

## ***Interactive comment on “Drought resistance increases from the individual to the ecosystem level in highly diverse neotropical rain forest: a meta-analysis of leaf, tree and ecosystem responses to drought” by Thomas Janssen et al.***

**Anonymous Referee #1**

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Janssen et al. examine whether a meta-analysis of leaf-, tree- and ecosystem-level data can help understand, and predict, neotropical rainforest responses to drought. They ask two questions: (i) how does drought impact the vegetation from the leaf to the ecosystem scale?, and (ii) can different hydraulic behaviours at different locations or among species explain differences in the responses to drought? They find that episodic drought effects compound on dry season effects at both the leaf and tree scales. However, vegetation responses are buffered at the ecosystem scale and, notably, are often not significant during episodic drought. Finally, independently

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compiled wood density data are used to explain some of the variability observed at the leaf and tree scales during the dry season (and to a lesser degree during episodic droughts).

I commend the authors for this undertaking (138 studies!) and for the quality of their writing. The study will make an important contribution by explaining the eco-physiological impacts of drought on a key region's rain forests, at a range of scales. However, I have several major methodological concerns that should be addressed in revision.

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### Main comments

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My first observation is that, according to the number of measurements / estimates compiled by the authors, episodic droughts data (624) represent 9% of the total amount of data (6956) and to 17% of the dry season data (3006). This feels like a very high number of episodic drought observations compared to the rest of the observations. Looking at Figure 1b and c, the number of observations per month appears biased towards the more recent years. Does this bias explain the frequency increase in the average of episodic drought months per year in the more recent years? Looking at Fig. 1d, I am also questioning the definitions used for the wet season, dry season, and episodic droughts. For example, in 2000, the K34 site starts off by being in the wet season for 5 months, then in the dry season for 1 month, then in the wet season again for 1 month, then in the dry season for 2 months, wet season for 2 months, dry season for 1 month, wet season for 2 months, dry season for 1 month.... This pattern of oscillating wet and dry season is seen repeated within the following years, but how likely is it to represent the “real” wet and dry season? And so, how can dry season effects on the vegetation be captured on time scales that make sense? Again, if we look at the dry season and episodic drought between 2015 and 2016, we

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see a transition from episodic drought to wet season although the relative extractable soil water is very close to 0. I understand from the authors' definition of the wet season that this is because the soil moisture has started to be replenished. Realistically, if the vegetation had just gone through an episodic drought, then would the next month's measurements of stomatal conductance, photosynthetic rate, etc. be representative of a wet season month?

Therefore, owing to potential hydraulic function damage sustained during the drought, the authors might want to rethink their definitions of the wet and dry seasons, as well as of the episodic droughts, in terms of what makes sense when considering potential multi-weeks (but not multi-years) legacy impacts on the vegetation. One solution would be to classify some of the data as being within "recovery months" (i.e. from a drought or from the dry season to the wet season) and to analyse them separately. The authors should also consider testing the sensitivity of their results to different quantile threshold definitions for what consists in the wet and dry season, as well as in an episodic drought.

My second concern relates to the method used to calculate the percentage changes shown in Figs. 3 and 4. It is very clear from Figs. S2, S3, and S4 that wood density is a good proxy for leaf- and tree-level hydraulic behaviour. So why not cluster the analysis of the rates of change by types of wood density (e.g. low vs high), to ensure that opposite types of leaf- and tree- level behaviours are not compensating and cancelling each other out when looking at the rates of change?

I understand that this is what Figs. 5 and 6 attempt to do, but I do think the broader narrative would be more successful had the meta-analysis differentiated between isohydric and anisohydric behaviours from the start. Clustering by behaviour might also help reconcile and explain the current inconsistencies in the findings from the leaf-level up to the ecosystem scale.

My third point has to do with the VPD values used to estimate changes in leaf-

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level transpiration. The leaf-level transpiration is estimated using the relationship  $E = g_s \times D$  where  $D$  is VPD.

Here, the authors use monthly averaged atmospheric midday VPD derived from the ERA5 reanalysis data. I am surprised because the VPD values present in the database are very low, with a maximum of 2.35 kPa across all 6956 data points and the 95th percentile < 1 kPa. Given that > 50% of the total data is classified as corresponding to either the dry season or to an episodic drought, I would at least expect the 95th percentile value of the average monthly midday VPD to be > 1 kPa! It is unclear to me whether these low values are due to using the Buck method to calculate VPD, or to the ERA5 data themselves.

Additionally, using atmospheric VPD rather than leaf-to-air VPD (which the relation  $E = g_s \times D$  is designed for) ignores feedback effects from the leaf to the atmosphere above. When plants transpire during a drought (or a heatwave), they also cool the air immediately above them, leading to lower leaf-to-air VPD than atmospheric VPD.

