We kindly thank the referees for taking our discussion paper under consideration and for their helpful and constructive comments. We performed a thorough revision of the manuscript by taking into account all issues pointed out by the referees, as well as their suggestions to improve methodology, statistical analyses, and the discussion sections. Our proposed changes are listed next to the points raised by the referees. We also added in the Acknowledgements section a project reference number (GRC2015/008) that had not been included in the former version.

REFEREE#1

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.

Answer: Hypotheses were more accurately defined in the revised manuscript. In this regard, we included that our interpretations were only referred to stem sapwood, rather than to the whole-tree NSC pool. For further detail, see the response to the final comment of referee#1.

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

Answer: We are grateful for this comment. The discussion of our results was carefully revised. Reiterative ideas were removed and the remaining text reorganized within the sub-sections. In addition, we changed the order of the hypotheses in the Introduction (page 2, lines 36-38), and modified several sentences in the summary in order to clarify key ideas of our study.

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. It has been properly included in the Materials and Methods section of the revised version (page 3, lines 23-24).

Correlations between DBH and tree height was not described statistically.

Answer: We performed Pearson's correlations (two-tailed test of significance and 95% confidence interval). This information is now included in Materials and Methods (page 4, lines 18-19).

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 (2) at each site (3)) throughout the manuscript. For the sake of clarity we clarified that NSC, phenological and anatomical measurements were performed "from all the selected trees" in page 3, line 23 and page 4, line 4. Moreover, we provided sample size for each species in Table 2 and Figures 3-7 captions.

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. Hence, we replaced "fast-growing trees" by "dominant trees" in page 2 line 4, and "than their slow-growing counterparts" was removed. Similarly, in page 4 line 26 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 positively correlated (page 5 lines 33-35 of the revised manuscript). We replaced, however, "tree size" by "stem diameter" in Figs. 2, 5a and 6 in order to avoid confusion.

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 substituted "Mean SS concentrations at the sites ranged from 3.88 to 5.08 % dry matter in *Qrob*" by "Mean SS concentrations along the gradient ranged from 3.88 to 5.08 % dry matter in *Qrob*" (page 5 line 17).

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 was removed from this sentence.

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 intended to compare mean values of both species together among study sites. However, we removed this comparison regarding total NSC from the manuscript because it was reiterative and confusing.

page 5 line 17 – Fig is not referenced correctly;

Answer: The reference to Figure 4a, b should have appeared in the following sentence. It has been now included in the proper position.

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 sentence as follows: "The highest D_h values were found for *Qpyr* at the humid (both years) and subhumid sites (2012), while *Qrob* had a more reduced variation along the gradient (2012 $F_{[2, 117]}$ = 2.89, 2013 $F_{[2, 117]}$ = 0.18, $P > 0.050$) (Fig. 4b)." (page 5 lines 26-28).

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

Answer: This paragraph was ambiguous. We rewrote it in a clearer form (page 5 lines 32-42).

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 in the revised version are those corresponding to min/max values for each species.

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

Answer: We rewrote this paragraph as follows: "*Qrob* exhibited an earlier budburst than *Qpyr* ($F_{[1, 236]}$ = 527.83, P < 0.001), occurring from early March to late April for the former, and from mid April to late May for the latter. In both species, budburst occurred earlier at the subhumid site than at humid and hyperhumid locations (Fig. 5b)" (Page 5, lines 35-37).

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

Answer: The correlation provided was performed after pooling the data from the three study sites. As the referee rightly stated, this correlation was not consistent across sites (Table R1), being thus related to a site effect. Thus, we removed this calculation from the manuscript and the corresponding sentences in Results and Discussion (page 8 lines 27-28 of the former version).

Table R1 Pearson's correlation coefficients for each species and site. * P < 0.05.

Spp	Hyperhumid	Humid	Subhumid
Q. robur	-0.317*	0.103	0.197
Q. pyrenaica	0.034	0.044	-0.306

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.

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 had been 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 had been 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 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 Lacointe et al. (2004, *Plant, Cell & Environ*) for a 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.

Hypotheses in page 2 were more accurately defined by specifying that interpretations are only referred to stem sapwood. Thus, we rephrased the sentence page 2, lines 37-38 as follows: "We also hypothesized that the more drought-tolerant *Q. pyrenaica* will have a more reduced xylem growth than *Q. robur*, but larger stem sapwood NSC concentrations". Likewise, in page 2, lines 39-42, we specified more clearly: "(i) stem diameter influences earlywood vessel size, which in turn affects NSC content in the stem; (ii) higher sapwood SS content in winter predisposes trees to advance growth resumption in spring, as well as to produce more earlywood vessels; and (iii) earlywood vessel n and size are key predictors of latewood growth in oaks". In addition, in page 7, lines 13-16, we included a sentence highlighting the need for further research concerning the NSC pool size at the whole tree level (with a special focus on roots) in order to confirm or reject our hypothesis about divergent carbon use strategies in study oaks.

