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Biogeosciences Discussions

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

Anonymous Referee #3

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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 relation

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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 modelers 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.

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

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.

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.

Maybe check how these ideas link up with the theoretical model of Kull and Kruijt, (1999, Functional Ecology) who show that fast growers (pioneers) should acclimate less than slow growers. 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.

2.2: what is the added value of (‘to increase confusion’) calculating

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GPP and annual carbon gain in stead 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.

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?

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. 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?

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

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a sentence in the discussion, and so is the Mg variation. The physiological significance of Ca and K gradients is not discussed at all.

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? The word ‘significant’ is used throughout the text rather loosely, without mentioning significance levels etc. Should not an ANOVA test be more appropriate here?

Results: Fig 6 is spaghetti. Any information on the distribution of shapes (as well as the heteroscedascity 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?

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

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

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

Table 1: caption way too long

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).

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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!

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 …ing…). 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.

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