One finding of this paper is that "the data shows no significant decline in leaf transpiration from the wet to the dry season [...] as the average increase of VPD from the wet to the dry season is of the same magnitude as the decline of stomatal conductance". Instead, higher estimates of midday VPD (e.g. from a different reanalysis product) could lead Janssen et al. to predict an increase in transpiration during the dry season. Or, conversely, using leaf-to-air VPD might lead to a smaller magnitude increase in leaf-to-air VPD than the decline in stomatal conductance, thus leading to predicting a reduction in leaf-level transpiration in the dry season!

It is very hard to tell what the implications of the VPD estimates are, but they currently make it hard to trust the leaf-level estimates of transpiration, Potential ways forward are:

1. to use a different method than the Buck method and to quantify the uncertainty;
2. to compare the current VPD estimates with different reanalysis products (e.g. ERA-Interim which has been evaluated more) or other products, such as the

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CRU data, and to quantify the uncertainty;

3. to calculate a proxy of leaf-to-air VPD using atmospheric VPD and leaf water potential to account for a degree of leaf-atmosphere feedbacks.

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Minor comments

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L. 22: it's hard to see how the results could be used as a benchmark for LSMs, given e.g. the unexplained differences in transpiration responses from the leaf- and tree- scales to the ecosystem scale. Instead, do the authors mean that the relationships they find between the different variables and wood density could help guide LSM parameterisation efforts in neotropical forests?

L.32: maybe consider citing Yang et al. 2018 (<https://doi.org/10.1038/s41467-018-05668-6>), which uses LiDAR and allometric relationships, in place of Zhao and Running? The Zhao and Running paper has temperature dependencies which are problematic and have been discussed in several technical comments....

L.54: I suggest starting a new paragraph at "Episodic droughts"

L.55-56: do tropical North Atlantic SST anomalies affect all the neotropics? Or do they primarily affect the easternmost region?

L. 75: "stomates progressively close" is more exact than "stomates close"

L.76: also:

1. Martin St-Paul et al. 2017 (<http://doi.wiley.com/10.1111/ele.12851>),
2. Drake et al. 2017 (<https://doi.org/10.1016/j.agrformet.2017.08.026>),  
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3. Choat et al. 2018 (<https://doi.org/10.1038/s41586-018-0240-x>)

L. 84-85:  $E$  can either stay the same, increase, or decrease during a drought, all of which could result on a decline in  $\Psi_l$ .... Also,  $k_{sl}$  declines as a result of a decline in  $\Psi_s$

L. 87-88: stomatal closure (described above) and stomatal downregulation are not the same, so the link isn't clear from the current phrasing. Also, using the words "potential" and "potentially" could lead to misinterpretation

L. 88-90: Is this meant as a global statement? Or is it still in the context of neotropical forests? Generally, this is quite variable depending on species, ecosystem, and timing... with different responses being observed at different stages of a drought

L. 104-106: I think the paragraph would be clearer if this sentence came right after the reference to Sayer et al 2007, L. 102

L. 107: here, maybe repeat what the three spatial scales are

L. 114: change "drought avoiding and drought tolerating strategies" to "drought avoidance or tolerance strategies"?

L.114-115: xylem embolism doesn't always substantially damage the hydraulic pathway, maybe consider rephrasing as "Drought avoidance strategies aim to avoid dangerous declines in  $\Psi_l$  that could lead to significant xylem embolism and thus damage...?"

L. 118-120: consider rewriting as: "Conversely, drought tolerance strategies imply [...] without significant and/or irreversible embolism-induced losses of hydraulic function"?

L. 120-123: the isohydric vs anisohydric (why use “non-isohydric” rather than anisohydric?) need a bit more explanation, e.g. isohydric species maintain a constant midday  $\Psi_l$  but also down-regulate their stomatal conductance. It would also be worth mentioning that the spectrum of isohydric and anisohydric behaviours is quite large, with some species having the capacity to oscillate between more-or-less isohydric or anisohydric behaviours depending on the environmental conditions...

L.131-133: this is a very nice hypothesis! To introduce it, the authors could refer to the work of Rosas et al. 2019 (<https://doi.org/10.1111/nph.15684>)

L. 136-138: I think that moving this sentence to line 133 before “In neotropical...” would make the text flow better

L. 138-140: this is very useful contextualisation, maybe it could make it into the abstract?

L. 153: typo: “it” to “they”

L. 156: what about measurement techniques and errors? Were those also included in the database? I imagine there would be different margins of error depending on the measurement technique. Also, were there quality checks or did all the above described data make it into the database?

L. 157: was the time of day not reported? This would highly impact measurements of stomatal conductance and leaf photosynthesis...