REFEREE#2

Overall, this was an interesting and useful contribution to the ongoing discussion about the roles of NSCs and plant hydraulics on tree phenology, growth, and survival. In this paper the authors studied two congenator oaks of that contrast in their ecological strategies to compare the impacts of winter NSC storage, hydraulic diameter, and budburst on earlywood vessel production (EVP) and the subsequent impacts of EVP, hydraulic diameter, foliar density, growing season length, and NSC on latewood production. Species were evaluated at three sites that form a moisture gradient in northwest Spain.

This paper was generally well written and well cited and most of my concerns are moderate and should not change the overall results.

Page 2, Lines 22-24: Here you describe one of your study species, but you fail to describe the other. I know Q. robor is more common, but not all your readers will be familiar with its ecology.

Answer: In the revised version, this paragraph was rewritten as follows: "This is the case of the ring-porous oaks *Quercus robur* L. and *Q. pyrenaica* Willd., which coexist in NW Iberian Peninsula. The former is widespread in Europe, being abundant in areas with mild-oceanic climate. By contrast, *Q. pyrenaica* is dominant in various mountainous ranges of the sub-Mediterranean area, hence exhibiting multiple adaptations to cope with summer drought and winter frost, such as late flushing (Pérez-de-Lis et al., 2016)" (page 2 lines 20-23 of the revised version of the manuscript).

Page 3, Line 21: No description is given as to HOW the trees were selected. In particular, I have no idea if the authors put out plots of some standard design, picked 'representative' trees, or picked the 40 biggest, healthiest trees they could find. No description is given of the size threshold or other criteria for inclusion (we could in theory be comparing a sapling at one site to a 100cm DBH tree at another). Unfortunately, ample evidence exists to show that trees and locations chosen subjectively to be 'normal' or 'representative' tend to be far better off than random, which unfortunately would cause all of the ANOVA-based comparative analyses to fall into question and require very careful interpretation of the regression-based analyses. I think in any revision the authors need to provide considerable more information about sampling and the editor should pay careful attention this information in assessing the validity of the work. For the remainder of the review I'm going to assume the sampling was done correctly (randomized locations, randomized trees within location).

Answer: A north-to-south transect was set following a gradient of decreasing humidity. The experiment was carried out at three sites situated along this transect. Both study species were present at the selected locations. At all the sites, *Qrob* and *Qpyr* trees were randomly selected, although highly suppressed and juvenile individuals were disregarded. In the revised version, we included a more detailed description of tree selection in page 3 line 5 and page 3 lines 21-22.

Page 3, Line 32: How was sapwood area determined?

Answer: Sapwood can easily be distinguished by colour. Heartwood in oaks is brown-coloured while sapwood has a pale tone (Figure R1). For the sake of clarity, this information was included in the revised version of the manuscript (page 3, lines 35-36).

Figure R1 Transverse section of a wood core of *Q. pyrenaica* showing the colour boundary between heartwood and sapwood.
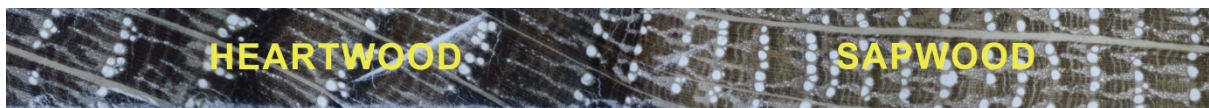
Page 4, Line 37: I'm going to assume growing season length is an individual-level measure and not a site-level measure (as is commonly done), otherwise this effect is confounded with the site random effect.

Answer: Indeed, growing season length is an individual-level parameter. In the revised manuscript, we cleared up this issue by modifying the paragraph regarding the methodology for phenological monitoring (page 3 lines 24-26).

Page 5, Lines 1-2: Here you're talking about averaging over a set of models, but in the paragraph above you only describe a single model. Where does this other set of

models come from? Why do you need another set of models? Why is the sum of Akaike weights an appropriate measure of the relative importance of a variable? This quantity is quite challenging to interpret, especially in a GLMM, and fairly unintuitive. I'm all for sophisticated analyses when needed, but why not stick to a simpler analysis (e.g. the proportion of the variance [R2] explained by each covariate),which in my mind would be much easier to interpret and a more direct measure of importance. As I tend to look at the figures before I read a paper, I'll also note that the meaning of 'relative importance' (essentially a weighted number of times that a variable was included in the model) is not clear in the figure.

