Biogeosciences Discuss., 7, C5412–C5423, 2011
www.biogeosciences-discuss.net/7/C5412/2011/
© Author(s) 2011. This work is distributed under
the Creative Commons Attribute 3.0 License.

Biogeosciences Discussions

Interactive comment on "Change in hydraulic properties and leaf traits of a tall rainforest tree species subjected to long-term throughfall exclusion in the perhumid tropics" *by* B. Schuldt et al.

B. Schuldt et al.

info@plant-ecology.de

Received and published: 18 April 2011

We kindly thank Dr. Ambrose for his very comprehensive and thoughtful review of the manuscript. We have addressed each comment individually.

Both reviewers pointed out, that our statistical calculations unfortunately were based on pseudo-replication. To exclude possible pseudo-replication, all statistical calculations were redone. Branch hydraulic, anatomical and leaf-related variables were tested for significant differences between the drought and control treatments with linear mixed ef-

fects models with treatment as a fixed variable. We assumed the non-independence of different branches and leaves within a tree, and of different trees within the plots in the models by adding plot and tree nested in plot as random effects. Linear mixed effects models were also applied in the analysis of stem increment data and morphological and anatomical traits related to trunk wood. These detailed results are presented in the appendix.

Further, the scope of the MS had to be changed due to the incorporation of several new data sets. Many chapters have been adjusted or completely re-written. The Methodology chapter has been improved according the reviewers' comments.

Comments by A. Ambrose (RC):

RC: However, there are a number of issues with the manuscript that need to be addressed before publication. Specifically, the introduction and discussion sections were not well structured, the hypotheses were not well matched to the actual experimental data, some important details of the experiment were not presented while other information that was presented was extraneous and did not add anything meaningful to the manuscript, some data interpretations were not clearly presented, some conclusions were not readily supported by the data, and the language needs improvement and editing throughout.

AC: Introduction and discussion section have been reorganized or rewritten including new hypotheses, and we removed the extraneous data. Further, the manuscript was corrected by a native speaker.

Specific Comments

RC: Page 8554, line 8 (and throughout the manuscript): The term "roof" is a confusing and poor choice to describe the plots subjected to experimental drought. I suggest using another alternative term that more accurately describes this treatment such as "drought" or "throughfall exclusion" plots.

AC: We have changed the term “roof” to “drought” throughout the text.

RC: Page 8554, line 8 (and throughout the manuscript): Similarly, the term “desiccated” is also a poor choice to describe the throughfall exclusion treatment. Desiccate implies a thorough drying out of something, but in this experiment only soil moisture levels were reduced while atmospheric moisture remained high. Thus, the trees in this study were not truly desiccated, only deprived of soil moisture. I suggest using an alternative term similar to the one used to replace “roof.”

RC: Page 8554, line 9: The hypotheses was tested that C. acuminatissima was “particularly sensitive to drought” – compared to what? Drought sensitivity is a relative term and this hypothesis should be reformulated to make explicit the basis for judging the relative drought sensitivity of this species.

AC: We assumed that tall-growing tropical tree species are particularly sensitive to drought compared to the bulk of medium- to small-sized trees in tropical forests as has been suggested in previous studies mentioned in the introduction.

RC: Page 8554, line 11: The rationale for the use of twig xylem hydraulic conductivity normalized to vessel lumen area should be explained. I also suggest that sapwood specific conductivity is a more appropriate measure for comparative purposes both among canopy positions and treatment plots in this experiment as well as other species reported in the literature.

AC: Indeed, sapwood-specific conductivity is easier to compare among different canopy positions than vessel lumen-area specific conductivity and all presented data of ks are related to sapwood-area, not lumen-area. Unfortunately, this wrong terminology must have been missed during our proof reading and has been corrected.

RC: Page 8554, lines 17-18: It would be good to state how much vessel diameter, conductivity, and wood density changed (e.g., in percent).

AC: The significant or marginally significant changes have been incorporated into the

new text.

RC: Page 8554, line 20: This sentence is poorly worded and does not necessarily reflect the results of the experiment. See more detailed comments on this hypothesis below.

AC: The abstract has been rewritten, and this sentence excluded.

RC: Page 8555, lines 15-16: I understand that this experiment is part of a larger study but the term “Displacement” is a poor choice for the type of experiment that was conducted here. A better term would simply be “exclusion” or “partial exclusion.”

