

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.

Thomas Janssen et al.

t.a.j.janssen@vu.nl

Received and published: 18 February 2020

Author response to Referee #1

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

[Printer-friendly version](#)

[Discussion paper](#)



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 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 ecophysiological 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.

Response: thank you very much for your extensive report. We appreciate the thorough review of our manuscript and your acknowledgement of the relevance of our work. Below we reply to the comments raised in the referee report.

Main comments 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?

Response: yes, there is a sampling bias in our meta-analysis towards the more recent years and this does result in more months being classified as episodic drought months than would be expected based on the 10% cut-off point. The sampling bias however does not explain the trend of increased episodic droughts (Figure 1 b) because the entire time series of ERA5 soil moisture was used to count the episodic droughts, whether we have field data in those months or not (see also specific comment on Figure 1). This will be made more clear in the revised version of the manuscript.

For the purpose of this meta-analysis we defined "episodic drought" as a month where

[Printer-friendly version](#)[Discussion paper](#)

the relative extractable soil water (REW) was lower than the 10% quantile of REW in the entire ERA5 soil moisture time-series (1979-2019). If the data retrieved from the literature was evenly distributed over the entire timespan of the ERA5 data we would expect that around 10%, so 363 of the 3630 initially classified dry season months would be classified as episodic drought. As pointed out by you, we classified almost double that amount, 624 months, as episodic drought. This is indeed explained by the bias of the retrieved data towards recent years (2009-2019) that were also drier compared to the previous decades (Figure 1b and 1c). Elaborating on this, we find that before 2009 ~14% (346 out of 2503) of initially classified dry season months were classified as episodic drought while in the decade 2009-2019 ~25% (280 out of 1125) of the dry season months were classified as episodic drought. *Note that the total amount of data slightly changed since the previous version because of the use of a new digital elevation model*

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?

Response: the separation of months into wet and dry season was indeed based on the depletion or replenishment of ERA5 soil moisture for a specific site. We will more elaborately discuss our choice of wet season and dry season definition when introducing the classification procedure in the Methods of the revised version of the manuscript. The rationale behind our definition is that when evapotranspiration exceeds precipitation, there is a precipitation deficit resulting in the depletion of soil moisture. This definition is often used to distinguish wet and dry season in neotropical forests and also used

[Printer-friendly version](#)[Discussion paper](#)

to calculate drought metrics such as the cumulated water deficit (Aragão et al., 2007). Although our definition is simple and might not always capture the complete ecophysiological responses to the dry season at every site in every year, we think that it does capture the general wet season and dry season states across the different sites. For example, the vapor pressure deficit is clearly higher during the dry season compared to a wet season (Figure 1d and 2d) indicating both a dry soil and a dry atmosphere during the dry season. For some years with an exceptional weak dry season (as in the year 2000 at the K34 site) the classification results in a rapid sequence of wet and dry season months. We partly tried to correct for these small changes in soil moisture by classifying all months with REW higher than 65% of REW as wet season months despite a reduction in REW (Methods L211-L213) but this did not entirely prevent that in some exceptional years there is a rapid sequence of wet and dry seasons in a single year. Nonetheless, the wet-dry season classification method resulted in that months classified as dry season are actually dry and are not just classified as dry season months because it is a particular month of the year.

Again, if we look at the dry season and episodic drought between 2015 and 2016, we 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.

[Printer-friendly version](#)[Discussion paper](#)

Response: on the leaf scale, the available literature reported no clear legacy effects of episodic drought on stomatal conductance, leaf water potential and photosynthesis (Alexandre, 1991; Santos et al., 2018). However, on the tree scale there are legacy effects reported, for example reduced hydraulic conductance and transpiration directly following episodic drought (Fontes et al., 2018) and changes in stem growth and leaf flushing (Doughty et al., 2014, 2015; Hofhansl et al., 2014). We discuss observed legacy effects reported in the literature in the Discussion (L486-L496) and acknowledge that the method used by us is only able to capture instantaneous responses and not the legacy effects, which is a limitation. When revising this manuscript we will more elaborately discuss the presence of legacy effects in our meta-analysis.