Answer: What we meant with "set of models" is that we calculated the AIC of the models containing all the possible fixed-effect combination. In the former version we used an information-theoretic approach to identify the most influent fixed effects of the model. According to this procedure, models were compared using their AIC scores (the lower the AIC, the better the model fit). Hence, models were ranked and averaged in order to assess the relative weight of each variable (we averaged 95% of all the fitted models according to their AIC scores). As we mentioned in the former version, this method was detailed in Burnham and Anderson (2002), and has been used in a recent paper analyzing possible limitations of carbon supply on secondary growth published in Biogeosciences (Guillemot et al. 2015). In order to provide more confident results, we included the estimates, variance partitioning, the variance explained by each fixed factor (as a percentage of the total variance explained by the fixed effects), proportion change in variance, and R^2 for mixed-effects models (marginal and conditional). This information is presented in Table 2 of the revised version.

Page 5, Line 8: You should report the degrees of freedom in the F test (and all other tests). If this is going to be the same for all subsequent analyses state that here at the first usage, otherwise make the df explicit for each analysis.

Answer: We agree to the referee. *df* values were included in brackets next to *F*, χ^2, and *r*.

Page 5, Line 34: Be consistent with notation. In all other places you refer to sites by their moisture status, and here you've reverted to a site code, and I'm not sure which site you're referring to.

Answer: We apologize for this mistake again; we put "ATL" instead of "Hyperhumid site". This error was corrected in the revised version.

Page 5, Line 35: Were trees with powdery mildew included or excluded? Why wasn't this included as a covariate? Why is there not more in the discussion about how this could be affecting results?

Answer: Unfortunately, powdery mildew infestation has not been quantified. Yet, it is relevant to take into account that all the trees were more or less affected by the pest (it would not be considered as a covariate, but as a part of the site effect). This is a very frequent disease at oak forests in the study region, but their effects during the humid spring of 2013 were higher than usual at the hyperhumid location. Thus, we decided to provide this information, which probably helped us to interpret the lower growth noted at this latter site. The possible effect of powdery mildew infestation is discussed in page 6 line 40 of the revised version. Since we did not perform any measurement, we marginally commented this issue.

Page 5, Line 37 to Page 6, Line 3: In the Results (here) and Discussion (below), I'm concerned that the authors are over-interpreting the biological significance of results that are statistically significant but have low R2. Looking at Figure 5, about all I'm comfortable concluding is that SS and tree size have a negative impact on budburst in both species, and that SS had a positive impact on EVP in Q. pyrenaica. Effects in the

R2 of 3-6% range (Starch, Q robor EVP) don't seem worth discussing, and those in the 10-16% range (Dh, SS) should be acknowledged as weak.

Answer: Thanks for the comment. In the revised version, we included a more careful interpretation of the relationships accounting for a low variance (in both SEM and GLMM) in the observed parameters with several changes in the Results and Discussion sections (particularly in Subsections 3.2, 4.2, and 4.3).

Page 6, line 31: Tree density effects are speculative

Answer: We acknowledge that direct measurements on tree competition were not carried out. But this idea was based on differences in stand tree density (reported in Pag 3 line 13) and basal area (according to stem diameter measurements in Figure 5a) among locations. In this regard, recent work modelled a strong effect of competition in *Q. pyrenaica* secondary growth (Fernández-de-Uña et al., 2016). For the sake of clarity, we rearranged the paragraph concerning differences among sites in subsection 4.1. In addition, the sentence in page 6 lines 35-36 of the revised version was rewritten as follows: "Complementarily, a lower tree density at the subhumid site might be associated to a reduced inter-tree competition, which is assumed to favour both carbon uptake and xylem growth".