AC: Has been changed to “Exclusion”.

RC: Page 8555, lines 27-28: It would be good to mention the effects of drought on turgor pressure and consequent consequences for cell expansion and leaf morphology here.

AC: Has been included in the new introduction.

RC: Page 8556, lines 1-3: Is this the conclusion or hypothesis provided by the authors of the other cited papers which found higher mortality in taller trees? The findings of the previous referenced studies should be described here.

AC: The introduction has been rewritten and this hypothesis was removed.

RC: Page 8556, lines 1-10: This entire paragraph is not clearly articulated and the relationship between mortality, xylem conduit tapering, atmospheric humidity deficit, tree size, forest productivity, and tree mortality is not well developed or presented. This paper is not explicitly measuring or addressing carbon starvation or tree mortality in an experimental framework, which would require measuring the range of important factors influencing carbon metabolism and transport (e.g., carbohydrate levels and phloem transport dynamics) and directly measuring mortality rates. I suggest that the authors focus the introduction instead on describing what we know about the effects of soil

drought on the xylem and leaf traits that were actually measured in this experiment but which are not adequately addressed in the current introduction. Because this paper addresses the issue of drought sensitivity and how the upper versus the lower canopy responds to soil water deficit, the introduction section needs much more background on these topics to provide adequate context for the experiment.

AC: Has been rewritten.

RC: Page 8556, lines 7-8: The statement that tall trees are normally more productive than short trees needs some citations for support (e.g., Sillett et al. 2010, Forest Ecology and Management 259: 976-994).

AC: Has been added.

RC: Page 8556, lines 3-8: Xylem tapering is considered a compensating mechanism for the effects of hydraulic limitation and is a much more complex subject than this paragraph presents. This paragraph invokes xylem tapering but only discusses vessel diameter at the tree base which does not really address the scale that tapering occurs at (i.e., the whole tree). Other mechanisms compensating for the increased effects of gravity and friction on water supply in tall trees (e.g., changes in Huber value, capacitance, and minimum water potentials) are not addressed but will play a large role in determining the effects of soil drought on tree performance with increasing height and size.

AC: Since we did not measure conduit tapering with height, this paragraph has been removed.

RC: Page 8556, line 17-Page 8557, line13: These two paragraphs are poorly structured. The hypotheses and the background information on the study site are distributed throughout the two paragraphs in a seemingly haphazard manner. I suggest that the paragraphs need to be reorganized and consolidated. In addition, the hypotheses are poorly developed and need to be reformulated to more closely match the measure-

ments and data actually obtained in this experiment.

AC: Has been reorganized.

RC: Page 8557, lines 4-6: This study does not directly measure variables of direct relevance to the carbon starvation hypothesis. In addition, it does not really even measure variables related to xylem dysfunction such as cavitation vulnerability. While the xylem hydraulic conductivity measurements in this study can provide insights into water transport dynamics in response to soil water deficit it does not explicitly address xylem dysfunction per se.

AC: The carbon starvation hypothesis has been removed.

RC: Page 8557, lines 19-21: It would be good to cite the source of these climatic data. Were they measurements made by the authors or some other source? Based on the measurements presented in this experiment, there is large inter-annual variability in precipitation at the study site (i.e., 3156 mm in year 1 and 2309 mm in year 2 – page 8565). How is it possible to calculate mean annual climatic values based on only one year (2008) of data? Are there any historical climatic data (at least more than a single year) available for the study site or region? What is the degree of variation in climatic conditions for the site?

AC: The measurements were done by the authors. Unfortunately, we do not have any historical climatic data from the study region.

RC: Page 8558, line 21-Page 8559, line 10: The multiple references for Campbell Scientific equipment in this paragraph list the location of this company as both the UK and Logan, UT, USA.

AC: Has been changed.

RC: Page 8559, line 2: Goff and Gratch (1946) is not included in the references.

AC: Has been included.

RC: Page 8859, lines 10-11: Why are the TDR probes only calibrated for 4 soil depths while the actual measurements were made at 6 depths?

AC: This was a mistake; the probes were calibrated for all 6 depths.

