

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

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

Indeed, sapwood-specific conductivity is of much greater interest than vessel lumen-area specific conductivity, and all presented data of ks were actually based on sapwood-area, not lumen-area. Unfortunately, this wrong methodology description in section 2.8 must have been missed during our proof reading and has been corrected.

We could prepare supplementary raw data for the appendix, or change the ratios of Table 4 to mean values per treatment.

The analyzed stem wood was produced after the beginning of the experiment according to the stem increment data, and monitored trees did not shrink (dehydrate). We assume that the slow soil desiccation, whereby atmospheric vapor pressure deficit was constantly low due to the perhumid conditions, did not provoke a step decrease in stem water potential and thereby causing stems to shrink.

Specific comments

RC: It is somewhat difficult to understand how you “desiccated” the plots from your abstract. Perhaps it would be better if you actually said, “soil desiccation in “roofed plots” was achieved by diverting throughfall (and stemflow?) with aluminum panels”.

AC: Has been corrected

RC: Page 8554, line 19: But this result wasn't significant (20% reduction in increment), right?

AC: We included, that this reduction in stem increment was not significant.

RC: Page 8554, line 20: Do you mean, “Drought treatments did not increase mortality in mature trees”?

AC: By ‘drought sensitivity’ we mean, no direct signs of drought stress whatsoever were observed after 24 month of soil desiccation among tall trees. This includes tree mortality, leaf shedding and canopy dieback etcetera.

RC: Page 8556, line 8: absolute growth is higher in large plants, but not relative growth. Per unit biomass, growth actually declines as plants get bigger. So.. I guess I don't understand why vessel size should increase with plant size (or height). Actually, I might suggest ending the paragraph after the Zach et al reference and omitting the last sentence. However, if you want to link productivity with hydraulics you could site one

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of Tim Brodribb's recent papers on the subject. He works with vessels in leaves rather than wood, but shows a close correlation between K_s (leaf) and C assimilation.

AC: Averaged per species, we found a good linear correlation ($p < 0.01$, $r^2 = 0.61$) between tree height and mean vessel diameter at the stem base. According hereon, and the statement by Melvin Tyree, assuming that a high hydraulic conductance is an essential prerequisite for a high plant productivity, we assume tall tropical tree species generally to possess larger vessels at the stem base compared to the understory, especially since conduits need to taper with increasing path length. We included the paper by Brodribb et al.

RC: Page 8557, line 26. Basal area is a much better description of stand structure than stem density. Do you know the basal area in your control and treatment plots?

AC: Basal area for the control and roof plots has been included (AB control: 46.46 m² ha⁻¹; roof: 40.26 m² ha⁻¹).

RC: Page 8558, line 10: When you say "close gaps around tree stems", do you mean that your roof captures stemflow as well? It sounds like you've done a wonderful job (what a huge effort!) setting up the plots. I am just trying to figure out how much of the throughfall (100%) and stemflow (?) has been captured by the roof.

AC: We did not measure or capture stem flow. According to a previous work (Dietz 2007, PhD thesis) stem flow is negligible compared to throughfall in this forest stand with a canopy height above 40m. In the beginning, we only used bamboo panels which were 4m long. Therefore, many gaps were still present in the beginning if trees were in the way. In the end of 2007, we closed these gaps by custom made panels for the specific gap and increased throughfall exclusion from 50% to 80% (measured with rainfall gutters above and below the roof).

RC: Page 8559, line 10: what were the TDR probes calibrated for... soil water potential?

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AC: The TDR probes were calibrated for the site and depth specific soil material. According to Campbell, Time Domain Reflectometry probes need to be calibrated gravimetrically for the site specific soil properties ranging from field capacity until below permanent wilting point.

RC: Page 8559, line 26. I am curious why you cite unpublished data for using a pressure plate to measure soil water desorption. It's a pretty standard method – I'm sure you could find the procedure in most soil methods texts.

AC: These data were obtained by van Straaten. We cited his PhD thesis.

RC: Page 8560, line 24: I think you mean “water displacement”. It would also be nice to cite a methods paper. I know water displacement sounds simple enough, but it is not as intuitive as most people think.

AC: We indeed mean water displacement and corrected the sentence. We could include a RAINFOR Field Manual by Chave. (http://www.geog.leeds.ac.uk/projects/rainfor/manuals/wood_density_english%5B1%5D.pdf).