Feedbacks between earlywood anatomy and non-structural carbohydrates affect spring phenology and wood production in ring-porous oaks

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Abstract. Non-structural carbohydrates (NSC) play a central role in the construction and maintenance of the vascular system, but feedbacks between the NSC status of trees and wood formation are not fully understood. We aimed to evaluate multiple dependencies among wood anatomy, winter NSC, and phenology for coexisting temperate (*Quercus robur*) and sub-Mediterranean (*Q. pyrenaica*) oaks along a water-availability gradient in NW Iberian Peninsula. Sapwood NSC concentrations w~~as~~ere quantified at three sites in December 2012 (~~n~~ _N_ = 240). Leaf phenology and wood anatomy were surveyed in 2013. Structural equation modelling was used to analyze the interplay among hydraulic diameter (D_h), winter NSC, ~~date of~~ budburst date, and earlywood vessel production (EVP), while the effect of D_h and EVP on latewood width was assessed by using a mixed-effects model. NSC and wood production increased under drier conditions ~~in~~ for both species. *Q. robur* showed a narrower D_h and lower soluble sugar (SS) concentration (3.88–5.08 % dry matter) than *Q. pyrenaica* (4.06–5.57 % dry matter), but *Q. robur* exhibited larger EVP and wider latewood (1,403 µm) than *Q. pyrenaica* (667 µm). Stem diameter and ~~Trees of both species with large~~ D_h had ~~showed higher SS concentration in winter~~ a positive effect on SS concentrations, which were related to an ~~and~~ earlier leaf flushing in both species. Sapwood sugar content ~~Q. pyrenaica~~ appeared to ~~exhibited a carbon saving strategy~~ limit EVP exclusively in *Q. pyrenaica*~~, as evidences the fact that EVP was in tune with SS content in winter~~. In turn, ~~Latewood production was controlled by~~ D_h and EVP were found to be key predictors of latewood growth~~, rather than by foliage density and growing season duration~~. Our results ~~suggest that high SS con~~ confirm that sapwood SS concentrations ~~tent in oaks with high conductive area favours an earlier spring phenology, as well as earlywood growth~~ are involved in modulating growth resumption and wood formation in spring. *Q. pyrenaica* exhibited a tighter control of carbohydrate allocation to ~~xylem~~ wood formation than *Q. robur*, which ~~is probably related to the acquisition of~~ would play a role in protecting against ~~physiological resistance to~~ environmental stress in the sub-Mediterranean area.

1 Introduction

Non-structural carbohydrates (NSC) have multiple key functions in trees, such as fuel maintenance respiration, osmoregulation, cryoprotection, or growth control (Morin et al., 2007; Sala et al., 2012; Wang and Ruan, 2013; Deslauriers et al., 2014; Dietze et al., 2014). The asynchrony between carbon assimilation and consumption is solved by the active accumulati~~ng~~onof non-structural carbohydrate~~s~~ (NSC) ~~reserves~~ (Chapin et al., 1990; ~~Sala et al., 2012~~ Dietze et al., 2014), which are mostly stored in stem, branches and coarse roots as soluble sugars (SS) and starch (~~Barbaroux et al., 2003~~ Salomon et al., 2016). A large part of the NSC budget of the tree is invested in construction and maintenance of the vascular system, as well as in fine roots turnover, and crown development (Wang and Ruan, 2013; DeSoto et al., 2016). The hydraulic network in ring-porous oaks is highly vulnerable to dysfunction due to cavitation of their large vessels, which operate at a narrow safety margin (Delzon and Cochard, 2014; Urli et al., 2015). The refilling of ~~these~~ embolized vessels needs restoration of osmotic gradients through releasing SS into the conduits (Salleo et al., 2009; Brodersen and McElrone, 2013).

Alternatively, the hydraulic function can be recovered through the formation of new conduits in the following spring (Brodribb et al., 2010). In ring-porous species, earlywood vessels are generally functional during only one year (Urli et al., 2015), and cambial resumption precedes leaf formation (Pérez-de-Lis et al., 2016). ~~Large~~ Stored NSCs ~~reserves~~ are therefore needed ~~in order~~ to provide energy and materials for leaf expansion and cambial activity at the onset of the growing season (~~Barbaroux et al., 2003;~~ El Zein et al., 2011).

Large vessels are presumed to boost carbon gain because stomatal conductance increases with the hydraulic capacity (Fichot et al., 2009). Concurrently, more carbohydrates may be allotted to hydraulic purposes in trees with wider but more vulnerable vessels (Salleo et al., 2009; Brodersen and McElrone, 2013). However, little is known about feedbacks between wood anatomy and short-distance NSC mobilization, which are probably influenced by tree vigour. Large ~~Tall trees are thought to form wider vessels at the tree base in order to compensate height-related hydraulic resistance in the stem (Petit et al., 2008). Probably, larger vessels boost carbon gain in dominant individuals since stomatal conductance increases with the hydraulic capacity (Fichot et al., 2009). In fact, fast growing~~dominant trees commonly exhibit ~~larger~~ higher NSC levels and a faster NSC turnover ~~than their slow growing counterparts (Sundberg et al., 1993;~~ Sala and Hoch, 2009; Carbone et al., 2013; DeSoto et al., 2016), but also. ~~Probably, larger vessels boost carbon gain in dominant individuals since stomatal conductance increases with the hydraulic capacity (Fichot et al., 2009).Tall trees are thought to form~~ wider vessels at the tree base ~~in order~~ to compensate height-related hydraulic resistance in the stem (Petit et al., 2008).~~Concurrently, more carbohydrates may be allotted to hydraulic purposes in trees with wider but more vulnerable vessels (Brodersen and McElrone, 2013).~~ However, little is known about how feedbacks between wood anatomy and short-distance NSC mobilization affect growth. In turn,