RC: Page 8560, lines 7-15: It would be good to include some information on the study trees in relation to the forest stands in which they were located. How deep were their crowns relative to the forest canopy? What was the tree crown and forest canopy density? How many other tree species were growing in the forest? Also, what were sample heights in the upper and lower crowns of these trees? How much variation was there in tree and sample heights? This type of information would greatly assist in interpretation of the results from this study.

AC: Two publications (Culmsee and Pitopang 2009, Culmsee et al. 2010) are presenting a complete overview of all occurring tree species. According to their results, C. acuminatissima is the most prominent and abundant tree species. Further biometrical details are given in chapter 2.1. We have included the height of crown base in Tab. 2.

RC: Page 8560, lines 18 and 20 (and elsewhere such as on Page 8561, line 22): Information is provided on the mean values for core length and other variables. What does the variation term ($\pm$) of these values represent? Standard deviation?

AC: Yes. For all methodology chapters and throughout the text the variation term represents mean $\pm$ standard error.

RC: Page 8560, line24: I suggest changing "replacement" to "displacement" and reference Archimedes' principle.

AC: Has been corrected.

RC: Page 8561, lines 6-9: I am not familiar with the Pilodyn wood testing method and suspect many other readers won't be either. Some more description of this is warranted. On the other hand, line 6 states that this method was used for comparison with the volume displacement technique of measuring wood density but no results or

discussion of this comparison are presented later in the manuscript except in Table 2. It is impossible (or at least difficult) to know how these two independent methods compare with each other from a simple listing of their values in Table 2 (what units are the Pilodyn hardness values?). I suggest that this comparison be explicitly addressed in the results and/or discussion sections if relevant to the overall findings or that these data be dropped altogether.

AC: We have removed the Pilodyn data.

RC: Page 8561, lines 13-14: DBH should be prefaced with "diameter-at-breast height" and this information would be more appropriate in section 2.5 describing the study trees. I assume that the 16 trees measured for annual stem diameter increment were also the trees uses for the other measurements but there are 2 more trees measured for stem diameter increment than the other measurements – which trees are these and why the difference?

AC: The tree individuals used for stem diameter increment were not entirely the same as used for the other measurements. We additionally investigated a few trees with smaller diameters for stem diameter increment.

RC: Page 8562, lines 12-13: Some rationale should be presented for the inclusion of vessel lumen area-specific hydraulic conductivity, and simple sapwood-specific hydraulic conductivity should be included. What additional information or value does vessel-lumen area-specific conductivity provide beyond sapwood- and leaf-specific conductivity?

AC: Indeed, sapwood-specific conductivity is more appropriate for comparison than vessel lumen-area specific conductivity, and all presented data of ks are related to sapwood-area, not lumen-area.

RC: Pages 8563, lines 2-14: It is not clear what the measurements on hydraulic mean diameter or theoretical hydraulic conductivity contribute to the paper, as these values

are only presented in Table 2 but not presented in the results section or discussed in relation to the overall findings. If these measurements contribute meaningfully to the findings then they should be explicitly discussed and if not then I suggest they be dropped altogether.

AC: The hydraulic mean diameter is calculated by weighting each conduit according to its contribution to total kh. We assumed that possible differences between treatments might be more pronounced for dh than for d, which, however, could not be confirmed. Nevertheless, dh is used in other papers on tree hydraulics and might serve for comparison (e.g. Pockmann et al. 2000, Martinez-Vilalta et al. 2002, Gonzales-Benecke et al. 2010). Therefore we have not excluded this variable from the MS.

RC: Page 8563, line18: what do the control and roof "n" values refer to? Typically, "n" values refer to the statistical replication sample size, which in this experiment are the plots with trees nested within the plots, not just the number of leaves, twigs, branches, or stems measured (which would be pseudo-replication). This applies to all of the other statistical analyses as well. More clarification on how the statistical treatment of the data in relation to replication and sample size seems warranted.

AC: We agree that pseudo-replication cannot be excluded if interactions between the branches and trees are occurring. We thus have completely recalculated the statistics. Branch hydraulic, anatomical and leaf-related variables were tested for significant differences between the drought and control treatments with linear mixed effects models with treatment as a fixed variable. We assumed the non-independence of different branches and leaves within a tree, and of different trees within the plots in the models by adding plot and tree nested in plot as random effects. Linear mixed effects models were also applied in the analysis of stem increment data and morphological and anatomical traits related to trunk wood. These detailed results are presented in the appendix.

