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Biogeosciences Discussions

Interactive comment on "Branch xylem density variations across Amazonia" *by* S. Patiño et al.

S. Patiño et al.

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Responses to I. Wright Referee 1 (IW)

Firstly, we thank the reviewer for his comments and suggestions. Now we address his main concerns.

1) *The Introduction lacks a logical context.*

We agree and have rewritten the introduction. In the new version we include a description of the physical, structural and functional importance of xylem density. We then draw a distinction between the density from the main trunk (Dw) and the density from branches (Dx) and comment on the possible causes of similarities and differences. Thirdly, we discuss how wood density has been associated with different physiological strategies of trees and the influence of climatic and soil-site factors on Dw. Finally, we introduce the Amazon basin and the motivations of the work, our particular questions, hypotheses and predictions as suggested by the reviewer.

2) *Lack of discussion and interpretation of the main results and issues.*

Again we agree. In both the results section and in the discussion we have added some paragraphs explaining the main results of this study. For example, we now discuss the possible causes of the observed regional variation based on studies showing Amazonian scale climatic and geochemical patterns. We explain (using supporting references) why those climatic and geochemical patterns may explain in part the observed regional variation of Dx. We argue that variations and patterns across the basin may be due to long-term morphological and physiological acclimation to the physical environment as has been suggested to occur for the hydraulic system. We also discuss the possible meaning of the slopes presented in Figure 5 (see below for further details). For instance, we found that among families, genera and species there was a common slope. We explore the possible causes of exceptions. Then we test for a shift in elevation and a shift along the fitted line and find significant evidence for both. We suggest that these changes reflect both species-specific and environmental effects. For example, if Dx were strictly genetically determined, the hypothesis would be that the slope of each examined taxa is not different from zero i.e. Dx of each examined taxon does not change from plot to plot no matter the average density of the plot. The average density of the plot would be determined by the species composition in that plot since Dx is *phylogenetically* conserved, and roughly in a plot -there are exceptions of course- usually there are more than 200 species including high, low and intermediate density species. The proportion of high and low density species in that plot would determine the plot average. On the other hand, if Dx were not only genetically determined but also influenced by the environmental conditions imposed in each site, the hypothesis would be that there is a common slope which is not different than one i.e. Dx change from plot to plot according to the average density of the plot. In this case the average-plot density would be determined by the species composition and by the plasticity of some species to cope (adaptation/long term acclimation) with the environmental constrains of the site. Our data supports the latter suggesting that the majority of examined species are responding structurally and functionally to environmental requirements, perhaps sea-

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sonal drought, or poor soils wich are reflected in *increase density*. Below, we explain the possible meaning of slopes steeper than one.

3) *Conclusions regarding the importance of site climate and soil properties on wood density are unsubstantiated.*

In the original manuscript we did not include any formal discussion of the environmental factors that may have an effect on xylem density. In the new version we have brought this material together and include a rather simple analysis of the large-scale factors that may contribute to the described across basin patterns. We leave more detail analysis of the possible factors influencing Dx for a second paper which will be submitted soon. At an Amazon-wide level, the main factors seem to be climatic and geological factors, physical barriers such as rivers, soils or biogeographical factors influencing species distributions/composition. We then present some relevant evidence from physiological and ecological studies in which the importance of climate (altitude/temperature, water availability, soil physical and chemical properties) and soils have been shown to influence tree and ecosystem functioning.

4) *Coauthors.*

We raise this point because Anonymous referee 1 also had mentioned of the number of co-authors.
In the new version of the manuscript we order the authors list according to the type of contribution to the manuscript. For example the first author (SP) was involved in every aspect of the manuscript: sampling, measurements, analysis and writing, the second author provided all the resources to be able to sample trees all across Amazonia, and also contributed to sampling, data analysis and the writing. We then present an alphabetic list of all the people that contributed to obtain the primary data: students, field assistants, colleagues. This list is followed by a second alphabetic list including all the people who contributed with plot tree-by-tree data and finally we include the two last authors who led the initiation of the RAINFOR project and contribute logistically.

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We now respond to the specific issues raised by IW

IW:
The most interesting results compare variance within families, genera or species in relation to plot-mean wood densities; these indicating that much of the time the two properties scale isometrically. Oddly, in other cases the within-taxon wood density variation varied more than plot-mean WD (i.e. SMA slopes were significantly steeper than 1), perhaps counter to what one would expect. Disappointingly, there is little discussion of what these slopes mean, or what the implications are of isometric or allometric scaling between these variables.

