by Erwin Dreyer, 2020-07-05 07:39

Request for minor revisions of the preprint "A new mechanism for tree mortality due to drought and heatwaves" by Hervé Cochard

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 very interesting 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:

I thank you for your very positive feedback on my manuscript. Please find below my answers to the many points made by yourself and the referees.

1. check for very minor language issues (like "a heatwave" and not "an...");

corrected

this is very minor as the language is otherwise very clear; a list of abbreviations would also be useful;

added as appendix 1.

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;

The reference list has been updated with more recent references.

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);

Done. The source of the program is in the data INRAE public depository: https://data.inrae.fr/dataset.xhtml?persistentId=doi:10.15454/6Z1MXK

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

These references have been provided.

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 stomatal 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;

This is a good point. In the current version of SurEau stomata respond instantaneously to different drivers like leaf water potential. Their own dynamics may indeed exacerbate the risk of runaway embolism. I do not think the problem is very acute in the morning because the delay in stomatal opening would also delay the increase in transpiration. But the situation is probably more critic when stomata are open and expose to a sudden pulse of dry air (reducing the leaf boundary resistance and increasing the VPD and hence increasing transiently leaf transpiration). This is clearly a point that should be addressed in the future.

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);

I've added sentences in that direction saying that "The results of the model are of course strongly determined by the initial conditions of the simulations. It is therefore necessary to pay more attention to the relative variations of the different simulated variables than to their absolute value."

6. 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.

I gave some suggestions to test the model predictions.

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.

I thank you and the referees for your positive feedback and the constructive comments. Before replying point-point to the referees' comments, I would like to clarify that this manuscript was very specifically devoted to the analysis of temperature effects on plant hydraulics and water relations. The full description of the SurEau model will be the purpose of a companion paper already available as BioRxiv manuscript (Cochard et al 2020). The code of the program is made available on Data INRAE.

Reviews

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.

I thank you Sabine for your encouragements!

What I am missing is a list of abbreviations, some traits are not explained, for instance some of those provided in the tables.

A list of abbreviations is given in the Appendix 1.

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.

Correct, there is no active osmotic adjustment in the model (no osmoregulation). The osmotic potential changes however with temperature (equation 9) or when cells dehydrate (according to a pressure-volume curve). The impact of osmoregulation is to decrease the osmotic potential and, therefore, to increase of turgor pressure. But, under steady state, the water potential remains unchanged as well as the negative pressure in the apoplasm. Leaf will then be more turgid but this will not make will water much more available for available for transpiration. This may favor growth however.

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.

Good point. I have added this sentence in the discussion:

"The causes of mortality in drought-prone trees are multiple and complex. Droughts may be the sole cause of tree mortality, but they are also often factors predisposing trees to lethal attacks by pathogen infections."

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.

I agree with these remarks. But again my objective here is to analysis the physiological consequences of temperature variations. I would say that temperature is not interacting strongly with processes not already described in the paper.

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".

Corrected

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

It is the energy budget of the leaf that determines its surface temperature.

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.

Done. More logical this way indeed!

Best regards, Sabine

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

This paper describes an interesting new hypothesis for the increase in tree drought mortality risk during heatwaves, and explores the consequences of the hypothesis using a mechanistic model. I suspect this hypothesis probably don't stack up when compared to field data on transpiration rates during heatwaves, but feel that it is nonetheless worth recommending in order to encourage experimentalists to test properly.

There is clearly a sharp increase in cut branches transpiration rates exposed to high temperatures so I don't see why this would not occur in the field. I suspect that this phenomenon has been overlooked and it is probably worth looking more into the details of flux data during heatwave episodes.

Before recommending, however, there are a number of things that should be done to improve the quality of the presentation.

Some major things about presentation:

- - Units should be added throughout, particularly in the methods where many terms are introduced without giving their units. Check that all units are consistent (e.g. is Kplant in mmol s-1 MPa-1 (Figure 1) or in mmol m-2 s-1 MPa-1 (Table 1)?).

  An appendix is now provided with definitions and units

- \- Citations should be given to support model equations and assumptions.

  Good point. Citations have been added, often as a reference to a classical text book.

- \- More details of the underlying model need to be given. There are many assumptions that are not described that determine the outcome of the simulations. What are the basic assumptions of the model framework? E.g. How is soil moisture depleted? How does stomatal conductance respond to soil drought? How is cuticular conductance incorporated? Is there hydraulic isolation of the plant from the soil at some point, and if so when? Is there refilling of the stem overnight? Etc.

  Again, the full description of the model is given in a companion paper. My objective here is to explore only the mechanisms involving a temperature effect. I have added a sentence in the introduction to make this point clear.

- \- The code should be made publicly available, and a link given in the text.

