

# ***Interactive comment on “Feedbacks between earlywood anatomy and non-structural carbohydrates affect spring phenology and wood production in ring-porous oaks” by Gonzalo Pérez-de-Lis et al.***

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REVIEWER: Pérez-de-Lis et al put forth a commendable study on the correlations between NSC reserves and tree physiology, particularly xylem structure and function. This topic first within the scope of BG and presents some novel concepts. While the authors formulate conclusions to hypothesis put forth, there appear to be significant limitations in their support for hypotheses (i) and (ii) (p2, lines 38-40). The description of the experiments is adequate with some significant issues (see below). Proper credit is given to related work. The title is appropriate for the research.

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ANSWER: We strongly appreciate the comments by the referee, which give us the chance to improve the quality of our work.

REVIEWER: I urge the authors to reduce the discussion in a effort to strengthen support for their findings.

ANSWER: We thank this comment. Indeed, sub-section 4.1 “NSC allocation to xylem growth reflects contrasting stress-tolerance strategies in oaks” can be reduced by re-ordering some of the ideas presented there. We will perform these modifications accordingly upon receipt of the other reviewers’ suggestions.

REVIEWER: Regarding methods, there is no indication on how DBH or tree height was measured.

ANSWER: This information was missing in the former version of the manuscript. Stem diameter was measured by using a diameter tape, while we used a Blume-Leiss hypsometer to estimate tree height. This information is properly included in the Materials and Methods section of the revised version.

REVIEWER: Correlations between DBH and tree height was not described statistically.

ANSWER: We performed Pearson’s correlations (two-tailed test of significance and 0.95 confidence interval). This information is included in Materials and Methods of the revised version.

REVIEWER: In the methods section, the authors state that 40 trees per species were selected, but in the methods or results sections, there is no indication on sample size for NSC or anatomical measurements. Can the reader assume  $n=40$  for all comparisons?

ANSWER: Sample size is 240 (40 by species at each site) throughout the manuscript. At the beginning of the sub-section entitled “2.2 Phenology and NSC concentration” we stated that “40 trees per species were selected for sampling”. For the sake of clarity we added the expression “in all the selected trees” in page 3 line 28 of and page 4 line1.

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REVIEWER: Authors fail to account for age of the trees when estimating growth rate by measurement of DBH. Authors state that DBH scales with tree height, but no statistics are offered to justify such allometric scaling. Thus, I find it problematic to use only DBH as an indication of tree size because of the disregard to growth rates. Furthermore, calculations of BAI would be useful in correlating NSC reserves with growth rate and subsequent parameters such as EVP, bud break, latewood production, etc...

ANSWER: As the reviewer rightly commented, growth rates were not considered in our study. Actually, our SEM model was focused on relations between NSC, hydraulic capacity, and vessel production, rather than on growth rates. In order to avoid misunderstanding, we removed both “fast-growing” and “slow-growing” expressions from the manuscript. We also replaced “fast-growing trees” by “dominant trees” in page 2 line 3, and “than their slow-growing counterparts” was removed in line 4. Similarly, in page 4 line 23 we replaced “fast-growing trees (larger stem diameter)” by “bigger trees”.

The reason for us to consider “tree size” in our study was because it is assumed to affect wood anatomy, as well as to carbon economy and storage (i.e. Petit et al. 2008, New Phytol; McDowell et al. 2005, Oecol; Sala and Hoch et al. 2009, Plant, Cell Environ). In addition, large trees are frequently dominant, having a different timing of xylogenesis and phenology than small trees (Rathgeber et al. 2011, Ann Bot). In our view, “stem diameter” is a good indicator of tree size in this study because tree height and stem diameter were noted to be positively correlated (Page 5 line 22; but see also the response to the comment: page 5 line 29 – this correlation does not appear to be consistent across all sites). However, if the referee still judges it necessary, we will replace “tree size” by “stem diameter” in the revised version.

