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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 Anonymous Referee 2 (AR2)

After consultation with my co-authors I now respond to the points raised one-by-one.

Major concerns AR2:

1) *Overestimation of branch xylem densities.*

AR2:
In this study samples were dried at a temperature of 70-90 °C. But temperatures of 103-105 °C are necessary (Ketterings et al. 2001, Chave et al. 2005, Schöngart et al. 2005) to determine wood densities representing an oven dry mass with about 12 % moisture content (the residual water in the xylem is mainly bound by capillary forces in the cell wall).

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Answer SP:
References provided by AR2 show that as part of the methodology, temperatures of 103 to 105 °C have routinely been used to dry wood samples from the main trunk of trees which include sapwood and heartwood. No explanation is provided of why these temperatures should be used to dry small samples of wood from branches. We are interested in *branch* xylem density as one of the physical properties of trees that is directly linked to tree physiological processes. Most of the relevant literature for our work shows that temperatures from 60 to 75 °C have been used to dry wood from branches (see for example Hacke et al 2000; Hacke et al 2001; Santiago et al 2004; Pratt et al 2007; Swenson and Enquist 2008; Schenk et al. 2008).

By definition, 12 to 18 % moisture content corresponds to air-dry wood samples. The moisture content of air-dry samples depends on the air vapour pressure deficit of the surroundings where samples are dried. It is stated that in any air-ventilated oven at any temperature higher than ambient, wood will warm up and start to dry (Kollmann and Cote-Jr., 1984). Therefore, after 3-5 days in an air-ventilated oven at 70-90°C, branch wood samples should have water contents lower than 12 %.

It is well known that heartwood is more difficult to dry than sapwood. This is because sapwood is generally permeable in all species and because tyloses, aspirated pits and depositions of extractives on pit membranes make heartwood more impermeable, inhibiting movements of water (Bowyer et al. 2003). Also, lighter species in general dry faster than heavier species, because their structure contains more openings per unit volume (Simpson 1981). Vessel elements of branches for many tropical trees are longer than 40 cm (S.P. unpublished data). For our samples this means that no water should have been trapped in cell lumens, making them easier to dry. Drying times and temperatures also depend on the size of the samples and whether they are soft or hard woods (Kollmann and Cote-Jr., 1984; Simpson 1981; Bowyer et al. 2003). Wood from branches < 2 cm diameter does not have heart wood. Instead it has pith which is composed of primary parenchyma, a tissue containing only free water which is easily

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removed. Pith larger than 2 mm was removed from the samples increasing the speed of drying since wood would have dried in two directions: from the outside to the inside and from the inside to the outside.

Nevertheless, we agree that there may have been an overestimation of sample dry mass and therefore of branch xylem densities because some bound water may have remained attached to the cellulose structure of the wood after drying. Still this *error* would have been small and approximately the same for all the samples in our data set because the density of every single stem was measured using exactly the same methodology and was performed always by the same person(s) (S.P. and others).

AR2:
However, drying at 70-90 °C results in higher moisture contents and thus the presented data have strong bias to overestimate xylem density (Dx). Even if the samples have been dried until achieving constant mass after 3-4 days, the moisture content is still much higher than a sample that has been dried for the same period by a temperature of 103-105 C. It is not understandable that the same authors determine xylem densities of branches (this study) by another methodology as xylem density of the bole (Chave et al. 2005).

Answer SP:
The methodology used in Chave et al. (2005) was for bole densities and not for branch xylem densities. Some differences between these type wood have been mentioning above.

