Peer Community In
Forest & Wood Sciences

An important contribution to the description of growth stresses in branches of adult trees based on a new model and an optimisation process with digitised branches.

Erwin Dreyer *based on peer reviews by* ***Jana Dlouha*** *and 1 anonymous reviewer*

Arnoul VAN ROOIJ, Eric BADEL, Jean Francois BARCZI, Yves CARAGLIO, Tancrède ALMERAS, Joseph GRIL (2023) Modelling the growth stress in tree branches: eccentric growth vs. reaction wood. HAL, ver. 4, peer-reviewed and recommended by Peer Community in Forest and Wood Sciences. https://hal.science/hal-03748026

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This interesting article (van Rooij et al, 2023) proposes an innovative modelling approach to the question of the biomechanics of a growing branch. The main aim is to model the "growth stress" (Fournier et al, 2013) it is exposed to while developing its radial structure in response to increasing weight. The proposed model is very interesting and novel with respect to the existing literature on this important topic in tree biology. The model bases on two major components of the structure of a growing branch: the eccentricity (the branch is usually thicker vertically than horizontally, which may provide the strength to resist the weight) and the production of reaction wood (Barnett et al, 2014) on one side of the branch which produces asymmetric forces against gravity. The reaction wood is either tension wood (in hardwood trees, e.g., angiosperms) or compression wood (in softwood trees, e.g., gymnosperms). The model is clearly described and based on a number of explicit and already described concepts with some simplifications (no local irregularities like nodes or holes, only vertical bending taken into account, branch growing straight at a constant angle, ...) whose potential effects are nicely discussed and on a reliable and detailed set of analytical equations. The model addresses the dynamic changes resulting from branch growth, i.e., mainly radial growth which results in an accumulation of wood and in increasing mass and "growth stress".

The model is tested during a virtual experiment using a small set of data from a large pine tree (taken as an example of a softwood conifer tree) and a cherry tree (taken as an example of a hardwood tree). The optimisation test uses the mean allometric values from 30 branches of each individual tree as an entry to the model. This test of the optimality of the model is a very useful prerequisite for the adoption of the model. One might however argue that some replicate examples from other tree species would have been welcome to better represent the potential inter-specific variability in the two groups (softwoods vs. hardwoods). Indeed, there is a lack of suitable data available to properly test the underlying hypotheses under different conditions (growth angles, wood densities, growth rate, branch aging, ….). However, the presented computations allow testing the plausibility of the model and of its main conclusions, with respect to some "growth stress" values reported in the literature. The results confirm that the contribution of reaction wood is dominant, even if the eccentricity of the branches bears a significant contribution in the two tested cases.

The present preprint has the potential to act as the foundation for some additional research that might challenge its main conclusions and provide (hopefully) more support to the main conclusion that eccentricity plays a minor but still significant role in ensuring the stability of the growing branches and that the main stabilising effects are produced by reaction wood.

This version of the preprint is now suitable for a recommendation. However, it still suffers a few minor typos and language issues that the authors might correct during further steps in the publication process (a final version as a preprint, or submission to a journal chosen by the authors). Among those typos, the fact that *Prunus avium* is a cherry tree and not a birch. Similarly, several references need be corrected and completed, and more care should be in general given to the scientific species names….

In conclusion, this modelling exercise and the optimisation procedure used here underline once more the importance of reaction wood as a stabiliser of the three-dimensional architecture of trees not only in the trunk (where it has been studied in detail), but also in the lateral and sometimes quite heavy branches.

Anyway, I believe this preprint (and the version potentially published in a journal) will become an important reference for future research about the biomechanics of branches and of tree crowns in general, and that it will trigger further research in this direction.

References:

Arnoul van Rooij, Eric Badel, Jean-François Barczi, Yves Caraglio, Tancrede Almeras, and Joseph Gril. (2023) Modelling the growth stress in tree branches: eccentric growth vs. reaction wood. HAL, ver. 4 peer-reviewed and recommended by Peer Community in Forest and Wood Science. https://hal.science/hal-03748026v4

Mériem Fournier, Jana Dlouha, Gaëlle Jaouen, Tancrède Almeras (2013). Integrative biomechanics for tree ecology: beyond wood density and strength. Journal of Experimental Botany, 60 (15), pp.4397-4410. https://doi.org/10.1093/jxb/ert279

J.R. Barnett, Joseph Gril, Pekka Saranpää (2014) Introduction, In: The Biology of Reaction Wood, Springer Series in Wood Science, Springer (pub), Gardiner B., Barnett J., Saranpää P., Gril J (eds), p. 1-11. https://doi.org/10.1007/978-3-642-10814-3_1

Reviews

Evaluation round #2

DOI or URL of the preprint: https://hal.science/hal-03748026
Version of the preprint: 3

Authors' reply, 18 April 2023

Dear reviewers, dear recommender,

Thank you for your review and your opinions. We have corrected all minor remarks. Also, we have noticed an error in the analysis, which has been corrected in the new version. In attachment you will find: 1. a response document in which we answer the comments. 2. a new commented version so that you can track the changes. In this version, corrections in blue follow your remarks, those in red follow the error previously mentioned.