REVIEWER: For the results section, comparisons are not adequately stated. Examples include: page 5 line 8 – is this comparison on NSCs combined across all sites;

ANSWER: We performed comparisons across sites, indeed. We will substitute “Mean SS concentrations at the sites ranged from 3.88 to 5.08 percentage dry matter in Qrob”

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by “Mean SS concentrations ranged along the gradient from 3.88 to 5.08 percentage dry matter in Qrob” (page 5 line 6).

REVIEWER: page 5 line 11 – the figure implies no significant difference between species at hyperhumid in the SS:starch ratio;

ANSWER: Thanks for the comment. In the revised version, hyperhumid location is removed from this sentence.

REVIEWER: page 5 line 12 – NSC (being a total of SS and starch) is not indicated in the figure and is this a comparison of species across all sites?

ANSWER: Actually, we compared values of both species (together) among study sites. We removed the reference to Figure 2 from this sentence.

REVIEWER: page 5 line 17 – Fig is not referenced correctly;

ANSWER: The reference to Figure 3a,b should have appeared in the following sentence. In the revised version, it is included in the proper position.

REVIEWER: page 5 line 18 – fig implies that hyperhumid does not differ from subhumid;

ANSWER: Actually, differences between the hyperhumid and the subhumid locations are significant in 2012, but not in 2013. In the revised version, we rewrote this phrase as follows: “In Qpyr, Dh at the hyperhumid site was substantially lower than at the humid and subhumid locations in 2012, but only than at the humid site in 2013. By contrast, much less variation was found among sites for Qrob”.

REVIEWER: page 5 line 19 – it is not clear which species are being referred to here;

ANSWER: We rewrote this phrase in a clearer form as follows: “EVP values decreased from the subhumid to the hyperhumid location in Qrob ( $F = 5.55$ ,  $P = 0.005$ ; Fig. 3c) and Qpyr ( $F = 4.12$ ,  $P = 0.019$ ). Trees of both species exhibited wider latewood at the subhumid than at the hyperhumid site (Qrob  $F = 11.88$ , Qpyr  $F = 14.25$ ,  $P < 0.001$ , Fig.

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3d)”.

REVIEWER: page 5 line 26 – clarification is needed here as to what species is being referred to for the budburst range, furthermore, are these comparisons referring to min/max, as the figure implies means of only end of March (90 days) to early May (130);

ANSWER: Dates provided are those corresponding to min/max values. In the revised version we specify that such information is referred to both species.

REVIEWER: page 5 line 27 – clarify what is being compared here;

ANSWER: We rewrote this sentence as follows: “Budburst at the hyperhumid and humid sites occurred synchronously (Qrob  $t=1.92$ , Qpyr  $t=-0.54$ ,  $P>0.05$ ), but later than at the subhumid location (Qrob  $F=128.45$ , Qpyr  $F=79.49$ ,  $P<0.001$ )”.

REVIEWER: page 5 line 29 – this correlation does not appear to be consistent across all sites;

ANSWER: Correlation coefficients at the former version of the manuscript were calculated at species level, after pooling the data of the three locations. Actually, stem diameter and tree height are strongly correlated at the hyperhumid and subhumid sites, while correlation is not significant at the humid location (See supplement to the comment, Table 1). The low variance in both stem diameter and height values measured at this latter location, which could be attributed to low age variability, likely obscured the scaling association between these two variables (See supplement to the comment, Fig. 1). Since this study is not focused on relations between stem diameter and tree height, we propose to include this information as Supplementary material.

REVIEWER: page 5 line 34 – what is “ALT” referring to?

ANSWER: We apologize for this mistake; we put “ATL” instead of “Hyperhumid site”. This error has been corrected in the revised version.

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REVIEWER: While the authors acknowledge limitations of this study, in particular the need to include more tissue types for NSC analyses and subsequent comparisons, using only stemwood NSC reserves as a proxy for hypotheses put forth in this research is possibly flawed. A primary concern is that stores of NSC reserves in the root system could have a huge impact on growth, budburst, etc, and cannot be ignored. Such analyses would need to be conducted in order to present this research as acceptable.