Answer SP:
We agree that there was little discussion about what the meaning of the slopes. In the new version of the manuscript we have included a paragraph in the discussion explaining and interpreting the SMA slops and the significance of the isometric scaling. Briefly, when comparing the variance within family, genera of species with plot-mean densities it is expected that plot average would tend to be lower than the average of the examined family/genus/species because plot-average includes both low and high density species. This effect seem to be stronger in family/genus/species with intrinsic high density growing in a site where the average plot is higher than the global mean of the data set (619 kg m-3) this can be seen by observation of the mean X and mean Y given in the SMA outputs (Appendix B). Still the average site will be smaller (for the reasons explained above) than the average value of the examined level. The effect that contribute to the high slopes seems to be less influential when analysing family/genus/species with intrinsic low density. Although there is plasticity the average of family/genus/species is smaller than that of the site because the plot-average includes high and low density individuals.

IW:
The text in many places rather poorly written, and certainly in need of basic proof-reading: there are spelling and grammatical mistakes in many places, and incomplete

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(and even incorrect) figure captions.

Answer SP:
The new version has been revised by English-speaking coauthors. Text and figure captions have been carefully corrected. (However, a few original mistakes regarding figure captions were made in the editorial office after proof reading!)

IW:
More effort needs to be spent on ensuring that the Introduction effectively sets the scene for the upcoming analyses, i.e. so that it clearly logically explains the motivations for the research and - most importantly for a manuscript such as this ? the expectations (slopes etc) for the results that are presented

Answer SP:
The introduction has been changed: it now clearly sets the scene and explains the motivations and expectations of the work. For example we give more importance to the definition of *xylem tissue* rather than concentrate in what is known about species distributions in tropical forests. We also discuss references that relate variation in wood density to variation in soil and climate. Also, present the hypotheses to be tested and the predictions for them i.e. slopes = 0 or slopes = 1, shifting slops and shifting elevations.

IW:
In the Discussion more attention is needed on interpreting the results and providing the reader with insight into the issues dealt with in the study.

Answer SP:
We have rewritten part of the discussion. We explain regional patterns and place more attention to explaining the meaning of the slopes.

IW:
At times the description given of specific results seems at odds with the results them-

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selves (details below), and conclusions that are drawn in regard to the supposed importance of site climate and soil properties on wood density are unsubstantiated: no analyses concerning climate or soils are presented in this manuscript.

Answer SP:
We have avoided descriptions of specific results. Instead we have focus on giving a functional interpretation to the variation of xylem density across Amazonia. We argue that these differences may reflect differences in tree functioning, due to both genetic and environmental effects, as has been shown in a range of physiological studies. In a second paper we will present a complete analysis of the factors influencing branch xylem density and continue our discussion of the functional significance of Dx variations across Amazonia.

IW:
I suggest that the authors either engage in a serious re-write of the current manuscript, or (even better, perhaps?) combine the current manuscript with one or both of the others, and in doing so present a stronger, more compelling and potentially influential piece of work.

Answer SP:
We have rewritten the introduction and the discussion and have also included simple analysis on the possible environmental factors responsible for the regional variations in Dx.

Further specific comments by IW:

IW:
Abstract
1. L12-13. No soils or climate data were analyses, so this statement is out of place in the Abstract.

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Answer SP:
We Agree. The statement has been deleted from the abstract.

IW:
2. L15-17. How is variation predictable according to where it growing? No results are presented that support this statement.

Answer SP:
This statement is supported by the results presented in figure 5, where the majority of families/genera/species examined showed variable density and this variation was not random but systematic i.e. families/genera/species tended to increase density as the plot-average density increased.

IW:
Introduction
P2007
3. L15-27. This section should be re-written to improve readability.

Answer SP:
The whole section has been deleted.

IW:
4. L25: These theories.... Which theories are being referred to, specifically?

Answer SP:
As the introduction has changed this statement has disappeared.

IW:
P2008
5. L17-26. This is largely conjecture, thus the statement that WD effectively integrates plant ontogeny, edaphic and climate effects over a plant?s lifetime is a hypothesis, and not fact, and this should be indicated, and perhaps some evidence presented.

Answer SP:

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We have rewritten this paragraph using references to explain that Dx and Dw may be related but also explaining that there might be structural and functional differences between wood density from the main truck and xylem density from branches.

IW:
P2009
6. L11-19. Range size is not the same as abundance within sites, and the two may not even be correlated, yet the authors treat the two properties as being one and the same. Also, why should a species 8216;converge8217; to the site-average WD value?

Answer SP:
Yes, we agree. As we have rewritten the introduction the paragraph has disappeared
Species may converge to the site-average value because there is evidence of convergency of physiological options of different species growing in the same conditions (Meinzer, 2003).