Sincerely yours,
Arnoul VAN ROOIJ et al.

Download author's reply

Download tracked changes file

Decision by Erwin Dreyer, posted 13 February 2023, validated 14 February 2023

A last round of revision is required to settle very minor issues in the presentation of the preprint

The new version of theis preprint as submitted by the authors was reviewed again by the two former reviewers. Both were fully satisfied with the answers provided by theauthors and the changes brought to the preprint, which followed nicely their recommendations. I concur with this statement and believe the preprint is almost ready for final recommendation. However, during my own reading of the manuscript, I came across some typos and minor mistakes that require a last round of revision. I reported these mistakes and providedsuggestions directly in the attached version of the manuscript. I therefore recommend that the authors do a last proof-reading before I produce the final recommendation for this very interesting and solid manuscript.

With best regards

Erwin Dreyer recommender **Download recommender's annotations**

Reviewed by Jana Dlouha, 27 January 2023

The revised version of the paper is ok for publishing!

Reviewed by anonymous reviewer 1, 10 February 2023

The authors have answered to all my points. The text has been much improved. I recommand it for acceptation.

Evaluation round #1

DOI or URL of the preprint: https://hal.science/hal-03748026
Version of the preprint: 2

Authors' reply, 13 January 2023

Download author's reply

Decision by Erwin Dreyer, posted 10 November 2022, validated 14 November 2022

An interesting manuscript on the biomechanics of branch growth in trees that requires however a careful revision

This interesting manuscript proposing a modelling approach to the question of the biomechanics of a growing branch has been analysed by two specialists of biomechanics (which, as a recommender, I am not).

The two external reviewers provided a detailed analysis of the manuscript (see their comments below or in the attached document). I had a look at the general structure and the logic of the manuscript too, and provided some detailed comments and suggestions as annotations in the attached version of the manuscript.

The external reviewers found the model quite interesting and novel with respect to the existing literature.on this very specialised topic in tree biology. They in general agree wiith the approach used to quantify two components of the structure of a growing branch: the eccentricity and the production of reaction wood. They found the model to be in general clearly described and based on a number of clear analytical equations. One of the reviewers however wondered why allometric relationships were used as entry to the model, and this concern needs be addressed. The model is then tested against a small set of data combining a branch from a large pine tree (taken as an example of a softwood conifer tree) and a cherry tree (taken as an example of a hardwood tree). This test of optimality is very interesting. However, one of the reviewers was concerned by the fact that the procedure used to test the optimality of a given growth strategy needed to be made more explicit. This should be done with some details at the end of the introduction, when the experimental procedure (combining modelling and test) is described in more details; by the way, I found that the current description lacks some details about the ratinale and the demnstration to be made.

There are also concerns about the structure and organisation of the manuscript. One of the referees stated that the manuscript sounded like having been written in several steps, with changes in the wording of the concepts used; I had the same feeling. Furthermore, my suggestion would be to clearly separate the presentation of the results from the discussion: such a clear disctinction leads to the presentation of the results in a short manner, and a more structure discussion that can in places cover more than just putting the results into perspective.

A concept that requires a better definition and a more consistent use is that of "growth strategy": here, it is used in the sense of the relative contribution of two different processes: eccentricity (accumilation of wood on one side of the brach to counteract the effects of gravity) and the formation of reaction wood (accumulation of tension wood in softwood trees (angiosperms) and compression wood in conifers (gymnosperms) that also counteracts the effects of gravity by changes in the ultrastructure of the wood tissues. The "strategy" is meant here as the balance between the two effects if I understood well the aims of the research. This needs be made clearer in the text. The same wording should then be used consistently across the manuscript.

Finally there is a need to make clear that the experimental basis og the manuscript does not allow to oppose gymnosperms and angiosperms as there is only one sample per category. I am sure the authors are perfectly aware of this, but some wording in the manuscript might give the wrong impression they are not. This was highlighted in the attached copy of the text.