~~c~~Entangled relationships between tree vigour and growth are influenced by the timing of tree phenology, given that dominant trees show larger growing periods and more intense cambial activity (Rathgeber et al., 2011). Although the break of dormancy is mostly controlled by temperature and photoperiod (Basler and Körner, 2014), some studies suggest that high NSC concentrations in developing buds speed up leaf-out dates (Maurel et al., 2004). In winter, phloem of deciduous trees ~~was suggested to be~~ is probably non-functional, whereby sapwood might be involved in carbon translocation through the plant body (Lacointe et al., 2004). The influx of sucrose from xylem conduits in branches into the buds was reported to be tightly correlated to bud swelling rates (Bonhomme et al., 2010), whilst high sucrose concentrations in the stem of mutant poplars have been associated to advanced budburst (Park et al., 2009). Cascade effects of leaf phenology on secondary growth would be then expected, given that leaf and cambial phenology are coordinated at the whole-tree level (Pérez-de-Lis et al., 2016)

~~There is a tight association between the timing of primary and secondary growth at the whole-tree level (Pérez-de-Lis et al., 2016).~~

~~In winter, phloem of deciduous trees was suggested to be non-functional, whereby sapwood might be involved in carbon translocation through the plant body (Lacointe et al., 2004). The influx of sucrose from xylem conduits in branches into the buds was reported to be tightly correlated to bud swelling rates (Bonhomme et al., 2010), whilst high sucrose concentrations in the stem of mutant poplars have been associated to advanced budburst (Park et al., 2009).~~ In ring-porous oaks, winter temperature has been reported to affect earlywood formation, which has been attributed to thermal-induced changes in respiratory demands and NSC levels ~~direct effects of temperature on both the timing of phenology and carbon demand for maintenance respiration~~ (Gea-Izquierdo et al., 2012). However, ~~the influence of sapwood NSC levels in dormancy release is frequently precluded, and~~ the ~~possible effect of their~~ interplay between NSC, phenology, and tree growth~~in tree growth is~~ is poorly understood.

~~There is a tight association between the timing of primary and secondary growth at the whole-tree level (Pérez-de-Lis et al., 2016). In turn,~~ ~~E~~ecological requirements modulating phenology are linked to functional species-specific strategies (Basler and Körner, 2014). This is the case of the ring-porous oaks *Quercus robur* L. and *Q. pyrenaica* Willd., which coexist

2

in NW Iberian Peninsula. The former is widespread in Europe, being abundant in areas with mild-oceanic climate. By contrast, *Q. pyrenaica* is dominant in various mountainous ranges of the sub-Mediterranean area, hence exhibiting multiple adaptations to cope with summer drought and winter frost, such as late flushing (Pérez-de-Lis et al., 2016)~~This is the case of the ring porous oaks *Quercus robur* L. and *Q. pyrenaica* Willd., which coexist in NW Iberian Peninsula. The latter is a sub-Mediterranean species that exhibits late flushing (Pérez de Lis et al., 2016), along with several morphological and physiological adaptations to cope with summer drought and winter frost~~. Such differences could impact carbon metabolism and allocation to growth (Valladares et al., 2000; Piper, 2011; Guillemot et al., 2015), as well as the rate of developmental processes (Deslauriers et al., 2009), affecting the adaptive capacity to track rapid climate change (Jump and Peñuelas, 2005). Water shortage is deemed to influence carbon metabolism in a complex manner by constraining the activity of both source and sink organs (Sala et al., 2012), and changing .~~s~~ugar fractions (Deslauriers et al., 2014). ~~Whereas~~ While some studies suggested that~~reported~~ declining growth demand under drought causes NSC to be accumulated~~that NSC are accumulated under drought~~ (Sala and Hoch, 2009; Lempereur et al., 2015; DeSoto et al., 2016), other authors found ~~a~~ drought-induced reduction in starch concentration ~~, coupled with changes in the SS composition~~under long-term drought (Rosas et al., 2013~~; Deslauriers et al., 2014~~). Therefore, we need to understand how phenology and growth are coordinated with NSC ~~and wood anatomy~~ in order to better predict plant responses to climate in the context of global warming.