RC: Page 8561, line 6: What is the purpose of the additional wood density measurement? I suggest just choosing what ever measurement you think is best and present only those data.

AC: Meanwhile, the non-destructive Pilodyn wood tester is more and more used to determine above ground biomass. Nevertheless, the Pilodyn wood tester needs to be calibrated. We therefore included this dataset.

RC: Page 8561, line 11: I would suggest using the term “dendrometer” or “dendrometer bands”, as this is probably a more familiar term.

AC: Has been corrected to dendrometer bands.

RC: Page 8561, line 16: I don't understand why you calculated “relative stem increment” by dividing the gross increment by the basal area. This is not a procedure I

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am familiar with and you don't reference it. I agree that you have to control for plant size, but I don't think this would work. There are several approaches to standardizing diameter increment for plant size. One thing you might consider is to use a correlative approach. In my experience, taking the \log_{10} of both original diameter (at the start of the experiment) and diameter increment will yield a linear relationship for data of your sort. You can then plot diameter increment (y axis) against stem diameter (x axis) using OLS regression (using the \log_{10} -transformed data). Assuming your data do not violate any correlation assumptions, the residuals from this correlation represent diameter increment that is unassociated with stem diameter. You need to make sure you use ordinary least squares (OLS) regression for this and not standardized or major axis regression, as the residuals from these later two procedures are not orthogonal to the x axis (original diameter).

AC: Our calculations were mainly based on changes in above-ground biomass rather than absolute stem increment. Depending on the second reviewer, we will either recalculate the stem increment data or leave them in the present form.

RC: Page 8561, line 15: Did the trees in the roof plots decrease in diameter after banding? Rainforest trees often do this during dry periods. This could be misinterpreted as reduced growth.

AC: We observed no shrinking after diameter increment measurements started. We assume that the slow soil desiccation under constantly low evaporative demand did not provoke stem shrinking due to a decrease in stem water potential. We assume this phenomenon only to occur in presence of a pronounced drought period with a strong increase in atmospheric vapor pressure deficit, causing a strong decrease in stem water potential and thereby the observed stem shrinking.

RC: Page 8561, line 22: Are you sure the wood in these branches were produced during the experiment? When did you collect them? Also, your branch lengths are very short and I would assume that you did not have closed vessels during your Ks

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measurements. I don't think this is a huge issue, but should probably mention it.

AC: The twig segments were harvested in June until August 2009, more than 2 years after the experiment started. Even if these twigs were not completely developed during the experiment, most of the active xylem (due to radial increase, the oldest parts of the xylem also occupy the least space) should have been produced during the experiment in these small and terminal twigs. Indeed, mean segment length of approximately 15 cm (12-22 cm) is the lower limit for hydraulic measurements in the tropics. Open vessels have lately been shown to have a negative impact on established high pressure vulnerability curves with the spinning technology. However, these measurements were done with relatively short stem segments (Cochard et al. 2010). The stem wood is known to consist of the largest vessels along the flow path for water, and vessel length is auto-correlated to vessel size. For *C. acuminatissima*, the stem wood shows a mean vessel size 4-times as big compared to the terminal twigs. For the twigs, we found a mean vessel size of 50 μm (ca. 8000 vessels measured). Jansen et al. (2011) studied vessel length distribution for several angiosperms. For example, *Quercus robur* as a temperate member of the family Fagaceae had an average vessel size of ca. 50 μm and a vessel length of 10 cm. Nijse (2004) explained the mechanism of vessel length distribution, indicating that with increasing segment length exponentially less and less vessels will be open cut. According to these two and other studies, we cannot preclude that segment length was sufficient to guarantee all vessels to be closed, but assumed that even if few some vessels might have been open cut, this would not have a strong effect on our low pressure hydraulic measurements.