ANSWER: As the referee pointed out, we are aware of the limitations of our study, which were detailed in the Conclusion section. Despite this, we think that the work presented in our manuscript is novel and supposes an incremental advance in this topic that may be interesting for a broad audience. In this regard, we would like to point out that several anatomical and phenological parameters (vessel size and number, ring width, budburst dates, stem diameter) were assessed simultaneously with carbohydrate reserves for the first time in ring-porous species. In addition, our data set is large, involving two species and three sites along a rainfall gradient (and 240 trees).

Carbon reserves in deciduous trees are mostly stored in the stem, as well as in coarse roots and branches (Barbaroux et al. 2003, *New Phyt*). Probably, additional NSC measurements in roots and branches would have been essential if our objective were to analyze changes in the total NSC pool, as it has been done in studies testing the carbon starvation hypothesis (i.e. Anderegg and Anderegg 2013, *Tree Phys*; Galvez et al. 2013, *New Phyt*; Hartmann et al. 2013, *Func Ecol*); or if we were interested in analyzing carbon fluxes among different tree compartments (Regier et al. 2010, *Tree Phys*). However, although we recognize that NSC measurements in roots would have been valuable in this study, our objective was to disentangle the interaction between xylem growth and short-distance NSC content, rather than focusing on the differences in NSC storage patterns among populations or species.

According to Steppe et al. (2015, *Trends Plant Sci*), a mechanism of xylem growth is dependent on the incorporation of carbon resources, and thus requires information on sugar concentrations in the stem. In this regard, a number of recently published studies

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analyze the interplay between carbohydrate content and xylem growth by sampling the cambial zone (Deslauriers et al. 2009, *Tree Phys*; Deslauriers et al. 2014, *Ann Bot*), stem sapwood (Galiano et al. 2011, *New Phyt*; El Zein et al. 2011, *Tree Phys*; Oberhuber et al. 2011, *Can J For Res*; Carbone et al. 2013, *New Phyt*), or several above ground compartments (Sala and Hoch et al. 2009, *Plant, Cell Environ*; Fajardo et al. 2012, *New Phyt*; Saffell et al. 2014, *Tree Phys*). It is interesting to note that NSC translocation through the different plant compartments may be strongly reduced during dormancy if phloem becomes non functional, as suggested by Lacoïnte et al. (2004, *Plant, Cell Environ*) for the deciduous walnut. Therefore, the contribution of local stem carbon reserves might probably be considerable in fuelling xylem growth before the sink-to-source transition of leaves (Begum et al. 2010, *Ann Bot*). This is related to the fact that initiation of cambial divisions in roots and stem precedes budburst in deciduous oaks and is consistent with the strong decline in stem NSC concentration frequently reported in spring (Barbaroux and Bréda, 2002, *Tree Phys*; El Zein et al. 2011, *Tree Phys*). For these reasons, we think that relations between stem sapwood NSC content and earlywood growth dynamics are especially relevant.

We agree that hypotheses in page 2 can be more accurately defined by specifying that interpretations are only referred to stem sapwood. Thus, in the new version, we rephrased the sentence in line 35, page 2, as follows: "In this regard, we hypothesized that the more-drought tolerant *Q. pyrenaica* will have larger stem sapwood NSC concentration but lower wood production than *Q. robur*". Likewise, line 39, page 2, we specified more clearly: "(i) tree size influences earlywood vessel diameter, which in turn affect NSC content in the stem; (ii) higher sapwood SS content in winter predisposes trees to advance growth resumption in spring, thereby fostering earlywood production [ . . . ]".

Please also note the supplement to this comment:

<http://www.biogeosciences-discuss.net/bg-2016-227/bg-2016-227-AC1-supplement.pdf>

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