In this research, data from stem sapwood NSC concentration in winter 2012, xylem anatomical traits, and leaf phenology in spring 2013 (as a proxy for cambial phenology) are used to disentangle the influence of their mutual interactions on the radial growth of ring-porous oaks growing along a water-availability gradient in NW Iberian Peninsula. We focused on the possible differences in xylem anatomy and NSC levels between *Q. robur* and *Q. pyrenaica* along the gradient. In this regard, ~~we hypothesized that the more drought tolerant *Q. pyrenaica* will have a larger NSC pool and more reduced growth than *Q. robur*. Wood~~ wood production and stem sapwood NSC concentration are expected to vary along the gradient, with reduced growth but increasing NSC storage under drier conditions. We also hypothesized that the more drought-tolerant *Q. pyrenaica* will have a more reduced xylem growth than *Q. robur*, but larger stem sapwood NSC concentrations. At the species level, we aim to test the following hypotheses: (i) ~~tree size~~stem diameter influences earlywood vessel size~~diameter~~, which in turn affects NSC content in the stem; (ii) higher sapwood SS content in winter predisposes trees to advance growth resumption in spring, as well as to~~thereby~~ ~~foster~~produce more~~ing~~ earlywood vessels~~production~~; and (iii) earlywood ~~anatomical features~~vessel number and size are ~~important~~key predictors of latewood growth in oaks.

2 Materials and methods

2.1 Study sites

~~The study area is located in NW Iberian Peninsula, at the transition between the Atlantic and Mediterranean biogeographical regions (Fig. 1a). Three mixed stands of *Q. robur* (hereafter *Qrob*) and *Q. pyrenaica* (hereafter *Qpyr*) were selected along a north to south gradient of decreasing water supply (Fig. 1B).~~ The study area is located in NW Iberian Peninsula, at the transition between the Atlantic and Mediterranean biogeographical regions (Fig. 1a). The experiment was conducted at three mixed stands of *Q. robur* (hereafter *Qrob*) and *Q. pyrenaica* (hereafter *Qpyr*) located along a north-to-south transect of 120 km, following a gradient of decreasing water supply (Fig. 1b). Annual rainfall declines from 1,461 mm at the northernmost site Bermui (hyperhumid), to 996 mm at Labio (humid), and to 832 mm at the southernmost site Moreiras (subhumid). Mean annual temperature is lower at the hyperhumid (11.3 ºC) and humid (11.6 ºC) sites than at the subhumid site (14.4 ºC). Sampled stands are dominated by *Qrob* at the hyperhumid and humid sites, whereas *Qpyr* is more frequent at the subhumid location. Forests at the hyperhumid and humid sites include temperate trees and understory shrubs, such as *Betula alba* L., *Castanea sativa* Mill., *Pyrus cordata* Desy., *Ilex aquifolium* L., *Daboecia cantabrica* (Huds.) K. Koch, and *Vaccinium myrtillus* L. By contrast, thermophilic Mediterranean flora, such as *Q. suber* L., *Laurus nobilis* L., *Arbutus unedo* L., *Osyris*

alba L., and *Daphne gnidium* L., dominates the subhumid location. Stand tree densities are 1,178, 1,082, and 530 ha⁻¹ at the hyperhumid, humid and subhumid sites, respectively. Drought episodes can ~~appear~~ occur at the study region in summer, particularly at the subhumid site ~~, which is the driest location within the gradient~~ (Fig. 1b). Incident rainfall in 2012 ~~at the hyperhumid, humid, and subhumid locations~~ was ~~respectively~~ 8, 14, and 33 % lower than the 1981–2010 average, respectively at the hyperhumid, humid, and subhumid locations~~lower than the 1981–2010 average~~, whereas it was 35, 36, and 3 % higher than the average in 2013 (Table 1). However, in summer 2013, there were only 34 (45 mm), 11 (20 mm), and 8 (35 mm) days of precipitation at the hyperhumid, humid and subhumid locations, respectively. Furthermore, mean maximum temperature ~~in the same period~~ was 22.0 ºC for the same period at the hyperhumid and humid sites, but 25.3 ºC at the subhumid location.