To summarize, there is a consensus that the manuscripts will ultimately deserve a recommendation, but that there is a need to improve its structure and clarity before this positive recommendation might be issued by the Peer Community in Forest and Wood Sciences. The manuscript has the potential of becoming a very nice and important contribution in the field of tree biomechanics.

Erwin Dreyer, acting as recommender for this manuscript. **Download recommender's annotations**

Reviewed by anonymous reviewer 1, 28 October 2022

The aim of this article is to explore which strategies minimize internal stresses during branch growth. The main hypothesis (which is verified later on Figure 12) is vertical bending moment prevails over the torsional moment, and horizontal bending moment. Based on this hypothesis the growth kinematic is simplified to specifically resist such vertical bending moment: the branch section remains circular during growth and the only degree of freedom is the position of the center of the circle along the vertical line coined eccentricity. A linear relationship between elastic strain, bending strain, radius increments, force and moment increments is derived from static force balance and Hooks law (12a,12b); the coefficients of the linear relationship are

expressed as function of the two maturation stresses and the eccentricity. Force and moment are supposed to depend on the radius R following allometric laws whose coefficients are estimated through simulations of trees with AMAPsim (Figure 4, Table 1). Equation 12a combined with the allometric laws for force and moments provides the elastic strain. Bending strain are also supposed to depend on the radius R following allometric relationships thus Equation 12b provides an equation between the two maturation stresses and the eccentricity (21a for hard wood and 21b for soft wood). Based on these allometric laws an analytic formula is provided for the stresses as a function of r (19). The two growth strategies derive from the fundamental equation (20), either supposing a constant eccentricity while the maturation stress difference (varying with r) drives the postural control or supposing a constant maturation stress difference while the eccentricity (varying with r) drives the postural control.
Once allometric law have been determined the model is fully analytical: For each strategies stresses are computed with formula (19) for increasing radius (the radius being the proxy for growth) as well as the driving variable (eccentricity or maturation stresses difference). The optimal strategy is the one which minimizes stresses at the periphery which are compressed to maximal stresses observed in the literature; stresses at the pith are not considered as they diverge due to an oversimplified model (discussed in the section Limits of the model). The strategies are compared for one hardwood species Prunus avium and one softwood species Pinus pinaster.

The article is interesting and globally well-written but I feel there were several phases of writing; the article is long and not completely coherent. I recommend publication once the following concerns are addressed:

The model is clearly detailed and rigorous. In my eye, the main limitation is the use of allometric laws to complete equation 12a, 12b to get equation 19 and 21. I do not see why an allometric is used for b but not for a; I am not a specialist and I can't judge the robustness of such an hypothesis but from far away it appears as an adhoc simplification. It could be more quantitatively discussed (narrowness of the allometric distribution). Later on the growth is supposed to be stationary so the b does not depend on r except in the paragraph, « Influence of the orientation ... ». In this paragraph you should explain why for up-righting and passive bending curves you do not use allometric law fo bending strain but other driver (« increasing weight » or « maturation gradient »). The whole is a bit fuzzy for me.

I had more difficulties to follow the discussion which probably comes from the fact I am not a specialist. In my eyes, the criteria for optimality of a strategy are not sufficiently explained: Is it solely the stress at the periphery? Is there a cost when eccentricity or maturation stress are too high? For instance, I do not understand the following statement:
« When combined, it seems more efficient to vary the eccentricity and keep a constant difference of maturation stress than to keep a uniform eccentricity and to vary the maturation stress. « When I look to figures 6.a.i and 6.b.i: maximal stress for the strategy beta=0 seems to rank as well as for e=0.5.
The figures and legend could also be improved:
- The use of r for b foth figure 5b and 5c (and all the following figures 6,7,8,9) was confusing: I would use x for 5b and r for 5c.
- The legend should be more homogeneous Figure 5 « constant difference of maturation stress « , Figure 6 « constant maturation gradient ». It would more logical to represents sigmaNW-SigmaTW than beta in the legend.
I do not understand "In case of combined effects, although eccentricity alone ensures stationarity, it does not succeed anymore when combined to a uniform maturation (red dotted line in Fig. 8.b). " First there is no red dotted line on figure 8. I thought "stationarity" was an hypothesis to suppose b independant of r which is at the basis of the model. How can you contradict an hypothesis of the model?
In general, the Results and discussion should be clarified and a bit more structured.

Reviewed by Jana Dlouha, 20 October 2022

Download the review