IW:
Methods
P2011
7. L1. The finding, attributed to Lloyd et al 2008b (in prep), that there is no effect of height on WD within a given plant is reasonably crucial for interspecific comparisons to be made across plants sampled at a variety of heights, as is done here. Thus, it would have been helpful if this cited work had accompanied the manuscript. In my own experience wood density tends to increase with distance back from the branch tip, in contrast to the findings attributed to Lloyd et al. But perhaps this is not the case with tropical tree species; in support of this possibility (and in agreement with Lloyd et al),the authors might be interested in the recent paper by Swenson Enquist (Am J Bot,May 2008 issue).

Answer SP:
There are few things regarding this point. We collected *terminal branches* with ap-

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proximately the same basal diameter (0.8 to 1.5 cm) and length (aprox. 1.5 m) from three positions on the trees: upper, middle and lower crown. We did not examine the variation of xylem density from the tip to main trunk. We agree that many (but not all) tropical trees show an increase of density going down from the tip towards the main trunk. But as mentioned above we compared only external/terminal branches at three positions on the crown. Interestingly there was no statistical difference on twig density between the tree positions. One would have expected perhaps lower density for lower (shaded) branches. Because when one compares leaves at the three positions, sunny leaves (from upper branches) have about 10 In the reviewed manuscript we present the results of the ANOVA comparing branches from upper and lower crown. This information is used to sustain the point that the data from Guyaflux, French Guiana has no bias as was suggested by Anonymous Referee 2.

IW:
P2012. 8. L16-19. These statements regarding contaminated data seem rather at odds with the description in Methods of a standard methodology being used for data collection.

Answer SP:
We believe that in any research that implies large amounts of field measurements there would be human *measurement errors*.

IW:
P2016. 9. L2-5. If only one branch was sampled per plant, then the residual variation simply cannot reflect within-tree variation, as claimed.

Answer SP:
Corrected, we wanted to say it between-tree variation. There are factors such as light, and mechanical stress (the *touch* of neighbouring trees) that can modify the genetic determined architectural patterns of a given tree i.e. a tree growing alone without close neighbours shows the well defined architectural design of that species. While trees

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closed to neighbours have thigmomorphological responses such as inhibition of the developing bud (Nicolini, 1997). This may result in a reduction of the length of the branch, production of extra reaction wood that may lead to structural changes of the xylem tissue that may be reflected in its density value. See for example (Cochard et al., 2005; Moulia et al., 2006; Han et al., 2007; Cordero et al., 2007; Coutand et al., 2008).

IW:
10. L11-14. 27-33

Answer SP:
Agree. Statement deleted

IW:
P2016. 11. L20. Could the authors be more precise than using phrases such as *nearly all*. Not only is this needlessly imprecise, it is actually untrue in this instance: while the confidence intervals of slopes fitted to 15/24 families and 17/23 genera did indeed include 1.0, these proportions can hardly be said to be nearly all. Incidentally, all of the slopes that were significantly different than 1.0 were steeper than unity; I wonder if the authors could include some discussion interpretation of this point in the Discussion.

Answer SP:
Rephrased. We have included some discussion and interpretation of *steep* slopes as explained above.

IW:
12. L23. Why *somewhat surprisingly*

Answer SP:
We agree!!! Not surprising taking into account all the literature supporting the point that the same species growing in different site conditions show different wood densities (See for example: Parolin et al., 2004; Nogueira et al., 2007).

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IW:
13. L28-29. To my reading, Brosimum varied as much or more than other taxa, yet the authors describe this genus as varying less than all the genera examined.

Answer SP:
This particular example was deleted from the manuscript because we had one error in the calculation of the density of one individual in TAP-04. The mistake has been corrected.

IW:
Discussion
14. P2018, L11-12. Here the authors argue that knowledge of site conditions is necessary to predict wood density. This may indeed be true, but no data are brought to bear on this issue in this manuscript and so a statement such as this needs to clearly labelled as conjecture, or citations need to be given.

Answer SP:
We agree, we have changed the argument and have added further suggestions.

IW:
15. Fig5B 5C captions are at odds with the axis titles.

Answer SP:
Corrected.

IW:
16. RAINFOR is spelt RAINFOIR in caption to Fig 7.

Answer SP:
Corrected.

IW:
17. Table A1 lacks a title. Also, reference is made to Anderson Malhi 2008, yet I could not find this citation in the reference list.

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Answer SP:
Corrected. The title for table A1 is: *Description of forest-plots*. The reference was footnote No. 8. In the new version it will be in the references list.

IW:
18. Caption to Table B1 is incorrect. Is this actually the caption to Fig 2?

Answer SP:
Corrected.

IW:
19. Table C1 gives a long list of regression parameters, but no mention is made of what regressions these are.

Answer SP:
These tables have been edited and the meaning of them explained in the text.

We thank the reviewer again for his comments.

Sandra Patino

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