2.2 Phenology and NSC concentration

At each study site, 40 trees per species were randomly selected ~~for sampling (overall n = 240)~~ from those belonging to the dominant and intermediate crown classes (overall N = 240), while highly suppressed and juvenile individuals were disregarded.~~.~~ ~~Stem diameter was measured for each tree in~~ In October 2012, we measured stem diameter from all the selected individuals with a diameter tape, while tree height was estimated with a Blume–Leiss hypsometer. Leaf phenology was weekly monitored during 2013 using binoculars (10×) at *ca.* 10 m distance from ~~each tree~~the stem.~~.~~ For each tree, ~~b~~Budburst was identified as the day of year (DOY) in which the apical buds on the uppermost part of the ~~canopy~~ crown were green and expanding, but no leaves were distinguishable yet. We considered budburst to be an indicator for cambial resumption in the stem, according to the high correlations observed between these two events in our study sites (Pérez-de-Lis et al., 2016). In late autumn, leaf shedding was identified as the date in which at least 50% of the leaves were shed from the crown. In addition, foliage density was visually estimated in July 2013 by counting the proportion of gaps in the crown, being expressed as a percentage of the theoretical maximum foliage density.

In order to analyze feedbacks between NSC and xylem anatomy, we quantified the content of NSC in sapwood by sampling one 5-mm diameter wood core per tree with an increment borer at breast height. Cores were taken in mid-December 2012, soon after the completion of leaf abscission, which occurred between mid and late November for both species. After extraction, cores were immediately placed into a cool box, and subsequently stored at –20 ºC to prevent carbohydrate degradation. Before NSCs extraction, we identified the boundary between sapwood (pale-coloured) and heartwood (brown-coloured).~~Before NSCs extraction, bark~~ Bark and traces of heartwood were removed, and the cores were oven-dried at 60 ºC for 72 hours. Sapwood was then finely grounded with a mixer mill (Retsch MM 400, Düsseldorf, Germany). We quantified NSC concentration for the whole sapwood by using the anthrone method (Olano et al., 2006). SS were extracted from 20 mg of dry mass in 1 ~~ml~~ mL of ethanol (80%) at 80 ºC for 30 min. The extract was centrifuged 10 min at 4,000 rpm, and the supernatant was collected for the spectrophotometrical determination of SS concentrations, for which we used the anthrone reagent. Starch contained in the residue was hydrolized with 1 ~~ml~~ mL of perchloric acid (35%) for 1 hour, and determination was conducted by using the anthrone reagent, as previously described for SS. Total NSC, SS, and starch concentrations were expressed as percentage of dry matter.

2.3 Wood anatomical measurements

In October 2013, ~~One~~ one additional core ~~per tree~~ was collected from all the selected trees ~~in October 2013~~ to perform wood anatomical measurements. Cores were air-dried and mounted on wooden supports to be cut using a microtome (WSL Core Microtome, Zurich, CH) and polished. Cross-sectional surfaces were photographed with a digital camera (Canon EOS 600D, Tokyo, Japan), attached to a transmitted light microscope (Olympus BX40, Tokyo, Japan). Image analysis was applied on the rings formed in 2012 and 2013 using ImageJ 1.48v (Schneider et al., 2012), in order to quantify the lumen area of earlywood vessels, latewood width, and the number of earlywood vessels, which is a *proxy* of earlywood vessel production

(EVP). For each vessel, we estimated the diameter of the equivalent circle, obtaining the hydraulic diameter (D_h) at the tree level according to the following Eq.:

$$D_h = \frac{\sum_{n=1}^{N} d_n^5}{\sum_{n=1}^{N} d_n^4},$$

(1)

where d_n is the diameter of the n vessel (Sperry et al., 1994). According to the Hagen–Poiseuille equation, D_h is proportional to the hydraulic capacity.

2.4 Comparisons along the gradient

Variation among sites and between species for NSC, dates of budburst and leaf shedding, wood anatomical traits, and foliage density were evaluated by applying generalized linear models (GLM) for gamma-distributed variables. Multiple ~~pairwise Pairwise~~ ~~comparisons~~ Comparisons were also assessed to test differences among site factor levels. This analysis was performed by using the packages 'lme4' and 'multcomp' for R 3.1.1 (R Core Team, 2014). Moreover, we calculated the Pearson's correlation between stem diameter and tree height (two-tailed test of significance and 95% confidence interval).