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.

Response: the lack of a “sensitivity analysis” was also noted by referee #2 L212-213. In the revised version of the manuscript we will more elaborately discuss our choice for a 10% threshold. We opted for a threshold that provided a reasonably strict episodic drought definition while still yielding a large enough sample size for the statistical analysis to differentiate between episodic drought and a regular dry season. We have now also tested a wide episodic drought threshold of 15% and a narrow episodic drought threshold of 5%. The wider episodic drought definition resulted in a decline of the sample size for the wet season – dry season comparison as more dry season months were classified as episodic drought. Furthermore, the p-values of 14 out of 23 variables declined but none of the previous significant variables became not significant in the wide (15%) threshold wet season – dry season comparison. wide episodic drought definition resulted in the increase of the sample size in the dry season - episodic drought comparison but also a decline in the p-values of 15 out of 23 variables, while none of the previously significant variables became not significant in the dry season – episodic drought comparison. The narrow episodic drought definition (5%) resulted in larger

[Printer-friendly version](#)[Discussion paper](#)

sample size for the wet season – dry season comparison compared to the baseline (10%) definition because more episodic drought months are now classified as dry season, and the increase of p-values in about half (12 out of 23) of the variables, while one variable (soil-leaf hydraulic conductance) became not significant in the wet season – dry season comparison. Furthermore, the narrow definition resulted in a decline in sample size for almost all variables (19 out of 23) and a decline of the p-values in 15 out of 23 variables in the dry season – episodic drought comparison with 4 previously significant variables now showing no significant change (soil-leaf hydraulic conductance, leaf transpiration, leaf photosynthesis and ecosystem water use efficiency). These results confirm that our analysis of seasonal drought is quite robust, with no major changes in the magnitude and direction of change of any variables in response to seasonal drought with different threshold values for episodic drought. Also the responses to episodic drought show no major changes in direction or magnitude but we observe a decline in significance levels in some variables, mainly because of a reduction in sample size. We will add these results to the supplementary material and discuss the implication of the threshold in the discussion.

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.

Response: we agree that merging the drought responses of all the species and functional groups present in the database results in the loss of the variability in responses

[Printer-friendly version](#)[Discussion paper](#)

observed. In the case of transpiration this merging indeed results in that we observe on average no significant changes in transpiration from the wet to the dry season (Figure 4) while studies that measured mainly high wood density species or low wood density species did show a significant increase or decrease in transpiration, respectively (Figure 5 and 6). As you mention, showing this variability is the purpose of Figure 5 and 6 while for Figure 3 and 4 the aim is to show the average response. We did consider splitting the data shown in Figure 3 and 4 in studies measuring mainly isohydric and non-isohydric species, however, this distinction is not easily made. As can be seen in Figure 5 and 6, there are not really two clusters of hydraulic behaviour but it is rather a continuum, related to the continuum from strictly isohydric to extreme non-isohydric behaviour that is observed in plants globally (Klein, 2014; Martínez-Vilalta et al., 2014; Meinzer et al., 2017). We think that arbitrary splitting the data in isohydric and non-isohydric studies will not help to reconcile the inconsistencies in drought responses observed from the leaf to the ecosystem scale. However, the relationships found and shown in Figure 5, 6, S2 S3 and S4, could inform vegetation models that could then simulate the effect of a variability in plant hydraulic behaviour on ecosystem scale productivity and transpiration.

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

[Printer-friendly version](#)[Discussion paper](#)

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 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.

Response: thank you for pointing out the very low VPD that we used to calculate leaf transpiration in our meta-analysis! After reviewing our pre-processing steps that we used to obtain the ERA5 VPD at every site, we found the mistake that resulted in these low VPD estimates: instead of using local time (12:00) temperature and dewpoint temperature to calculate midday VPD, we erroneously used 12:00 UTC when downloading the ERA5 temperature data.

