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Interactive comment on "Variations in leaf physiological properties within Amazon forest canopies" *by* J. Lloyd et al.

J. Lloyd et al.

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We thank Referee 3 for his detailed comments. All points raised are addressed below:

REFEREE: This paper aims to describe a huge study, a large volume of data, and a complex modelling and sensitivity study. The model is sound and exciting. The data are of great value and the analysis is extremely valuable, needs publishing. The conclusions (or the messages) of the paper are important: as far as I can tell, a breakthrough vision on the ecology and spatial variation of leaf photosynthesis in (tropical) forests is given, explaining that leaf acclimation to local light does not occur as much as expected from simple optimality; arguments because top canopy leaves are limited in how much photosynthetic capacity they can accommodate. Why this should be so is not made very clear though. Unfortunately, I am afraid the authors will not succeed in getting this message across very well with the present paper. It is rather chaotically written, too

woolly, starting with a modelling section which complexity has no with its usage in the discussion section and from which it is hard to extract the main message. The data section is shrouded in complex statistics, while the main conclusions may not be even that hard to convey: only Ma, delta-13 and Cdw are related to height. The conclusion is enlightening, but hard to grasp. One would expect at least a hand stretched out to modellers what to do now: should they just use these empirical profiles, of is there maybe any predictability in this A0*, which seems to govern the degree of canopy variation? What follows below is an also rather chaotic list of more specific comments.

RESPONSE: We agree that many of the arguments the submitted version may have appeared as somewhat obtuse. Considerable effort has now been made in trying to make the manuscript more readable, though it should also be appreciated that some of the arguments, maths and statistics are necessarily complex (even for the first author) and that irrespective of style, this is a manuscript that will almost certainly require careful reading and conceptual effort by any reader interested in obtaining a full comprehension and appreciation of the arguments presented.

We have also added a new section (6.2; Extrapolation to the stand level) which we hope provides more than just a stretching hand to modellers.

REFEREE: Appendix: equations are (seem) very complex. Hard to verify. Proof of message (N/ Amax does not have to follow light) absent or perhaps swamped by the equations?

RESPONSE: The model equations are not really that complex at all (except for the presence of a hypergeometric function). They are also correct.

REFEREE: Does the reason for the non-optimality lie in the fact that Rd decreases with light?

RESPONSE: No, but this point is now discussed in Section 6.3 (Model and data uncertainties).

REFEREE: Section 2.1 is hard to follow. Based on one set of equations many sensitivity tests are shown, but the main message remains to be guessed by the reader, and it leaves the suspicion that not all of the assumed conditions are realistic.

RESPONSE: A summary paragraph is now included at the end of Section 2.1. Not clear to us what could be considered “unrealistic”.

REFEREE: p. 4656 why would photosynthetic capacity be so fundamentally limited to a maximum? Except for a reference to Turner, this should be elaborated a bit more because it is a rather fundamental assumption in the reasoning.

RESPONSE: This point is considered with more detail and care in Section 6.1 (Gradients in nitrogen, phosphorus and photosynthetic capacity: fifth paragraph)

REFEREE: In the discussion it is said (p. 4666 l. 3) that in case of optimality trees would be at an advantage always with shallow crowns, accumulating all photosynthetic capacity near the top. But, this implies that production of height supporting tissue is not an issue, while of course only fast-growing species possess the strategy to grow tall and explore the canopy tops. Slow growers (shade tolerants) can have an advantage in exploring a canopies lower regions.

RESPONSE: This is obviously a complex issue, but now considered as a discussion point in 6.3 (Model and data uncertainties). We also point out here, however, that sharper gradients (expressed as a function of LAI) do not necessarily mean a shallower crown (as leaf area density may also mediate such changes). One also needs to take into account variations in wood density between fast and slow growers which probably give rise to less variation in stem construction costs with height than would appear to be the case at first sight.

REFEREE: Section 2.2: what is the added value of to increase confusion calculating GPP and annual carbon gain instead of assuming and average, steady state situation? Especially considering the fact that in this annual simulations many simplifications are

assumed, such as constancy of Cc and A0, leaf life time on 1 year, etc. I can imagine that calculation with real data is worthwhile if also variable A0 etc are assumed (causing covariances of e.g Ao and light) but in this case it seems to me that this is exercise is indeed only adding to confusion. It would be nice to look at seasonal variations in all the parameters researched as well, to see if there is any relationship with relative variation of resource availability over a year. But of course this is a different study altogether ..In this context, pretending to be comprehensive. with varying SLA, would it not make sense to account for a relationship between leaf thickness and longevity, as a factor in optimality ? If one would consider the productivity of a leaf over its life span (higher with higher Ma and/or lower Ndw), this would be another factor in considering optimality.

RESPONSE: Yes, it would be a different study altogether. But (to avoid confusion) we have now removed out flippant comment at the start of Section 2.2 and explained more clearly our rationale for doing these calculations over the 3+ year period.

REFEREE: Section 2.3: I have the impression that there is repetition here and a lot of woolliness. What is the main message? I see optima increasing with A0* but is there some sort of maximum optimum? Would this have anything to do with available radiation?

RESPONSE: Radiation would have an effect, though we have not considered it here. Yes, mathematically there would be an optimum probably dependent on the annually integrated $Q_{„}$ but probably also existing beyond the usual physiological bounds. But we think to go into all that would merely serve to increase the confusion most readers.