To quantify the extent to which our Dx may have been overestimated we performed a test in French Guiana.
Experiment.
Wood samples (14-26 mm long and 4-17 mm diameter) from upper crown branches of 276 trees 10-104 cm DBH were used from the BRIDGE project ANR, UMR-ECOFOG, French Guiana: http://ecofog.cirad.fr/BRIDGE/index.html (Carolina Sarmiento, S.P. et

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al, unpublished data). Samples were dried for two days at 75 °C and their dry mass obtained (m75). Then they were re-dried for two days at 103 °C, and the new dry mass was obtained (m103). There were no statistical differences between the two masses (ANOVA, DF=1, F=0.05, P=0.824, mean m75 = 0.793 +- 0.464 g, mean m103 = 0.784 +- 0.459 g) nor between the two densities (ANOVA, DF=1, F=0.51, P=0.477, mean Dx(75) = 0.608 g cm-3, mean Dx(103) = 0.601 g cm-3). Nonetheless we can observe indeed that there was a small overestimation of 1.1 % of the dry mass and 1.2 % of the Dx when wood samples from branches were dried at 75 °C for two days as compared to the higher temperature.

AR2:
Therefore the samples, if still available, should be dried at 103-105 °C and new data analysis should be performed.

Answer SP:
After observing the results from the previous test and the literature we are confident that there is no need to dry our wood samples again. Even if there is a problem in contrasting branch xylem density with bole density, we are presenting a novel dataset from all across Amazonia that is methodologically internally consistent. Therefore, we decided not to apply any correction to our original data set but to correct the new data from the BRIDGE project which includes 20 trees (selected as explained below) from 7 plots across French Guiana by multiplying Dx by 1.01. The correction was applied because all these samples were dried for at least three days at 103 °C.

2) *Claiming that branch density could be a surrogate for bole density.*

AR2:
The authors state at Page 2018 in the last paragraph that on the species levels the xylem density of the branches (Dx) is similar to those of the bole (Dw). I would expect much lower values in the xylem density of branches compared to those of the bole.

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Most tropical trees show density gradients from heartwood to sapwood (Wiemann and Williamson 1989; Fearnside 1997, Parolin 2002, Wittmann et al. 2006). This increase of specific wood density with increasing tree diameter can be explained by the incorporation of mineral salts and chemical substances (terpenes, essential oils, tannins, flavonoids, aldheydes, alcohols, and colored pigments) during the formation of heartwood to protect the wood against the attacks of predatory organisms such as fungi, insects, and xylophagous grubs. However branches of 1-2 cm diameter already have a wooden tissue, but still do not have heartwood formation and thus I am surprised that Dx and Dw are similar. This might be a hint that the xylem of the branch density is overestimated due to drying the samples at lower temperature as the samples used to determine the xylem density of the bole.

Answer SP:

Branch xylem density of many tropical species is higher than bole density (Sarmiento C., S.P. et al. in preparation). In general it is true that branches have lower density than the bole of the same tree. But on the one hand not only the presence of heartwood will increase the density of a wood sample. In general branches have large amounts of reaction wood which is denser than normal wood (see for example Baillères et al. 1997). On the other hand bole density could also be underestimated because some extractives can be driven off during drying at high temperatures i.e. 103 °C (Bowyer et al. 2003). Nevertheless, since submission of the paper there are reports already showing the correlation between trunk and branch density in tropical trees (Swenson and Enquist 2008; Sarmiento C., S.P. et al. 2008; Sarmiento C., S.P. et al. in preparation; Juliana Agudelo and others unpublished data). These works suggest that with some care branch density could be use to predict trunk density of tropical trees. Yet, the apparent similarity between the density of the main trunk and that of branches is an important issue that can not be explained by simple *overestimation* of branch densities (Sarmiento C., S.P. et al. in preparation). The key question unanswered (and which we were careful not to comment on too closely - though in retrospect it may have been wiser not to mention it at all!) is whether or not bole densities vary systematically with

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location to a similar extent as we have documented for Dx. Obviously, although then posing some interesting scientific questions, this would also present a great inconvenience to many researchers and foresters who have long considered bole densities to be a more or less site independent (i.e. solely species dependent).

3) *Not enough data to support the results.*

AR2:
An impressive dataset of 1466 trees comprising 503 tree species from 80 plots across the Amazon basin have been analysed for this study. But about 20 trees greater than 10 cm dbh per plot (P. 2010, line 5) is not very representative to indicate the variation between stand levels across the basin or between families, genera and species. Tropical rainforests have high species diversities of up to 300 species per hectare considering individuals >10 cm dbh. 1466 trees samples divided by 80 plots yields in 18,3 trees per plot in average (not 20 trees). This number is by far not representative for a stand considering also that the majority of the sampled trees were chosen by the possibility to climb them.