For the analyses in the revised version of the manuscript we will now use temperature and dewpoint temperature at four different times (15:00 – 18:00 UTC) that correspond with local 12:00 in four time zones covering our study area. The ERA5 results seem to correspond reasonably well with VPD observations from flux towers in our study area (Figure 1). Using the actual midday VPD logically resulted in changes in the range of

[Printer-friendly version](#)[Discussion paper](#)

VPD found in the meta-analysis (Figure 2). However, we observe no major changes in the direction or magnitude of the leaf transpiration response to seasonal (Figure 3) and episodic drought. The response of leaf transpiration to seasonal drought remains not significantly different from 0 and significantly declines in response to episodic drought. This can be explained because the new and correct midday VPD is higher compared to the previous VPD estimate in the wet season, in the dry season and during episodic drought which results in marginal changes in the relative response of leaf transpiration.

We recognise that atmospheric VPD and leaf-to-air VPD can be very different depending on the cooling feedback resulting from leaf transpiration. However, leaf-to-air VPD, leaf temperature or leaf water potential were not consistently provided in the original source papers that provided the stomatal conductance data, preventing us from calculating actual leaf transpiration. We agree that we have to be more careful with the results from this analysis. In the revised version of the manuscript we will discuss the implications of using atmospheric VPD instead of leaf-to-air VPD in calculating leaf transpiration.

Minor comments 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?

Response: yes, we agree with your suggested change of formulation: "We present new insights into the functioning of tropical forest in response to drought and present novel relationships between wood density and drought responses that can help guide the parametrization of land surface models."

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 prob-

[Printer-friendly version](#)[Discussion paper](#)

lematic and have been discussed in several technical comments....

Response: thank you for your suggested change in referenced literature, we will change this in the revision.

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

Response: this will be changed

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

Response: according to Marengo et al. 2011, the North Atlantic SST affected the position of the ITCZ, forcing the ITCZ anomalously northward during 2010, resulting in an episodic drought in the southern Amazon Basin.

L. 75: “stomates progressively close” is more exact than “stomates close”

Response: agree, better formulation. This will be changed.

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>) 3. Choat et al. 2018 (<https://doi.org/10.1038/s41586-018-0240-x>)

Response: agree, these references are a good addition to Buckley et al. 2019

L. 84-85: E can either stay the same, increase, or decrease during a drought, all of which could result on a decline in Ψ l.... Also, ksl declines as a result of a decline in Ψ s

Response: this will be reformulated.

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

Response: this will be reformulated.

BGD

Interactive
comment

Printer-friendly version

Discussion paper



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

Response: yes we agree this is confusing, this will be reformulated.

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

Response: this will be reformulated.

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

Response: this will be reformulated.

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

Response: this will be reformulated.

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 Ψ that could lead to significant xylem embolism and thus damage...”?

Response: yes we agree, this will be reformulated.

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

Response: this will be reformulated.

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 Ψ 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

[Printer-friendly version](#)

[Discussion paper](#)



behaviours depending on the environmental conditions...

Response: agree, we will elaborate on this

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>)

Response: thank you, we will read Rosas et al. 2019 and consider including a reference to this paper.

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

Response: agree, this paragraph will be restructured.

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

Response: we will consider mentioning this contextualization in the abstract

L. 153: typo: “it” to “they”

Response: this will be changed

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?

Response: no, we did not differentiate between measurement techniques in the database and this could indeed result in differences in uncertainties. However, since the meta-analysis deals with relative changes in a variable of interest or “effect sizes” the absolute values are less important. Furthermore, since our meta-analysis deals with values that are averaged for the different studies, which each included multiple tree species and individuals, the variability due to differences between species and in-

BGD

Interactive
comment

Printer-friendly version

Discussion paper



dividuals is much larger compared to measurement uncertainties (see e.g. Santos et al. 2018). It would indeed be very interesting to see how different measurement techniques have an effect on measured drought responses but this is beyond the scope of this study.