REFEREE: Summarising, section 2 is interesting on its own right, the analytical considerations lead to nice new insights, but it is hard to follow, and the authors make little effort to indicate clearly what the main questions and the main conclusions are of this sub-study, nor is there a bridging statement to section 3. and further.

RESPONSE: As stated above, we hope this section is now overall clearer and more concisely written. We have also now added the bridging Section 2.4 (Model validation)

to smooth the way from the theoretical Section 2 to the rest of the manuscript.

REFEREE: Its conclusions are again referred to in the discussion, but not much substance is added to it there, and the link to the observed data is mainly that, indeed, gradients with height of many leaf constituents are not significant. I might have missed it, but is there any estimate of the measured kp (extinction coefficients of photosynthetic capacity), based on Na or Pa gradients?

RESPONSE: Yes, you did miss it (Figure 8 and Table 2). Figure 9 is also with P on a leaf area basis and provides one line of support for the overall model.

REFEREE: Methods: There is a lot of detail on the analysis methods, but almost complete lack of justification of why this particular set of variables was measured. This may seem obvious, but, for example, variation of delta-13-C is only interpreted very briefly in half a sentence in the discussion, and so is the Mg variation. The physiological significance of Ca and K gradients is not discussed at all.

RESPONSE: Rationale for analysing cations and 13C are now given In Section 1 (Introduction) with 13C specifically discussed at the end of Section 6.1 ((Gradients in nitrogen, phosphorus and photosynthetic capacity: third last paragraph) with cations and carbon now having their very own Section 6.4.

REFEREE: Statistics: I am not a statistician. But what I see is a very complex multiple linear regression being done on many data. Somewhere it is mentioned that normality in the data is assumed (no justification) but later the data appear not normal and they are normalized using a log scale. A statistical t-test is mentioned only once. Some of the data then appear significant (gradients significantly different from zero) but, amid so many regressions, what is the probability that these significances are coincidental?

RESPONSE: It is first stated in Section 4 that the statistical analysis presented ssumes normality (not that the data were normal). Indeed, it is for this reason that in Section 5 (Results) we then make the transformation. There are only eight regressions (which

are hardly complex) and we see no reason for correcting for multiple testing.

REFEREE: The word significant is used throughout the text rather loosely, without mentioning significance levels etc.

RESPONSE: Fair enough, we now detail our standard level of $P<0.05$

REFEREE: Should not an ANOVA test be more appropriate here?

RESPONSE: No. In our view multilevel modelling provides a new, enlightened and more powerful way for data such as we collected to be meaningfully interpreted.

REFEREE: Fig 6 is spaghetti. Any information on the distribution of shapes (as well as the heteroscedacity mentioned) is lost. Would not box-whiskers plots, for example, be better? In several places it seems to me comparisons are the wrong way round. E.g. in results,5.2, conclusion 3.Fig 7: are slopes of Ma, Cdw and delta-13 really significantly different from zero here?

RESPONSE: It certainly would have been simpler for us not to present the raw data in Figure 6. But we thought it best that the actual data going into the model be presented in some way. It is also not at all obvious to us how we could have presented this data as a box-whiskers plot. And yes, when analysed with the multi-level technique we have described, then the gradients in LMA, C_DW and d13C are indeed significant. See our comment immediately above as well.

REFEREE: Fig. 8 seems to have lost its labels in the panels.

RESPONSE: Now fixed.

REFEREE: The arguments at page 4662, l. 20 etc, are hard to follow.

RESPONSE: These lines have now been deleted and the problems with estimating k_p in such a situation discussed more comprehensively in Section 6.2 (Extrapolation to the stand level: first paragraph)

REFEREE: 5.4 , the last sentence calls for some explanation on the assumed role of delta-13-C.

RESPONSE: The role of 13C is now specifically discussed at the end of Section 6.1 (Gradients in nitrogen, phosphorus and photosynthetic capacity: third last paragraph)

REFEREE: Table 1: caption way too long

RESPONSE: Our understanding is that a Table caption should be of sufficient detail for the reader to be able to understand it without having to refer to the text. If that end up making the caption rather long, then so be it.

REFERRE: Discussion: p. 4665, l. 6: to say that the question has been wrongly posed and is correctly posed here is a bit bold. The explanation that the authors bring up here is a nice one and a new one, but also only one more among other valid ideas, while some other are not dealt with (see above).

RESPONSE: Fortune favours the bold. That this is just one of several possibilities is however, now made more clear at several stages in the text (see also responses to Referee 2).

REFEREE: Conclusions: There is no conclusions section! The article now abruptly ends with a very technical statement on the roles of Mg in photosynthesis. After all this complex reasoning and all these data, we really at least need something to help us get the key messages of this paper!

RESPONSE: A conclusion Section has now been added.

REFEREE: General; In all humbleness about my own English, I have the impression that the paper was submitted somewhat immaturely. In many cases sentences do not flow well, words repeated. Check grammar. Superfluous use of present continuous(fact BEING because of such and such). The text is actually very hard to interpret in places. Long sentences, also Text is often repetitive. Much could be said with less words. It is my impression that this paper needs: - rephrasing of sections where the messages

should come out - addition of a conclusions section rethinking of the statistics, or better justification of significances and more strict usage of statistical terms. – Justification of the measurements taken, by putting them in their physiological context - Shortening(by removing superfluous words and repetitive arguments) - A thorough language check.

RESPONSE: We accept the validity of the above criticisms and have made considerable efforts to make the main messages clearer.

Interactive comment on Biogeosciences Discuss., 6, 4639, 2009.