**Biogeosciences
Discussions**

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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 2 for his/her comments. In what follows, each point raised is addressed.

REFEREE: Section 2.1 presents an elaborate analysis of the optimal Amax distribution, following the idea that plants are free to allocate a fixed amount of nitrogen. It points out that (1) this distribution should be steeper at high LAI, and (2) that this model predicts unrealistically high Ao and that if Ao is constrained more realistic predictions arise. (1) has been analysed and discussed by Hirose and Werger (1987) Oecologia 72: 520-526 and (2) by Pons et al. (1989) in Causes and Consequences of Variation in Growth Rat by Lambers H et al. pp. 175-186. .....This whole section can thus be reduced to a few sentences.

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RESPONSE: With respect to (1), we agree, not citing Hirose and Werger (1987) was an oversight. This has now been remedied in Section 2.1 (Simulations with a canopy of fixed photosynthetic capacity) with this paper being cited as appropriate.

With respect to (2), I was unaware of this chapter, but that study is now appropriately acknowledged in both Section 2.1 (Simulations with a canopy of fixed photosynthetic capacity) and in the Discussion (Section 6.1 Gradients in nitrogen, phosphorus and photosynthetic capacity).

Although we have attempted so shorten Section 2.1, the basic content remains as there are several issues included in this Section which are not covered in the above papers. First, the current paper provides a mechanistic explanation as to why high LAI canopies are more sensitive to imbalances in $k_p$ versus $k_i$ (second last paragraph). Second, we show that an increase in LAI can actually decrease canopy photosynthetic rates when canopy photosynthetic capacity is taken as fixed. Importantly, these explanations are critical for understanding the simulations which follow in Sections 2.2 and 2.3. Thus, whilst now appropriately citing previous work (the omission in the original for which we apologise), we have chosen to retain the bulk of this Section as it is fundamental to an understanding of the whole paper.

REFEREE: The model and measurement sections read a bit too much like two separate studies. Normally in one paper one would expect the measurements to test model predictions or the model to put the Measurements into perspective. At least they should be about the same parameters and general question. But in this study the two seem to be dealing with somewhat different questions and parameters. The model refers to optimization of the mean distribution of light, Amax and nitrogen at the whole-stand level. Conversely the measured data address the question about differences in distribution between nutrients and differences in distribution between and within trees. I understand that the data needed to test the model might be hard to obtain. Nevertheless I feel that splitting the paper into two much shorter papers might be an improvement.

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RESPONSE: Indeed, the modelling part was only started when it first appeared the gradient data might not really be enough for a stand-alone paper. It is, however, accepted the paper appears a bit segregated, but especially now that the literature review of gradients has been included in the Discussion and with a bit more effort towards a synthesis in the revision we think it is best everything stay lumped together.

REFEREE: I have some difficulty with the firm assertion of Ao having to be a fixed trait. The fact that a trait value is not observed does not mean that it is physiologically impossible. It could also be that it was selected against. The fixation of Ao should thus be treated with more care.

RESPONSE: We do not think we ever said it was strictly fixed, but this point is considered with more detail and care in Section 6.1 (Gradients in nitrogen, phosphorus and photosynthetic capacity: fifth paragraph)

REFEREE: Section 2.4. The authors attempt to estimate the extent to which inclusion of individual-based selection might affect predicted LAIs. I certainly commend the authors for making this attempt but I do not understand how they obtained their evolutionary stable LAI. First as far as I understand leaf area in this context is a strongly density dependent trait. That is the stable LAI would depend strongly on the degree to which neighbour plants influence each other light climate. If their crowns were separated simple and game theoretical solutions should be the same. So I cannot see how this was accounted for.

RESPONSE: We think there is probably a difference in the way competition for light is and should be viewed for woody and herbaceous types. Our point of view and rationale is now made clearer for this Section, which has also been moved to the Appendix (B); this reorganisation reflecting both the great uncertainties in the calculations and the fact that the other referee seems to have found this part paper of the paper somewhat distracting.

REFEREE: In conjunction with 4. competition for light does not only entail leaf pro-

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duction but also vertical leaf positioning. The dynamics of leaf turnover in relation to optimization of LAI have been analysed by Hikosaka (2003) American Naturalist 162: 149-164 and Boonman et al (2006) American Naturalist 168: 597-607.

RESPONSE: This is now mentioned in Appendix B (Evolutionary stable versus instantaneous solutions), though obviously beyond the scope of this analysis.

Minor points

REFEREE: Overall the writing is good and clear but there are a number of typos that need to be fixed.

RESPONSE: Yes, and embarrassingly large number of grammatical, typographical and spelling errors. This reflects the need to submit the manuscript by an immovable deadline and has hopefully now been fully rectified.

REFEREE: Top of the abstract, there is no need to list all nutrients measured, probably mentioning Ma, 13C N and a number of other nutrients suffices.

RESPONSE: Done

REFEREE: Page 4644ln 23: $k_p = k_i$ being optimal has been proven various authors.

RESPONSE : Indeed, but Field (1983) was the first and that is thus the appropriate citation.

REFEREE: Page 4645 lns 10-18: This point has already been made by Pons et al. (1989).

RESPONSE: As discussed above, appropriate acknowledgement of this prior work has now been made.

REFEREE: I did not understand eq. (3).

RESPONSE: The dependency on $k_p$ arises through the dual LMA linkage. This is now made clearer in the text.

REFEREE: The assumption that night time respiration is equal to 8% of the canopy photosynthetic capacity is a bit simplistic in my view

RESPONSE: Agreed, this is discussed a bit more now in Section 6.3 (Model and data uncertainties).

REFEREE: Pg. 4650 ln 21: If the ES-LAI is greater than the optimal one it means a greater leaf area and not a taller plant.

RESPONSE: See response to Major point 4.

REFEREE: Page4651 I could not find where in Fig. 4 the results for ES-LAI are presented.

RESPONSE: Yes, this was a silly oversight reflecting time constraints. See what is now Table B1(which is also now appropriately references in the text).

REFEREE: Page4660 para 1: The fact that you transformed data to improve homoscedastity, can be explained in one sentence or so.

RESPONSE: Now shortened.

REFEREE: Page 4662: I understand that an estimate of $k_p$ was not possible?

RESPONSE: Yes. The offending paragraph has actually 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: Pg 4664 ln 25: The costs of reallocating N were first mentioned by Field (1983)

RESPONSE: This citation now included.

REFEREE: Pg 4666 1st para: Indeed this would allow it to have a greater Cc; but a greater Cc also entails that more N should be taken up.

RESPONSE: Yes, this general point is considered briefly in Section 6.3 (Model and

data uncertainties)

REFEREE: Pg 4668 ln 15. To downplay the impact of the model approach in this study relative to alternative models (see Major point 1) replace show by give one possible answer for

RESPONSE: Done.

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