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

Response: very often the day and time of day were not reported for tree and ecosystem scale responses. For the leaf scale responses (stomatal conductance, photosynthesis and leaf water potential) we always used the value at maximum photosynthesis (at mid-day), except for pre-dawn leaf water potential, naturally. We will include this information in the methods of the revised version.

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

Response: this will be included in the revised version.

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

Response: agree, this will be omitted in the revised version. See also specific comment by referee #2.

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

Response: yes it should, this will be changed.

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

Response: we will consider including this suggestion.

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

[Printer-friendly version](#)[Discussion paper](#)

Response: we will clarify this in the revised manuscript

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

Response: yes, all stomatal conductance measurement were made at midday. Thank you for your insights. We will elaborate on the role of boundary layer conductance in tropical forest canopies in the revised version and also discuss the possible limitations of our crude estimate of leaf transpiration.

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)?

Response: multiple studies that were included in the database reported either maximum sapflux density (at midday) or daily tree transpiration, but not both. We used the linear relationship to calculate daily tree transpiration for the studies that reported only maximum sapflux density. We will elaborate on this in the revised version.

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

Printer-friendly version

Discussion paper



Response: yes, equation 3 assumes that the system is at steady state. Steady state conditions were not ensured and we doubt whether we could account for this in a meta-analysis. The “instantaneous soil to leaf hydraulic conductance” calculated here should be regarded a measure of whole-tree hydraulic conductance at midday (Love and Sperry, 2018).

L. 192: typo: “rooting zone” to “root-zone”

Response: this will be changed in the revised manuscript

L. 193-194: strictly speaking, difference between Ψ_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 Ψ_s ...

Response: this will be changed in the revised manuscript

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?

Response: the log response ratio is used to derive the test statistics following Lajeunesse (2011) and then back converted to percentage change.

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?

Response: yes, we agree that there can be large within genus variability in wood density and hydraulic behaviour. However, across neotropical tree species about 74% of the variation in wood density can be explained by genus level variability (Chave et al., 2006), so genus level wood density could be regarded a useful proxy. Genus averaged wood density was used in 127 cases out of a total of 786 individuals measured. As the wood density was averaged per study, we believe that the effect of using genus aver-

[Printer-friendly version](#)[Discussion paper](#)

aged wood density instead of species averaged wood density is small. The alternative would be to not provide a wood density value to this individual, which would probably cause more bias in the study averaged wood density than providing the genus average.

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

Response: this will be included

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....

Response: the result that on average leaf transpiration does not change from the wet to the dry season (see also final major comment and figures), follows from the averaging of study level responses of 25 studies from which 11 studies showed a (marginal) increase in leaf-level transpiration and 14 studies a (marginal) decrease in leaf-level transpiration from the wet to the dry season (Figure 5 b). Furthermore, the same result is found when looking at tree scale transpiration which is independent from our calculation of VPD and leaf transpiration. The bias towards studies measuring low wood density trees in sun-exposed canopy positions likely contributes to the overestimation of the dry season decline in stomatal conductance and therefore leaf transpiration (this bias is discussed in the Discussion).

L. 265: but a drop in Ψ is observed!

Response: yes, this is confusing and will be reformulated.

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)

Response: we will read Rosas et al. 2019 and consider including a reference to this paper.

L. 304 (and later): the “WUE_i” notation is inconsistent with the “iWUE” notation used in the introduction

[Printer-friendly version](#)[Discussion paper](#)

Response: This will be changed to iWUE in the next version of the manuscript.

L. 311: “we observe that” is not needed

Response: agree, this will be omitted in the next version.

L. 315: typo: “marginal” should be “marginally”

Response: this will be corrected.

L. 322: give the ranges of variation?

Response: this sentence is confusing and will be omitted or reformulated in the revised version.

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

Response: agree, only for stomatal conductance and leaf transpiration is the relationship with wood density significant ($p < 0.05$) during episodic drought and shows a similar relationship as during seasonal drought. We will highlight that this is not the case for leaf photosynthesis and midday leaf water potential.