L. 157-158: how many different species, genus, and/or different site averages?

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L. 160-161: the information on how the spatial data were extracted is probably not needed

L. 171: shouldn't “midday vapor pressure deficit” be “monthly averaged midday vapor pressure deficit”?

L. 173-175: the authors need to mention that this assumption largely ignores variations in root distributions

L. 177-178: please clarify what “ecosystem performance measures” means

L. 179: were all the stomatal conductance measurements made at midday? Also, it is worth mentioning that this relationship assumes a perfect coupling between the stomates and the atmosphere above, i.e. it assumes that the boundary layer conductance to water vapour,  $g_b$ , is much larger than  $g_s$ . But in forests with large leaves and dense canopies, decoupling is often observed because  $g_b$  is relatively small, such that when  $g_s$  and  $g_b$  are of similar magnitudes  $E \approx 0.5 \times g_s \times D$ . In the context of this study, it is impossible to estimate what the coupling/decoupling factor is at a given location and/or at a given time, but the authors should mention this (in the context of leaf shedding and flushing?), given their findings

L. 184-186: from the text alone, it is very unclear how transpiration was estimated. How does the RMSE represent the linear relationship?

Looking at Fig S1, I presume the authors have compiled tree scale measurements of  $E$  so, in the analysis, why not just use those measurements (instead of the estimates described by the linear relationship)?

L. 190: my interpretation of equation 3 is that it should only be valid at steady-state. How did the authors ensure steady-state conditions? Were the data filtered

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depending on VPD?

L. 192: typo: "rooting zone" to "root-zone"

L. 193-194: strictly speaking, difference between  $\Psi_l$  at midday and  $\Psi_{pre-dawn}$  is a proxy of the water gradient within the tree, from the root up to the canopy. For it to equate soil-canopy gradient, further information on tree height would be needed to account for gravitational effects and relate  $\Psi_{pre-dawn}$  to  $\Psi_s$ ...

L. 225-227: I realise it's common to use log response ratios when comparing large amounts of data, but why not directly use the percentage change to quantify drought effect size?

L. 242-243: given the large variability in hydraulic behaviour observed within a genus, is it reasonable to use the genus average as a proxy here? And how many of the location points are affected by this assumption?

L. 254: the reference to Figure 2a is needed here too

L. 260: I find hard to believe that this is an actual result and not simply a product of the methods used to calculate the leaf-level transpiration....

L. 265: but a drop in  $\Psi_l$  is observed!

L. 275-276: the authors could mention that this is in line with the findings of Rosas et al. 2019 along a mesic-xeric gradient (although their study is not on neotropical species)

L. 304 (and later): the "WUEi" notation is inconsistent with the "iWUE" notation

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used in the introduction

L. 311: "we observe that" is not needed

L. 315: typo: "marginal" should be "marginally"

L. 322: give the ranges of variation?

L. 320-328: the findings would benefit from being broken down in terms of the dry season (significant) vs episodic drought (mainly not significant)

L. 334: the authors need to state that the relationship is not significant...

L. 336: "intermediate response" is very vague, please reformulate

L. 337-342: these findings are very useful!

L. 344-346: How is it "similar"? Fig. 6a seems to show far less significance and way more scatter than Fig. 5b

L. 356: why "hydrological"? Do the authors mean hydraulic?

L. 358: please replace "cancelled out" by "offset"

L. 392-394: I don't follow this sentence.... these effects can be consistently observed for weeks, and even months? Do the authors mean that leaf effects are typically observed on shorter time scales due to the "life expectancy" of a leaf compared to a tree, or to an ecosystem?

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L.405-406: the mention of these “ENSO swings” would be a better fit L. 400, right after the list of references. But what is an ENSO swing? This is never defined...

L. 398-407: I’m not entirely clear why the increase in the frequency of episodic droughts is not first mentioned in the results section?

L. 538-540: this should come earlier, after L. 120-123

L. 546: but can also be explained by plant capacitance

L. 564: typo: missing “and” after “environments”

Fig. 1a: the K34 site should be indicated on the map given Fig. 1d and 1e

Fig. 1b: this is averaged across sites, right? I wonder whether it would make more sense to actually average the episodic drought months across the whole area of neotropical forests shown on the map. This would potentially reduce sampling biases in concluding that episodic droughts have been increasing in neotropical forests. Alternatively, the authors could consider weighting this by the number of monthly observations per year.

Fig. 1e: visually, it would be very nice if the ENSO index was coloured to match the wet and dry season and the episodic droughts

Fig. 2a: where do the top soil  $\Psi_s$  data come from? The caption says published data, but I didn’t find it in the methods?

Fig. 2a and 2b: yes to the mention of capital letters in the legend, but what does it mean when letters are coupled (e.g. AB in the dry season in Fig. 2a) or when the letter A or B appear during episodic droughts?

Fig.2: I imagine the horizontal lines in the box plots show the median, the boxes themselves interquartile ranges, the vertical lines the 5th-95th percentiles and the

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points are outliers? This needs to be mentioned in the legend

Figs. 3 4: what do the horizontal lines represent? Ranges?

Additionally, it would be useful:

1. to also mention the number of data points (or average number of data points per study/site) in brackets;
2. to visually separate the variables that were directly retrieved from the literature from those that necessitated further calculations.

Figs. 5 6: so bigger points mean smaller errors? Does that also play a role in the weighting of the solid and dashed lines?

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Interactive comment on Biogeosciences Discuss., <https://doi.org/10.5194/bg-2019-497>, 2020.