  The full code of the program has been made available (data INRAE public depository)

- The paper suggests that experiments are required to follow up on this hypothesis. It would be useful to indicate what kind of data would be helpful.

Suggestions to test the prediction of the model are now given at the end of the discussion.

One major thing about the science:
I'm concerned that the model is not representing the effects of high T/ VPD on transpiration correctly. For example, the introduction states « A rise in air temperature strongly increases leaf transpiration via its exponential effect on air saturation vapor pressure ». I am not actually sure that this is supported by data. It assumes that the plant does not shut its stomata in response to higher VPD, which most plants do in fact do. Monteith (1995, Plant Cell & Environ 18:357-364) highlights that in most cases there is a three-phase response of E to D - initially it increases, but then plateaus and decreases. Whole-tree chamber and sapflow data during heatwaves show that transpiration tends to decrease, not increase (e.g. Pfautsch & Adams 2012 Oecologia DOI 10.1007/s00442-012-2494-6; Duursma et al. 2014 Agric For Meteorol 189-190: 2-10; Drake et al. 2018 Global Change Biology DOI: 10.1111/gcb.14037).

This manuscript details only the direct impacts of temperature on plant physiology. In SurEau there is a great number of indirect effects, not given here, that capture well the typical behaviors mentioned by the referee. For instance, at high VPD, E becomes limited by the leaf water potential and gs decreases to keep leaf homeostasis. The maximum stomatal conductance itself shows a temperature dependence (see equation 44 in the companion paper) that captures the decline of E at high T. This response is even exacerbated under water stress conditions. This is illustrated for instance by the drop of E in figure 5. With regards to sapflow or whole-tree chamber data, the referee is mentioning classical plant temperature-response experiments.

We are not dealing with these kind of experiments here. We are dealing with experiments with plants having their stomata closed because of water stress and expose to a temperature above their cuticle Tp value. I'm not aware of published E data under such conditions.

It's not clear from the paper how stomatal conductance is being modelled. The paper must describe how the gs response to VPD, T and soil moisture content is being represented, and provide some evidence or rationale to support the approach. This lack of information seriously undermines the value of the paper, as the reader spends most of the time wondering what the model is doing and whether or not the outputs make any sense. The impact of the heatwaves, for example, appears to be dependent on transpiration increasing during the heatwave - contrary to evidence.

There are multiple ways to model how stomatal conductance respond to water stress in SurEau. These are described in the companion paper and therefore not in this one. However, I agree with the referee that it is important to detail the conditions under which the simulations were done (here gs respond to bulk leaf turgor pressure). It is important to note that embolism occurs beyond the point of stomatal closure and therefore the different option to model gs response to water stress have in fine little impact on the patterns described here as they occur post stomatal closure.

Another important point is that the paper is not quite as clear as it should be that the "ne" mechanism » is and what it adds. It is generally understood that plants die earlier during hot conditions because of the increased evaporative demand, which means soil moisture stores are depleted faster. That mechanism is very well known and incorporated in pretty much all process-based models. My understanding is that the author is proposing here an additional mechanism, namely that under high temperatures gmin increases, and that will cause plants to cavitate even faster, due to faster water loss. The author does not make clear why this additional mechanism is needed, and does not clearly differentiate what the new mechanism adds. I would suggest that the Introduction needs to make it clearer why this mechanism is needed, and outline the logic of how the simulations are going to explore this and other impacts of temperature on hydraulic function. The presentation of the results should be more careful to distinguish when this mechanism is under consideration in the simulations. The discussion should also take the time to explain how the new mechanism impacts on the simulated time to mortality, compared to the control case in which gmin is constant. The problem is that the discussion argues that runaway cavitation during a heatwave is caused by the increase in gmin but runaway cavitation would still occur if gmin were constant, just a bit later. Do we really need this new mechanism?

It is a pity that the referee miss these points because they were the purpose of the paper! For instance, figure 4 aimed precisely at showing the impact of gmin when considered constant or temperature-dependant. I will try to reinforce the novelty of the new mechanism that I describe here.

Detailed comments:

Introduction "These die-offs seem clearly driven by climate change" - this kind of unsupported speculative statement is unhelpful. There is a very worrying tendency in the literature to run ahead of our capacity to attribute tree mortality to climate change. I would omit this statement and instead focus on the (better-substantiated) observation that tree mortality appears to be higher during heatwave conditions. Some more appropriate citations could also be found (the Williams et al 2012 paper cited in the first paragraph refers to death of people, not trees, during heatwaves, which seems rather tangential?)

I've omitted this statement and referred to Adams et al instead of Williams et al.

Also avoid the word "drastic" which is too subjective to use in a scientific paper. Extreme is better, as it is quantifiable.

"drastic" removed throughout the text.