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

Response: yes, we will add that this relationship is not significant

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

Response: “intermediate response” will be omitted, “midday δ_{midday} declining parallel to a decline in pre-dawn $\delta_{\text{pre-dawn}}$ ” should be a sufficient description of the midday leaf water potential response to declining pre-dawn leaf water potential in the intermediate wood density group.

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

Response: thank you.

Printer-friendly version

Discussion paper



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

Response: we agree that this sentence is vaguely formulated. By “similar” we refer to the similarity in the relationships between wood density and the direction and magnitude of leaf and tree scale transpiration. Both show an increase of transpiration from the wet to the dry season in studies that measured high wood density species and a decline of transpiration in studies that measured low wood density species. This will be clarified in the revised version.

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

Response: yes, this is a vague term and will be omitted in the revised version.

L. 358: please replace “cancelled out” by “offset”

Response: this will be replaced.

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?

Response: yes, this is partly what is referred to here but not explicitly mentioned. Leaf shedding and flushing can be a mechanism that results in leaf scale responses being visible on shorter time scales but on even shorter timescales also the opening and closure of the stomates. The purpose of these two sentences is to highlight the presence of buffering in the system, in this case because of non-structural carbohydrates, that could result in the observed inconsistencies in drought responses going from the leaf to the ecosystem. This paragraph will be reformulated.

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...

[Printer-friendly version](#)[Discussion paper](#)

Response: this will be changed.

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?

Response: this is mentioned in results section 3.2, L289-L290. This will be highlighted in the next version.

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

Response: this will be moved.

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

Response: this will be changed.

L. 564: typo: missing "and" after "environments"

Response: "and" will be included.

Fig. 1a: the K34 site should be indicated on the map given Fig. 1d and 1e Response: the location of K34 will be indicated on the map in the revised version.

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.

Response: yes, this is averaged across sites. The number of episodic drought months counted in Fig. 1b are independent of the monthly observations retrieved from the literature as all months classified as episodic drought in the time series (1979-2019) at that each site are included. We will consider calculating also the number of episodic drought months across the neotropics in a rectangular grid and compare this to the

[Printer-friendly version](#)

[Discussion paper](#)



counted number of episodic droughts in Fig. 1b to check for sampling bias.

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

Response: thank you for the suggestion, we will look into this and see whether we can make the ENSO index more visually interesting.

Fig. 2a: where do the top soil Ψ s data come from? The caption says published data, but I didn't find it in the methods?

Response: the references are in the supplementary material (main database excel file) but this is presently not clear. References to the top soil Ψ s will be included in the Methods in the revised version.

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?

Response: for Fig 2a this indicates that there is a significant difference in topsoil water potential between the wet season (A) and episodic drought (B) but not between the dry season and either the wet season or episodic drought (AB). This will be elaborated on in the caption of the revised version of this figure.

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

Response: yes exactly. We will explain the ranges of the boxplots in the caption of the revised version of this figure.

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

Response: the horizontal lines are the 95% confidence interval range, this will be more clearly described in the caption of the revised version.

BGD

Interactive
comment

Printer-friendly version

Discussion paper



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.

Response: we will consider making these changes in the revised versions of these figures.

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

Response: yes, the size of the points is determined based on the inverse of the sampling variance of that particular study (i.e. precision) and yes, the model is also constructed using inverse-variance weights. These details will be added to the Methods and in the caption in the revised version of the manuscript.

References

Alexandre, D. Y.: Comportement hydrique au cours de la saison seche et place dans la succession de trois arbres guyanais: *Trema micrantha*, *Goupia glabra* et *Eperua grandiflora*, *Ann. des Sci. For.*, 48(1), 101–112, 1991.

Aragão, L. E. O. C., Malhi, Y., Roman-Cuesta, R. M., Saatchi, S., Anderson, L. O. and Shimabukuro, Y. E.: Spatial patterns and fire response of recent Amazonian droughts, *Geophys. Res. Lett.*, 34(7), L07701, doi:10.1029/2006GL028946, 2007.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Hans Steege, T. E. R. and Webb, C. O.: Regional and phylogenetic variation of wood density across 2456 neotropical tree species, *Ecol. Appl.*, 16(6), 2356–2367, doi:10.1890/1051-0761(2006)016[2356:RAPVOW]2.0.CO;2, 2006.

