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A very useful simulation of the impact of drought and enhanced temperatures on embolism in trees and on tree dieback

Erwin Dreyer based on reviews by Sabine Rosner and 1 anonymous reviewer

A recommendation of:

Hervé Cochard. **A new mechanism for tree mortality due to drought and heatwaves** *(2020), bioRxiv, 531632, ver. 2 peer-reviewed and recommended by Peer Community in Forest & Wood Sciences.* 10.1101/531632

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Water availability has been known to strongly modulate forest productivity and tree growth on an interannual basis (as revealed by numerous dendrochronological studies) and across biomes (Ellison et al, 2017). Recurrent episodes of severe drought lead to decreased soil water content and as a consequence to visible losses in annual growth increment, and in some cases even to tree death and forest decline. The occurrence of such drought events and of larger scale tree dieback, seem to be increasing over the last decades, albeit such processes are not new. The causes for drought-induced tree death are still disputed; in many cases, tree death occurs after the release of drought, and is caused by severe attacks by pests and pathogens. In other cases, tree death is caused by recurrent drought events over several years, leading to a depletion of stored carbohydrates, growth decline and ultimately death.

However, this understanding of drought-induced tree dieback, which applies to drought events that occurred in temperate climate biomes during the end of the 20th century, seems inadequate to explain the increasing occurrence of large-scale dieback induces by recent drought episodes (Allen et al, 2015). In these recent cases a direct impairment of hydraulic functions seems responsible for tree death. Such impairments (cavitation and resulting massive embolism) have been well documented through extensive research that started in the 90s. Up to now, the consensus was that trees are fairly well protected against such potentially lethal dysfunctions: an efficient stomatal closure limits transpiration and the risk of runaway embolism. Many tree models based on the known hydraulic properties of trees (vulnerability of different organs to cavitation, hydraulic conductance of these organs, transpiration, stomatal conductance…) were developed since the seminal work of Tyree and Sperry (1989) and only seldom predicted the occurrence of runaway embolism (Cochard and Delzon, 2013).

These models considered the impact of drought through reduced soil water availability, which is indeed the central process during drought, but overlooked to some extent the fact that drought is frequently and increasingly associated to higher temperatures, which may change rather severely model parameters and result in a higher risk of runaway embolism.

The present preprint proposed by Cochard (2020) bases on such a new hydraulic model (the model SurEau, Martin StPaul et al, 2017; Cochard et al, 2020) integrating more explicitly the impact of temperature on different parameters. Two parameters appear particularly relevant and highly sensitive to temperature:

(i) the vapor pressure deficit of the air (VPD), which increases exponentially with temperature and results in increased transpiration and more rapid soil water depletion; this effect is well known and has been the matter of many research and modelling;

(ii) (ii) the cuticular conductance to water vapor, which becomes the most important limit to transpiration once stomata are closed, and which is much less well documented with respect to mean values and temperature sensitivity (mainly because this process is difficult to record). Recent advances (Schuster et al, 2016) provided some insight into the importance of this parameter and showed how it may rapidly increase with temperature (see references in the preprint).

The presented work bases on this new model to document more precisely how enhanced temperature may increase water loss through transpiration and consequently induce runaway embolism in trees more rapidly than usually expected. The hypothesis that the temperature response of cuticular conductance may play a central role in the sensitivity of trees to a combination of soil water depletion and enhanced air (and leaf) temperature was tested through numerical simulations with SurEau. The results are very clear: temperature-dependent increases in cuticular conductance may accelerate the onset of runaway embolism at a rate that was not expected before.

The demonstration is indeed very clear and convincing. It remains however a simulation (or an “in silico experiment”. Data providing real values of cuticular conductance remain scarce, and data documenting its response to enhanced temperatures even scarcer. This opens an avenue for new research and investigations, and Cochard (2020) provides some clues about which data and which experiments could confirm the central role of temperature induced changes in cuticular conductance with temperature (eg new measurements of Tp, the phase transition temperature that matches the range of temperatures known to trigger mortality during hot-droughts, Billon et al. (2020)).

I believe this preprint is an important contribution in this field, and the reviewers were of the same opinion (see their reviews attached to this recommendation). Indeed, this preprint illustrates how simulation exercises can help us identify some key processes that require further attention and documentation. I believe this is an important contribution to our understanding of the rapid, drought-induced tree death observed in different parts of the world at alarming rates.

As such, and combined with a detailed description of the model SurEau, this preprint is a very important addendum to the corpus of knowledge that is currently gathered around the hydraulic functioning of trees.

References

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere, 6(8), 1-55.
doi: https://doi.org/10.1890/ES15-00203.1
Billon et al. (2020). The DroughtBox: A new tool for phenotyping residual branch conductance and its temperature dependence during drought. Plant, Cell and Environment, 43, 1584-1594.
doi https://doi.org/10.1111/pce.13750
Cochard, H. (2020) A new mechanism for tree mortality due to drought and heatwaves. bioRxiv, 531632, ver.

