same amount of light. This assumption is conservative, especially under direct illumination conditions, since it allows for the greatest possible utilization of absorbed light. This assumption is also practical, since we do not have the necessary data to represent individual leaves for Amazon forest species as facets (triangles) in the model. We have added a paragraph to the discussion section to consider the impact of this assumption and other model parameters (including light saturation, see below) on our results.

(ii) A further approximation is the assumption of the same leaf photosynthetic rate model for all positions in the canopy. In reality there is adaptation of leaves to higher/lower mean light conditions, both spatially and seasonally (Kitajima et al 1997; Valladares et al. 1997), which acts to reduce the variation of canopy level photosynthesis with light levels, making total canopy response more linear to light. While correct values may be difficult to obtain, and are typically sub-optimal in natural vegetation, ignoring variability may change the light utilization calculation by 10-15% (Haxeltine and Prentice 1996, Alton et al., 2007b). A full modelling study of these effects is beyond the scope of the paper, and would be a good topic for future research, but the authors should state clearly the approximations used and their likely impact on results in presenting conclusions.

Response: We agree with the reviewer that our use of a single light saturation curve is an important assumption in the experimental design. We also concur that the information needed to model variability in light saturation responses is an important area for future research. Light responses likely vary by species, canopy position, and season. We have added a more explicit call for more research on these topics in the revised manuscript.

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

(iii) Figure 3: The meaning of the numbers could be more clear: 'Leaf absorbed PAR' here refers to per m² of ground surface, compared with the same name in Figure 2 uses same terminology to refer to absorption per m² of leaf area averaged over 1m³ volume. The maximum intercepted PAR is shown to peak at 1300 $\mu\text{mol}/\text{m}^2/\text{s}$. This seems rather low, with direct sunlight values potentially in excess of 2300 $\mu\text{mol}/\text{m}^2/\text{s}$. Is the data used time averaged?

Response: The Referee is correct that the units for leaf absorbed PAR are inconsistent between Figure 2 and Figure 3. Figure 3 now indicates "Total Canopy Leaf-absorbed PAR." We have changed the x-axis scale for Figure 2 to indicate "Average Leaf-absorbed PAR ($\mu\text{mol LAI-1 s}^{-1}$).

(iv) Section 3, line 24 "including the fraction of leaves experiencing light-saturated conditions" – please clarify the definition of 'light-saturated' used here. Is it the case that all leaves within 1m³ voxel are either light saturated or not?

Response: Yes, light saturation effects are estimated for each voxel. Light saturation effects are calculated as the difference between absorbed and utilized light, based on

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the average light absorption by leaf area in each 1 m³ voxel. The statistical representation of leaf material in each voxel allows for greater absorption by some leaf elements than others. However, our post-processing of the simulations assumes equivalent absorption by all leaf elements in each voxel.

3. Conclusions/interpretation of results The conclusions are well drawn, and should be clarified to include the caveats noted in the methods discussed above ((2(i) & 2(ii)). A further point made which would benefit from greater quantification is the extent to which seasonal and diurnal variation is influenced by 3D structure (as opposed to light levels/diffuse fraction which have been previously modelled with 1D canopy models). In particular: (i) how sensitive are the results to the particular canopy structure (e.g. does it matter if leaf area is allocated differently, or voxel size changes)?

Response: The use of lidar data to allocate leaf area to 1 m³ voxels is a substantial increase in 3D detail compared to models that represent vertical profiles of leaf area (see Figure 5) or models that assume geometric crown shapes for all trees. The decision to model leaf area using 1m³ voxels is a compromise, based on 1) the motivation to characterize the impact of vertical and horizontal heterogeneity in forest structure on canopy light environments and 2) the ability to constrain forest 3D structure using airborne lidar data or field information. Although we do not include simulations with coarser depictions of forest structure, either in terms of voxel resolution or detail regarding leaf and branch distributions, the comparison of DART results to other models in Figure 5 does provide some insight into the role of canopy structure to estimate light levels throughout the canopy profile. A sensitivity analysis would be a promising direction for future research, especially if new data could be collected to support an analysis of changing light saturation effects by canopy position, species, or season.

Another way to consider the impact of the estimated forest structure in this study is to consider diurnal and seasonal differences in absorption by leaves and branches. Even though branches and stems are only included for canopy trees, the representation of woody material has a distinct contribution to total APAR (see Table S2). The decision

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to include only stems and large branches in our simulations follows the results from sensitivity analyses by Ramanczyk et al. (2013) on the role of fine branches in canopy radiative transfer simulations.

(ii) How important is 3D structure to the results? This could be discussed more critically, or ideally tested by reallocating LAI to a homogenous distribution (ie each cell contains same leaf area density), for same total scene LAI. For example we would expect to see increased total IPAR, since clumping is reduced, and impact also on canopy BRDF, but of interest here is impact on canopy light use efficiency and its seasonal pattern – how important is inclusion of 3D structure to model this?

Response: We compared DART model results to simulations using ED2 and a light extinction model (see Figure 5). The amount of 3D structure clearly impacts the vertical distribution of light absorption. Profiles of cumulative light utilization differ even more strongly than total light absorption, as 3D structure alters the influence of shadowing and light saturation effects. At low sun angles, the exponential model has no sensitivity to these impacts, and the ED2 model indicates higher light absorption than DART, even with 2500 patches, because there are no woody elements or interactions between patches (shadowing). Canopy 3D structure alters the diversity of light environments in the canopy, including the positions at which light saturation effects occur (top of canopy, mid-story, understory) and the variability in light environments for which acclimation at the leaf level would need to accommodate. We have added a new figure to better illustrate the role of shadowing under diurnal and seasonal changes in illumination geometry (see response to Referee 3). This figure better captures the influence of 3D structure on model simulations. Movies S1 and S2 also highlight the contribution from 3D structure to diurnal and seasonal differences in canopy light environments.

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Response: We appreciate the reviewer's direct references to previously published literature, and we have reviewed these papers in preparing our revised manuscript.

Interactive comment on *Biogeosciences Discuss.*, 12, 19043, 2015.

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