Doughty, C. E., Malhi, Y., Araujo-murakami, A., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., Pardo-Toledo, E., Mendizabal, L. M., Rojas-Landivar, V. D., Vega-Martinez, M., Flores-Valencia, M., Sibling-Rivero, R., Moreno-Vare, L., Jes-

sica Viscarra, L., Chuviru-Castro, T., Osinaga-Becerra, M., Ledezma, R., Javier, E., Arroyo, L., Heredia, J. P., Pardo-Toledo, E., Mendizabal, L. M. and Victor, D.: Allocation trade-offs dominate the response of tropical forest growth to seasonal and inter-annual drought, *Ecology*, 95(8), 1–6, doi:10.1890/13-1507.1, 2014. Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huasco, W. H., Silva-Espejo, J. E., Araujo-Murakami, A., da Costa, M. C., Rocha, W., Feldpausch, T. R., Mendoza, A. L. M., da Costa, A. C. L., Meir, P., Phillips, O. L. and Malhi, Y.: Drought impact on forest carbon dynamics and fluxes in Amazonia, *Nature*, 519(7541), 78–82, doi:10.1038/nature14213, 2015.

Fontes, C. G., Dawson, T. E., Jardine, K., McDowell, N., Gimenez, B. O., Anderegg, L., Negrón-Juárez, R., Higuchi, N., Fine, P. V. A., Araújo, A. C. and Chambers, J. Q.: Dry and hot: the hydraulic consequences of a climate change-type drought for Amazonian trees, *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 373(1760), doi:10.1098/rstb.2018.0209, 2018.

Hofhansl, F., Kobler, J., Drage, S., Pözl, E. M., Wanek, W., Ofner, J., Drage, S., Pözl, E. M. and Wanek, W.: Sensitivity of tropical lowland net primary production to climate anomalies, *Global Biogeochem. Cycles*, 28(12), 10585, doi:10.1002/2014GB004934.Received, 2014.

Klein, T.: The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours, *Funct. Ecol.*, 28(6), 1313–1320, doi:10.1111/1365-2435.12289, 2014.

Lajeunesse, M. J.: On the meta-analysis of response ratios for studies with correlated and multi-group designs, *Ecology*, 92(11), 2049–2055, doi:10.1890/11-0423.1, 2011. Love, D. M. and Sperry, J. S.: In situ embolism induction reveals vessel refilling in a natural aspen stand, *Tree Physiol.*, 38(7), 1006–1015, doi:10.1093/treephys/tpy007, 2018.

Martínez-Vilalta, J., Poyatos, R., Aguadé, D., Retana, J. and Mencuccini, M.: A

[Printer-friendly version](#)[Discussion paper](#)

new look at water transport regulation in plants, *New Phytol.*, 204(1), 105–115, doi:10.1111/nph.12912, 2014. Meinzer, F. C., Smith, D. D., Woodruff, D. R., Marias, D. E., McCulloh, K. A., Howard, A. R. and Magedman, A. L.: Stomatal kinetics and photosynthetic gas exchange along a continuum of isohydric to anisohydric regulation of plant water status, *Plant Cell Environ.*, 40(8), 1618–1628, doi:10.1111/pce.12970, 2017.

Santos, V. A. H. F. dos, Ferreira, M. J., Rodrigues, J. V. F. C., Garcia, M. N., Ceron, J. V. B., Nelson, B. W. and Saleska, S. R.: Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest., 2018.