2 peer-reviewed and recommended by PCI Forest and Wood Sciences. doi: https://doi.org/10.1101/531632
Cochard, H., Martin-StPaul, N., Pimont, F., and Ruffault, J. (2020). SurEau.c: a mechanistic model of plant water relations under extreme drought. bioRxiv, 2020.05.10.086678. doi: https://doi.org/10.1101/2020.05.10.086678
Ellison et al. (2017). Trees, forests and water: Cool insights for a hot world. Global Environmental Change, 43, 51-61. doi: https://doi.org/10.1016/j.gloenvcha.2017.01.002
Martin-StPaul, N., Delzon, S., and Cochard, H. (2017). Plant resistance to drought depends on timely stomatal closure. Ecology letters, 20(11), 1437-1447. doi: https://doi.org/10.1111/ele.12851
Schuster et al. (2016). Effectiveness of cuticular transpiration barriers in a desert plant at controlling water loss at high temperatures. AoB Plants, 8(1), plw027. doi: https://doi.org/10.1093/aobpla/plw027
Tyree, M. T., and Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. Annual review of plant biology, 40(1), 19-36. doi: https://doi.org/10.1146/annurev.pp.40.060189.000315

Revision round #1

2020-07-05

This preprint presents a very nice and interesting simulation study based on a new hydraulic model for trees, that integrates temperature induced changes in cuticular conductance to water vapour. As a result, the hydraulic safety margin of the trees severely declines with temperature, and runaway embolism able to induce tree death occurs much earlier in time under high temperatures. The model is elegant and nice, the simulation is very clearly presented, and the results build up a novel hypothesis awaiting for empirical confirmation by experimental data.

The preprint was reviewed by two experts in the field who provided the attached comments. You will see from their comments that they both found the preprints highly commendable and believe it makes a veryi nteresting contribution to the literature in this field. They also raised some in my eyes very relevant concerns that need be taken into account before a final recommendation should be made. I concur with most of these concerns and would recommend a careful revision (mostly minor) around following points:

1. check for very minor language issues (like "a heatwave" and ont "an..."); this is very minor as the language is otherwise very clear; a list of abbreviations would also be useful;

2. update in places the references (there have been recent addition to the literature that might be useful); moreover, some citations need a direct link to the reference;

3. as stated by one of the referees, it would be important to provide access to the code of the model; this may be done through deposition of a documented version of the code in a public repository (dataverse of INRAE for instance);

4. references should be systematically provided for all model equations, even more as some are empirically adjusted equations (widely used indeed, but still);

5. an important point for the discussion is that the model assumes that the response of stomatal conductance is not involved as the important step occurs with fully closed stomata; one of the referees questions this lack of contribution; from my point of view, I wonder whether transient stomaltal opening (in the morning for instance) might not happen at this stage, and whether this may have an impact on the induction of runaway embolism;

6. the simulation bases on a set of clearly defined initial conditions (including soil water availability); it might be useful to better insist on the fact that simulation outcomes severely depend on these conditions (particularly on the water storage capacity in the soil, as is mentioned in the text);

7. I feel, like one of the referees, that there is a need to propose in the discussion, some experimental approaches devoted to testing the hypothesis. This would be a major addendum to the preprint and could launch an avenue for future research in this area.

Once you have undertaken these, mostly minor changes, I have no doubt this preprint will constitute a highly recommendable preprint for the PCI Forest&Wood sciences. I do thank you for having submitted this preprint to the PCI.

Reviewed by Sabine Rosner, 2020-05-23 18:06

Dear Erwin, the study „A new mechanism for tree mortality due to drought and heatwaves" is highly recommended because it includes a so far overseen aspect in models dealing with survival of trees under the impact drought stress and heatwaves: the role of temperature on cuticular conductance (phase transition temperature). The approach is explained to the readers step by step and the model helps our understanding of mortality due to drought stress in trees. Moreover, such model predictions are extremely helpful for underlining the need for urgent action to reduce global warming.

What I am missing is a list of abbreviations, some traits are not explained, for instance some of those provided in the tables. As far as I understood it, osmotic adjustment per se is not included in the model, but it might be a strategy of the plant to actively decrease the osmotic potential to make soil water available when stomata are closed. In the discussion I would also mention that forest trees rarely die from drought tress alone, but drought stress predisposes them for insect or pathogen infestations, and this predisposition might be also higher in combination with heatwaves. For urban trees, this model approach is of very high relevance. What I am also missing in the discussion is that the leaves have a maturation process during the growing season, and, the prediction of the time to hydraulic failure might be even lower in juvenile leaves than in mature leaves. There are as well seasonal shifts in P50 over the season, as is was recently shown again for grapevine.

Some additional minor comments:

Page 2: "Similarly, the air vapor pressure is decreased by the air relative humidity RH (%)" is somehow confusing because it can be also increased when the RH is higher according to the formula. Would replace "decreased" by "influenced".

Page 2, last sentence: "was a function of its energy".

Figure 5: would use a different color code: red should indicate the highest stress (heat wave from day 13 on), green medium (heat wave days 5-12) and blue the lowest stress (heat wave on days 0-6) in Figures 6-7 this is more logical.

Best regards,

Sabine

Reviewed by anonymous reviewer, 2020-06-29 07:13

Download the review (PDF file)

Author's reply:

Dear Recommender, please find in the attached file my replies to the numerous comments made by the referee. I'm sorry that it took so long for me to send this reply. But this was not such a "minor" revision actually. I thank you again for considering my work for this PCI. Regards, H Cochard

Download author's reply (PDF file)