RC: Page 8564, line 7: It is not clear why _15N was measured in this study. As the

authors mention on page 8570, the _15N signature of leaves typically shows no strong drought signal. If confirmation of this is a major finding of this experiment it should be expressly stated as such and some mention of the significance of this issue should be included in the introduction, otherwise it contributes little or nothing to the manuscript.

AC: We have removed the d15N data from the manuscript, and included 18O instead.

RC: Page 8564, lines 12-13: This sentence should be moved up to line 7 before the sentence describing the stable isotope measurements.

AC: The paragraph has been reorganized.

RC: Page 8567, line 1: How old were the branches? What proportion of their growth occurred during the experiment?

AC: We do not know the exact age of the branches. Nevertheless, the branches were on average 1 cm in diameter and showed vigorous length growth which indicates that most of the active sapwood had been produced during the 24 months of the drought experiment. We accounted for this age-related problem by only analyzing the outermost radial quart of the sapwood for wood anatomical properties, on average the outermost 1 mm.

RC: Page 8568, lines 6-7: This sentence is unclear and should be re-worded.

AC: The paragraph has been reorganized.

RC: Page 8569, line 12: What is remarkable about impaired hydraulic performance in terminal twigs when exposed to drought?

RC: Page 8569, lines 12 – Page 8570, line 2: This entire paragraph on the observed changes in leaf number and leaf area per twig sapwood area needs improvement. The changes in leaf number are interesting but from a hydraulic perspective if the total leaf area per unit sapwood area (Huber value) did not change then the functional supply of water in the drought treatments did not change. If anything the smaller leaves would

have a different energy balance and would likely lose more water through transpiration, thus decreasing their water status, not improving it as suggested here. This study would have greatly benefitted from measurements of xylem water potential to better determine what the effect of the drought treatments had on leaf water status.

AC: The paragraph has been reorganized.

RC: Page 8570, lines 3-12: It would be good to provide some context for the importance of foliar nutrient levels in the introduction of the manuscript to help evaluate the significance of these findings.

RC: Page 8570, lines 11-12: But significant difference was observed in soil moisture in deep soil layers between the treatments which would indicate that the droughted trees were not necessarily accessing this more than the control trees.

RC: Page 8571, lines 6-10: This sentence is not clear and should be re-worded.

RC: Page 8571, lines 14-16: Your data do not necessarily indicate adaptive responses, which operate at evolutionary time scales, but rather plastic responses in the study trees. In addition, canopy leaf areas did not change so the data do not support the conclusion that this was a response to experimental drought. Also, you have no evidence that there was reduced canopy transpiration because this variable was not measured, leaf area of the branches did not change, and you did not measure any potential changes.

AC: We replaced the misleading term 'adaptation' in all relevant passages by 'acclimation' which describes the plastic responses of the trees more precisely.

RC: Page 8571, lines 16-18: The fact that adult C. accumininatissima trees did not die does not mean that the species is not sensitive to drought. First, sapling C. accumininatissima died (line 13). Second, mortality is not the only way to assess mortality, and your data suggest that drought did have an effect on leaf and twig traits.

AC: In order to concentrate on the physiological measurements, we dropped all sen-

tences related to mortality.

RC: Page 8572, lines 11-12: What was the difference in humidity between the upper and lower canopy that would support such a hypothesis? Your measurements in the midcanopy indicate that humidity is very high (i.e., > 88% RH average), so it seems that it would be difficult to find a enough of a difference in RH between the upper and lower canopy positions that would result in a functional effect on tree physiology.

AC: VPD doubles from the forest floor to a canopy height of 30 m. We have included these results as figure (Fig. 1).

RC: Page 8572, lines 19-21: this is a premature conclusion not necessarily supported by your data.

RC: Page 8572, line 26 and Page 8573, line 1: Was there a sufficiently large enough difference in evaporative demand or atmospheric drought between canopy positions to support these conclusions? It does not appear to be the case from the limited data you present.

AC: VPD doubles from the forest floor to a canopy height of 30 m. We have included these results as figure (Fig. 1).

RC: Page 8573, lines 17-21: This conclusion is premature given the data you present and the lack of xylem water potential data in your study.

AC: The conclusion has been rewritten.

Interactive comment on Biogeosciences Discuss., 7, 8553, 2010.