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

BGD

Interactive
comment

Printer-friendly version

Discussion paper



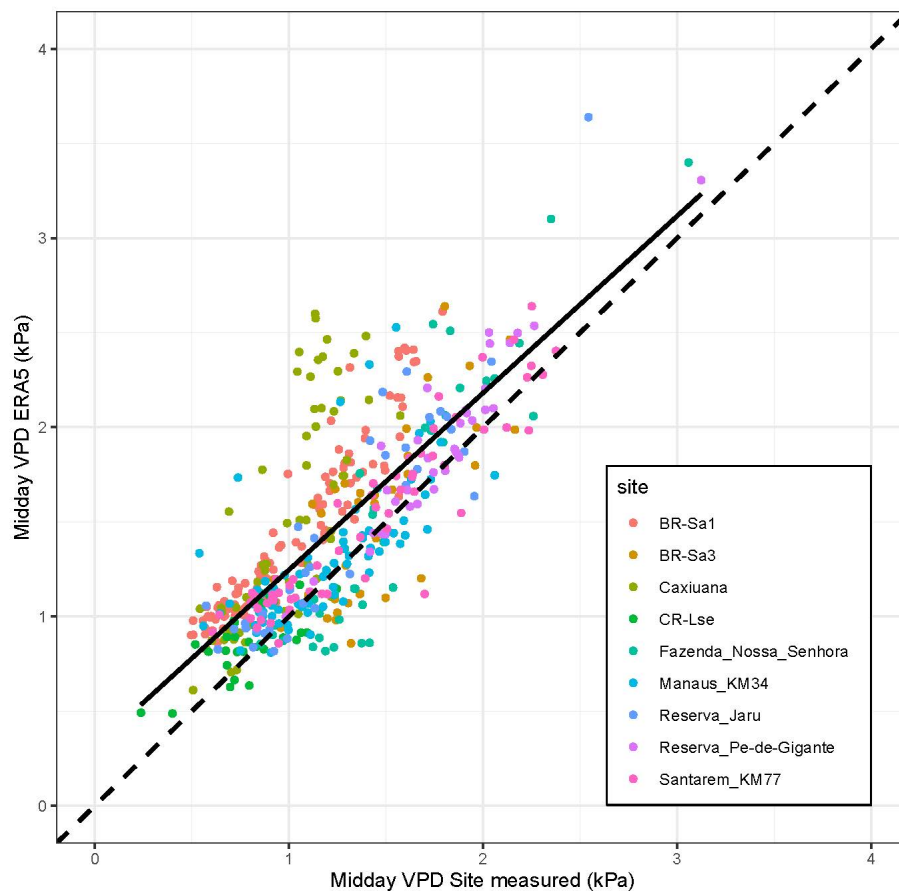


Fig. 1. The new ERA5 vapor pressure deficit at midday (12:00) compared with vapor pressure deficit measured at 12:00 at 9 flux tower sites in the study area. The dashed line represents the 1:1 line and the so

[Printer-friendly version](#)[Discussion paper](#)