RC: Page 8562, line 13: "Ks" usually refers to sapwood-specific conductivity. When people read your paper, they may not read the methods and will interpret your data incorrectly if you use "Ks". I would strongly urge you to use a different symbol to denote your measurement of lumen-specific conductivity (perhaps Klumen?). Also, it seems a bit strange to me to calculate conductivity in this way. Assuming I'm understanding your methods correctly, you measure Ks as the rate of flow (at a given length and pressure)

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per unit lumen area (no cell wall whatsoever)? Thus, K_s should simply be a function of the vessel area to density ratio. For example, if “ K_s ” increases, this must be due to an increase in vessel diameter and a decrease in vessel number (or increasing pit/end wall resistance). Because you measure both vessel diameter and density, I’m not sure what additional information your conductivity measurements give. I would strongly suggest that you at least include sapwood-specific conductivity in Table 4. You have all the data you need to calculate it. Because your data are so unique, they are also valuable, and other scientists will probably be interested in them.

AC: We indeed did measure sapwood-specific conductivity, which unfortunately was described wrong in this methodology section and has been corrected.

RC: Page 8562, line 25. Are you sure this increment was put on during the experiment? What was your absolute diameter increment prior to collecting these wood samples?

AC: We assured that the analyzed area of the outermost xylem (1 cm from cambium) was produced after the beginning of the experiment. Over the experimental time period (24 month), control trees increased in stem diameter by on average 1.95 cm, and drought-exposed trees by 1.53 cm.

RC: Page 8564, line 1: I don’t understand why you would calculate HV as a function of leaf number. I also don’t think it’s necessary for your argument.

AC: We tried this approach to account for the observed leaf morphological changes of the drought-exposed tree individuals. We found significantly larger leaves after the drought-treatment, contrary to the literature. Taking into account the total number of supported leaves revealed that it might be a common strategy for trees exposed to prolonged drought to reduce total number, but increase leaf size to optimize water use efficiency. To our knowledge, this has not been documented so far and therefore we consider this modified Huber Value as a valuable addition.

RC: Page 8566, line 4: From looking at figure 1, soil water potential only decreased by

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ca. 1.5 MPa. Also, don't need the “-“ in front of “3 MPa”. Ditto for following sentence.

AC: Figure 1 presents the data from three TDR probes averaged for 0.5 m soil depth. Only the top soil (10 cm) decreased up to 3 MPa. Most of the fine root biomass is located in the uppermost 20 cm.

RC: Page 8566, line 22: Please state how much lower (or higher). For example, here, did the conductivity decrease by 2% or 200%? Also, please use the symbol for conductivity after you define it. It is spelled out here. Alternatively, use a shorter, simple handle, such as, “hydraulic conductivity” rather than “axial hydraulic conductivity [es] in the xylem”. Actually, I think you mean conductivity of the lumen, not xylem.

AC: Has been included and corrected.

RC: Page 8567, line 5-9: I don't know what 15N has to do with your experiment. You don't discuss it in the introduction or the methods (unless I missed it) and I can't think why you include it here. I don't think it adds anything. Although the 13C makes sense for your experiment, I don't think you discuss what it means or why you measured it in the methods.

AC: Severe drought is often accompanied with N-limitation. Rainfall has been found to have a strong influence on foliar $\delta^{15}\text{N}$ largely due to the interaction of the growth stimulating effects of adequate moisture, the increased availability of dissolved soil N and the shift between predominantly organic versus inorganic N nutrition related to soil moisture (Handley et al. 1999). Depending on the second reviewer, we will either discuss 15N more detailed in the M&M section, or remove it.

RC: Page 8567, line 11: What are the absolute diameter increment values? Were your stem sapwood samples from only this increment?

AC: Yes, they were. Control trees increased in stem diameter by on average 1.95 cm, and drought-exposed trees by 1.53 cm during the experiment.

RC: Page 8568, line 4: How much higher?

AC: We included, that HV differed by 44 % between sun-exposed and shaded canopy, and LSC was 33 % lower as summarized in Table 4.

RC: Page 8569, line 3: Why do you say they must have grown during the experiment?

AC: We only sampled terminal twigs from the outermost canopy. We agree that it cannot completely be precluded that these twigs might have developed before the experiment and corrected the sentence. Nevertheless, most of the radial active xylem should have developed after the soil desiccation started.

RC: Page 8569, line 6: But you measured both vessel diameter and density. Can't you just plot each against K_s and tell the reader how much of the variance in " k_s " is explained by each? I actually think a more productive tack might be to calculate vessel lumen fraction (% sapwood that is vessel lumen) and S (vessel area / vessel density) and plot these against sapwood-specific K_s (viz Zanne et al. 2010). This is because it gets to your question about whether or not increases in conductivity result in lower WD – increasing VLF should directly compromise WD, but increasing S should not.

