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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 #2

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Loyd et al. present an elaborate study on the variation of leaf properties in tropical rain forest trees. They combine measurements of the vertical distribution of the contents of practically all major nutrients as well mass/area and 13C isotope concentration. Generally vertical gradients in mass based contents were less pronounced than those on an area base. Gradients within tree crowns were less pronounced than those among trees. In addition to the measurements Loyd et al analysed the optimal distribution of photosynthetic capacity (Amax) and associated resources. Current models have found optimal distribution patterns to be steeper than real patterns. Loyd et al. point out that this discrepancy might arise from the fact that these models do not consider constraints on the Amax of leaves at the top of the canopy (Ao). They suggest that there might be genetic limits on this value and that if Ao is constraint to values within the observed

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range, more realistic distribution patterns can be found. They further show an interrelation between the LAI, Ao and the steepness of the Amax distribution kp, pointing out that species with high Ao, should have high kp values and greater LAI. This is a very elaborate study with a broad data set and a rigorous mathematical analysis. It provides useful information for forest modelers and sheds a new light on the discussion around optimal canopy structure and resource allocation in plants. However, in its current version I feel the paper is too long, dwells in part on issues that have been extensively discussed in previous work, and not very well integrated.

1. 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 constrainede 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 Rate… by Lambers H et al. pp. 175-186. Several papers thereafter have reiterated these arguments (Grindlay 1997; Hirose 2005; Anten 2005 to name a few). This whole section can thus be reduced to a few sentences. 2. 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. 3. 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

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selected against. The fixation of Ao should thus be treated with more care. 4. 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 neighbor plants influence each other’s 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. 5. In conjunction with 4. competition for light does not only entail leaf production 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.

Minor points 1. Overall the writing is good and clear but there are a number of typos that need to be fixed 2. 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 3. Page 4644 ln 23: Kp = Kl being optimal has been proven various authors 4. Page 4645 lns 10-18: This point has already been made by Pons et al. (1989). 5. I did not understand eq. (3). 6. The assumption that night time respiration is equal to 8% of the canopy photosynthetic capacity is a bit simplistic in my view 7. 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. 8. Page 4651 I could not find where in Fig. 4 the results for ES-LAI are presented. 9. Page 4660 para 1: The fact that you transformed data to improve homoscedastity, can be explained in one sentence or so. 10. Page 4662: I understand that an estimate of kp was not possible? 11. Pg 4664 ln 25: The costs of reallocating N were fists mentioned by Field (1983) 12. 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. 13. 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”

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