There is an issue with the definition of eleaf (eqn 1),which is described as being the vapour pressure "at leaf level" and at « leaf surface" - presumably this is intended as the intercellular vapour pressure, not the leaf surface vapour pressure? These are not the same thing. The definition must be made precise. Please give citations for each of the equations in this section.

Yes, as e_leaf is also influenced by the leaf water potential it is the vapour pressure inside the leaf. References have been added.

Eqn 5, Tair will only have a strong effect on transpiration if it is assumed that gleaf is constant .. which it is most definitely not! Are these equations assumed only to apply once stomatal closure has been achieved, and we are only considering cuticular conductance? This must be clarified.

As explaine above, gleaf is not constant. I made clear that gleaf was composed of gs (stomatal) and gmin (cuticular) conductances.

« In Figure 1 I assume that root temperature is constant.." Clearly there are a number of other assumptions being made here. Clarify how conductance is being partitioned among the different organs.

Yes, this is an important missing information. I assumed that 50% of the conductance was above ground.

Define terms in Figure 1 caption.

done

As above, more details of the model framework need to be given, as do basic assumptions.

Why is the model timestep 1 millisecond? Seems excessive?

This is to avoid numerical instabilities associated with the Courant- Friedrichs-Lewy conditions

If there is a leaf energy budget module - then why is transpiration simulated using equation 5? Why not Penman-Monteith?

The leaf energy budget is used to compute Tleaf not E in SurEau.

It seems like the typical plant is a sapling growing in a pot? A plant of 1.3 m with a rooting volume of 50 L ? Any reason for this choice ? Perhaps rather than calling it a typical plant explain that the simulations refer to a potted sapling?

OK, corrected.

In Table 1, why are there two values of gsmax?

The values refer to gleaf and gmin. corrected

What is slope?

The slope of the VC. Corrected

Explain how the soil type (clay) is used to translate soil water content to soil water potential. What is the maximum soil water holding capacity?

I use pedotranfers functions for this (Van Genuchten's equation).

Explain what are Tair-min, Tair-max etc in the second Table 1 (perhaps make this Table 2!)

Added in Appendix 1

Figure 4 is nice. However, the conclusion drawn from this figure is not clearly supported:

The time to hydraulic failure appears clearly more determined by the water losses beyond the point of stomatal closure rather than the speed at which plant empty the soil water reserve when stomata are still open.

To better support this statement, add a second set of curves (or second panel) to show also time to stomatal closure, so as to understand where in the drydown the sensitivity to temperature principally occurs. (Also fix typo in y-label).

Good suggestion. I've added the requested figure, showing that most of the variation in THF is actually mostly dues to post-stomatal closure effect.

Figure 5: Add units to axis labels. Explain the dashed vertical lines? And consider more distinctive colours. I am not sure which is green and which is blue! Why are there several red lines?

Colors have been changed and units added. The legend was modified to be more explicit.

It would have been interesting to have a bit more exploration of the model behaviour during the heatwave simulations. The only thing that is shown is time to PLC. What about soil moisture content over time? Transpiration over time? Loss via cuticular conductance over time? Such exploration would be helpful in understanding what is really going on in the model, and might also help to identify the types of experimental data that could be used to test this hypothesis.

It would also be very interesting to show leaf temperature. I'm assuming there are no adverse impacts of high leaf temperatures in the model (it would be good to confirm this). It is possible that the increased gmin with high temperatures could serve to help cool the leaves - shortening the time to hydraulic failure, yes, but also avoiding lethally high leaf temperatures.

I agree that it would be nice to show all these details but this would mean adding a large number of graphics. I suggest join the dataset of these simulations and let the readers explore these data themselves.

Discussion: The paper overlooks the capacity for plants to modify gmin in response to warmer temperatures. There is some evidence that plants can down-regulate gmin in response to warmer or drier conditions (Duursma et al. 2019, New Phytologist). It would have been nice to explore the impact of downregulation of gmin in the simulations - failing that, a mention in the discussion of this mechanism would be appropriate.

The figures 6&7 explore this acclimation process actually (through Q10a, Q10b and Tp). This clearly shows that lower gmin values (mostly at high temperature) increases the time to hydraulic failure. I've mentioned in the discussion the importance of documenting the plasticity of Tp and gmin.

The discussion should touch on how these results could be tested. I would anticipate that potted plants would definitely experience hydraulic failure faster in hot conditions but how might one go about demonstrating that increased cuticular conductance was playing a role, above and beyond higher evaporation rates?

It would also be appropriate to consider how the results might apply to full-sized trees that are not limited by soil volume.

I've added some suggestions about possible ways to test the predictions of the SurEau model. Working with big tree in-situ is obviously more tricky. I propose to explore the emission of volatile compounds that also depend on gmin when stomata are closed.