AC: For the twigs, only total sapwood-area was determined. Only from the trunk wood cores anatomical traits were analyzed.

RC: Page 8569, line 9: Do you mean diameter? If not, how do they adjust their shape, and why would plant water status (xylem potential?) affect it?

AC: Yes, we mean vessel size.

RC: Page 8569, line 25: I'm not sure why this is an "alternative strategy". It seems to be the same thing, only said a different way. Maybe you can omit this sentence?

AC: To our knowledge, it is so commonly assumed that trees rather increase single leaf area, but decrease overall number. We called this adaptation an 'alternative strategy' to the more familiar leaf size and leaf number decrease during and after severe drought.

RC: Page 8570, line 7: But your table 4 shows a significant difference for N.

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AC: We changed significantly to considerably.

RC: Page 8570, line 21: I'm not sure you can say that stomatal conductance did not change as a result of desiccation. $\delta^{13}C$ data can be pretty unreliable, as a general rule, unless you have a long-term study and differences in g_s were considerable. Also, the carbon that went into the leaves that you harvested may have been fixed prior to the experiment (from starch reserves, which can be significant in trees). Do you have any gas exchange data?

AC: Unfortunately, we do not have any gas exchange data, which could have helped us explain the $\delta^{13}C$ results.

RC: Page 8570, line 22-23: I might suggest, "... , suggesting that stomatal conductance and rubisco concentrations were similar between roof and control plots."

AC: Has been changed.

RC: Page 8570, line 28: You use many different terms for conductivity (e.g., "axial conductivity", "axial hydraulic conductivity in xylem", etc.) , and sometimes you use a symbol (K_s) to represent it. I would suggest to try and use the same, short description (perhaps "lumen conductivity") consistently throughout the text.

AC: Has been corrected.

RC: Page 8571, line 1: The words "which" and "but" are always preceded with a comma. Also, I think you mean "roof plots, which also had higher wood density..."

AC: Has been corrected.

RC: Page 8571, line 5: You should be able to address the shrinkage question easily – did the diameters of the trees in your roof plots decrease after building the roof, or did their growth just slow down?

AC: Their growth just slowed down, we excluded the shrinking part.

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RC: Page 8572, line 24: What does SLA have to do with hydraulics?

AC: We deleted the SLA statement.

RC: Page 8572, line 26: ...presumably due to evaporative demand. Pretty much any of the other variables in Darcy's law could also be responsible for decreasing HV and KI (e.g., leaf potential, soil potential, sapwood-specific conductivity, or VPD).

AC: By lower evaporative demand we especially mean lower vapor pressure deficit, which automatically is reflected in an lower leaf water potential.

RC: Page 8572, line 28: I would suggest, "...lower wood density". Also, again, because you don't include sapwood outside vessel lumen, your conductivity measurements do not imply a tradeoff with wood density. For example higher lumen conductivity (as you calculate it) simply means that there are fewer, but larger vessels (similar to Amy Zanne's "S"). Really, only higher lumen fractions (percentage of sapwood area that is lumen) should compromise wood density... and even then, it usually only marginally affects density.

AC: Our Ks calculation included all active sapwood. We unfortunately described the methodology wrong, which has been corrected.

RC: Page 8573, line 16: But table 4 shows a significant decrease in leaf area.

AC: No, AL was increased by 29% for sun leaves, and 39% for shaded leaves.

RC: Page 8573, line 19: It may simply be the case that the roof plots just didn't get dry enough to result in differences between understory and overstory trees.

AC: We agree.

RC: Table 1: Did you measure soil temperature?

AC: No.

RC: Table 2: Your theoretical Ks appear far too high. Is there a mistake in your cal-

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culations? Are your n values correct? This should be the total number of replicates (individual trees), not samples, right?

AC: The calculated theoretical hydraulic conductivity is indeed so high due to the very large vessels. If we assume a mean vessel diameter of $250 \mu\text{m}$ and a mean vessel density of 3 vessels per mm^2 , based on the Hagen-Poiseuille-Equation this single vessel from an area of 0.33 mm^2 would result in a hydraulic conductivity of $287 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$.

AC: We will accomplish Sean Gleason comments as soon as the second review is available.

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

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