Answer SP:
In the case of the biased tree sampling, the obvious point that AR2 overlooks, as mentioned in the Material and Methods, for each tree climbed, typically three to five other trees were sampled. Often climbers used one tree to climb and move from there to different and/or larger trees. Thus there is unlikely to be implicit bias based on the actual sampling strategy. Secondly, although we could sample on average only 20 trees per plot, we have taken this into account to the maximum extent in our analysis by treating all variables as random terms (reflecting we could only manage to subsample some part of the population) and, especially as we have taken into account effects of genotype per se on Dx, then the conclusion that a significant proportion of the variance in the dataset observed is related where the trees were growing is statistically robust (note; one can also add the standard errors for each variance component pie chart

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as GENSTAT gives these in its output as well; all effects are significant). We have also estimated the mean species Dx effects for each plot weighting values according the actual species abundances observed which again means, that although our plot level estimates may not be as perfect as if we had somehow managed to sample all trees in all the plots, our estimates are as realistic and representative as possible -and certainly more realistic than many previously published estimates of stand level Dw where literature values for mean Dw rather than actual measurements for the plots in question have been used.

To address the issue of sampling bias at the plot level, we test whether a sample of 20 trees chosen in according to the method used in the present manuscript would represent the mean Dx of the community of trees > 10 cm DBH contained within one hectare plot. For this test we used data from the Trésor permanent plot in French Guiana (the BRIDGE project, Carolina Sarmiento, S.P. et al. unpublished data) were 95 % of the trees > 10 cm DBH were sampled for branch density (399 trees). We applied the 20-tree sampling design to this plot twenty times. Each set of trees was composed of 4 sub-groups of neighbouring trees distributed across the plot, to include trees from different landscapes of the plot. Note that for the test presented here, each set was chosen visually from the dot-plot of all the sampled trees and not in the field following physiognomic variations within the plot. We compared each set with the overall mean and with each other using Tukey HSD test. No statistical differences were found between any group and the overall plot mean, nor between any two groups (overall mean = 0.595 g cm-3, DF=20, F=0.71, P=0.819). We also used Mood Median Test because not all the sets had normal distribution. There were no differences in the median between the groups (overall median = 0.600 g cm-3, Chi-Square = 16.59, DF = 20, P = 0.679).

AR2:

The analysis of the dataset considers only differences of xylem density between taxons (family, genus, species) and geographical regions, but none of the 50 authors

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started the attempt to relate xylem density of branches with environmental data such as edaphic parameters (nutrient-rich floodplains vs. terra firme) and climatic parameters such as rainfall patterns (these data are available in the RAINFOR program for the majority of the plots) or even successional stages (as they occur frequently in the high-dynamical floodplain forests) or aboveground wood biomass stocks and production (Baker et al. 2004, Malhi et al. 2004, 2006).

Answer SP:
These are the subjects of an accompanying paper which will be submitted within this special issue and which is currently in preperation on the same subject(s) but with a different title to those mentioned in the concluding paragraph of the original version of the manuscript; and which will reveal how the site level effects shown in the current paper are to a large degree explicable in terms of variations in soils and climate and, even better, how these effects are linked with parallel changes in foliar nutrient status and other relevant physiological properties. The present manuscript is already long enough to include the results of all the factors that may influence branch Dx of Amazonian trees. Nevertheless as suggested by I. Wright (Referee 1) in this paper we will introduce the subject in the introduction as part of the literature review and in the discussion in a more concrete manner such as supporting evidence from many studies that show how wood density is influenced by climatic and edaphic conditions.

Minor concerns AR2:

AR2:
Abstract: Density values should be expressed as g cm-3 not kg m-3.

Answer SP:
Across the literature different authors use different units or unit systems i.e. g cm-3 in the metric system or lb ft-3 in the English system. For submission in Biogeosciences it is mandatory to use the metric system and, wherever, possible, SI units should be used, therefore we conserve kg m-3 whenever possible.