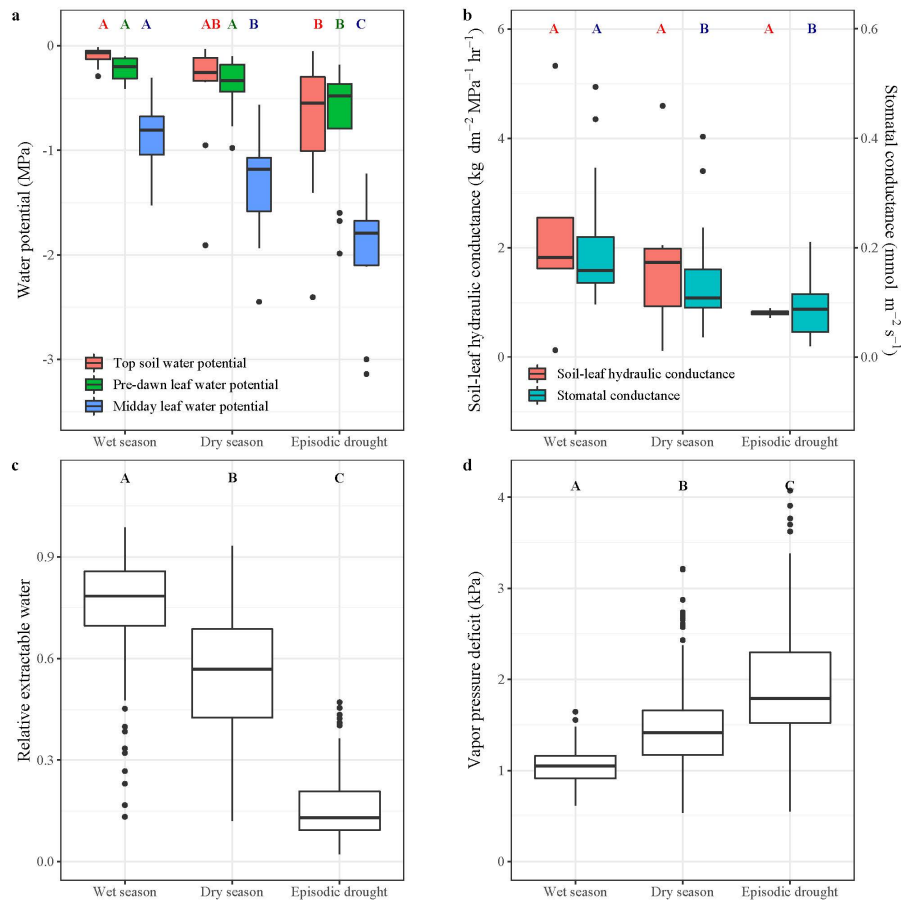


Fig. 2. Updated Figure 2 with new vapor pressure deficit estimates.

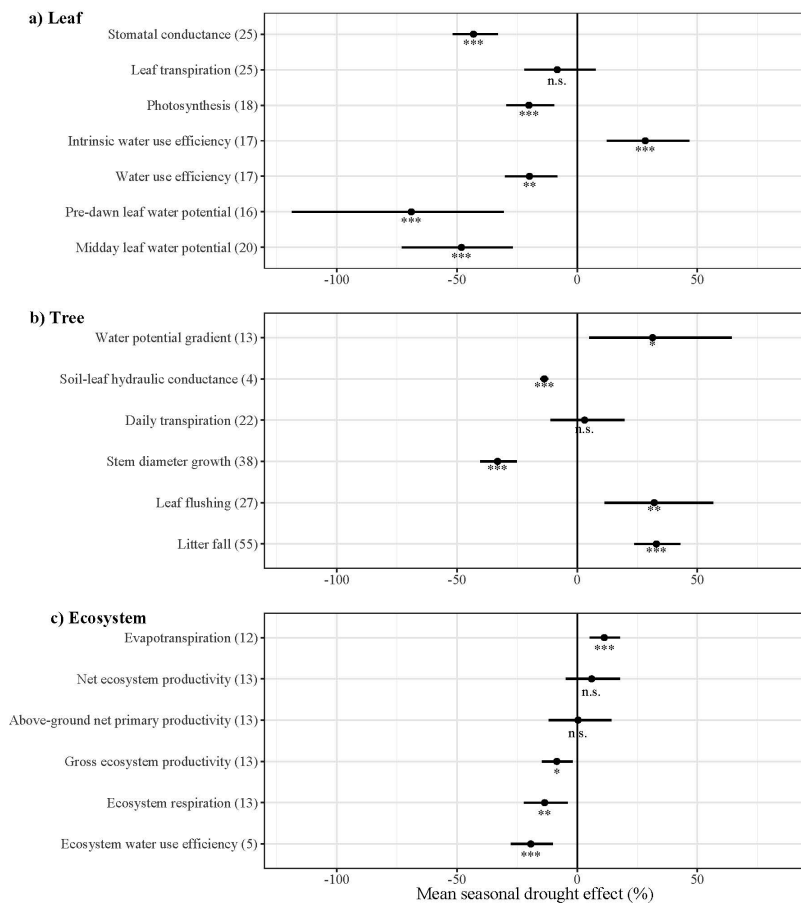


Fig. 3. Updated Figure 3 with new vapor pressure deficit estimates.

Printer-friendly version

Discussion paper