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Interactive Comment

AR2:
Introduction: The first 30 lines about species distribution patterns should be shortened.

Answer SP:
The introduction is being rewritten as suggested by I. Wright (Referee 1) in a more coherent manner with no inclusion of the 30 lines about species distributions. A new version of this manuscript will be submitted soon.

AR2:
Methodology: The two plots from the Paracou site (French Guiana) had another methodology, where only lower branches from subcanopy trees were sampled (Page 2010, line 26). This database should not be considered for this analysis. For instance, in the BCI 50-ha plot, large trees tend to have lower wood densities than small trees (Chave et al. 2004). Thus the data set from the Paracou site may overestimate xylem densities.

Answer SP:
The reviewer is assuming that density of branches and main trunk of small trees (> 10 cm dbh) is the same and that both are higher than branches and boles of large trees.

If the density of the main trunk of small trees tends to be higher than for large trees on BCI this finding can not be generalised for trees in the Amazon basin or any other tropical forest. For example Wittmann et al (2006) found the opposite tendency for high várzea trees in the Western Brazilian Amazon and Chave et al. (2008) did not find that small trees at Les Nouragues, French Guiana have higher densities than large trees. We found that the sampled trees in Paracou followed normal distribution, included the range of densities measured for sapwood of the main trunk and followed the same distribution of abundance of the main families present in the Guyaflux plots (Jacques Beauchene, personal communication). When weighting by species abundance, our sampled trees accounted for more than 50 % of the families present.

To determine if there was indeed an overestimation of Dx for the Guyaflux trees we

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compared Dx from upper and lower branches of the same trees from our sub-sample of 272 trees. We found no statistical difference between the density of branches from the two positions on the trees (ANOVA, DF=1, F=0.18, P=0.674, mean upper branches = 0.619, mean lower branches = 0.615).

Therefore we have chosen to retain the data from Guyaflux. Furthermore, since we have engaged in rewriting we will include data for 7 new plots from French Guiana.

AR2:
When comparing the xylem density of branches exposed to light, mid-light and shadow, it is also not understandable why only 200 trees have been considered and not the whole dataset? How have the 200 trees been selected from the total dataset?

Answer SP:
We have rewritten this part of the methodology to help readers to understand the collecting protocol. Briefly, in each plot we sampled branches from low, middle and upper crown from a sub-sample (three to 5 trees) of the 20 trees. Practically and logistically it was impossible to sample more trees and/or branches during the project. There was no rule on how to select these trees. It could have been the climbed tree or one of the neighbouring trees. The only rule we followed was that these trees had to have three types of branches: upper canopy = exposed to light, middle = mid-light and lower = shaded.

AR2:
P. 2011, line 16: Units should be given in mm or cm, not meters.

Answer SP:
For submission in Biogeosciences it is mandatory to use the metric system and, wherever, possible, SI units should be used, therefore we conserve meters (m) whenever possible.

AR2:

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Results
P. 2014, line 17: What is N for the Ecuador region?

Answer SP:
Corrected: typing error

AR2:
P. 2015, line 3: Bignoniaceae (for instance the genus Tabebuia) also have species with very high density. The same holds for Euphorbiaceae, which have wood densities varying from 0.33 to 0.93 g cm-3.

Answer SP:
The same might hold for the majority of families. In this paper we only report the results obtained for our own measured branch Dx. We do not claim the values reported here are absolute for any given species, genera or family. Although we have not been able to collect individuals of the same family, genera or species in all the plots we have enough data to support the main findings of this study: Dx of the same species, genera and families collected in different forests changes according to the mean density of each forest.

AR2:
P. 2016, lines 11-13: This sentence is not understandable.

Answer SP:
Changed

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1-Now to be: S. Patiño, T. R. Baker, N. M. Fyllas et al.: Relationships among ecologically important dimensions of neotropical plant trait variation as affected by soils and climate.

Interactive comment on Biogeosciences Discuss., 5, 2003, 2008.