2.5 Connections among earlywood anatomy, sapwood NSC content and spring phenology

We performed structural equation models (SEM) to disentangle ~~, at the species level,~~ the role of winter NSC as possible regulators of budburst and EVP in 2013 at the species level. Thereby, data from all ~~the~~ sites were pooled, and ~~a~~ a unique model was fit for each species. SEM approach provides an adequate representation for interacting systems, in which simultaneous influences and responses, including direct and indirect effects are explored (Grace, 2006). The structure of a hypothetical SEM, and its calculation, requires incorporating available *a priori* knowledge. According to the lines of evidence showed in the introduction, we hypothesized that ~~fast growing~~bigger trees ~~(larger stem diameter)~~ show higher SS and starch concentrations due to their larger D_h (~~Supplement,~~ Fig. 2~~S1~~). In turn, high SS and starch concentrations in winter are expected to speed up tree phenology (~~date of budburst~~budburst date) and boost EVP during the subsequent year.

Standardized coefficients were estimated by the maximum likelihood method, and model evaluation was performed using a χ^2 test. A *P*-value below 0.05 indicates that discrepancy between observed and expected covariance matrices is acceptable. The adjusted goodness of model fit index (AGFI), and the root mean square error of approximation (RMSEA) were complementarily performed in order to consider the effect of sample size on the model fit evaluation. Values of AGFI above 0.90 and RMSEA ~~respectively above 0.90 and~~ below 0.05 indicate an acceptable fit of the model in relation to the degrees of freedom. A χ^2 test for multi-group invariance was applied to evaluate differences between the models fitted for each species. SEM analyses were performed with AMOS 18.0 software (AMOS Development Corp., Mount Pleasant, South Carolina, USA).

2.6 Predictors of latewood formation

We performed generalized linear mixed-effects models (GLMM) to identify ~~which factors~~how earlywood anatomy, foliage density, phenology, and winter NSC levels affected latewood production in 2013~~at the species level~~. The effect of site was included as a random component, while winter NSCs, earlywood anatomy (D_h and EVP in 2013), growing season length, and foliage density were the explanatory variables of the model. Collinearity was surveyed by calculating the generalized variance-inflation factors for each species. GLMM models were fitted by a log-link function with a gamma distribution, being ranked according to the ~~second order~~corrected Akaike's Information Criterion (AICc) (Bolker et al., 2009). We averaged the 95% confidence set of models according to the Akaike weights, and the relative importance of a given variable was calculated as the sum of the Akaike weights across all the models in which it was contained (Burnham and Anderson, 2002). ~~We used the packages 'lme4' and 'MuMIn' for R 3.1.1 (R Core Team, 2014) to assess GLMMs.~~ Marginal (fixed effects only) and conditional R^2 (both fixed and random effects) were calculated by using the variance components of fixed

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and random factors and the residuals. The proportion change in variance (PCV) was quantified in order to provide the variability in latewood width explained by the full model (containing fixed and random effects), as compared to the null model (only containing the random component). Complementarily, we estimated the percentage of the variance explained by each fixed factor, and both full and null models were ranked according to the minimum AICc and Bayesian Information criterion (BIC) scores. Variance partitioning, R^2 and PCV calculations were performed by following the methods reported by Nakagawa and Schielzeth (2013). We used the packages 'lme4' and 'MuMIn' for R 3.1.1 (R Core Team, 2014) to assess GLMM model estimates, variance partitioning, and statistics.

3 Results

3.1 Variation in NSC, wood anatomy and leaf phenology along the gradient

Mean SS concentrations along the gradient ranged from 3.88 to 5.08 % dry matter in *Qrob*~~Mean SS concentrations at the sites ranged from 3.88 to 5.08 % dry matter in *Qrob*~~, and from 4.06 to 5.57 % dry matter in *Qpyr* ~~(Fig. 2)~~, being similar to those of starch, which ranged from 4.28 to 5.11 % dry matter in *Qrob*, and from 3.47 to 5.11 % in *Qpyr* (Fig. ~~2~~3). As a result, *Qpyr* exhibited ~~therefore~~ greater SS ~~content~~ concentrations than *Qrob* ($F_{[1, 238]}$ = 18.27, $P < 0.001$), while both starch and NSC ~~concentration~~ levels did not differ between species ~~, although were marginally significant for NSC~~ (starch $F_{[1, 238]\text{starch}}$ = 2.14, NSC $F_{[1, 238]\text{NSC}}$ = 0.62, $P > 0.050$). Such pattern resulted in a higher SS-to-starch ratio for *Qpyr* than for *Qrob* (F = 18.07, $P < 0.001$), especially at the ~~hyperhumid and~~ humid location~~s~~ (Fig. ~~2~~3), ~~whereas~~ although there was no variation along the gradient (F = 0.21, $P = 0.814$). In contrast, ~~NSC substantially varied among locations (F = 22.34, $P < 0.001$),~~ SS content decreased in both species ~~with decreasing concentrations~~ from the subhumid to the hyperhumid sites ~~(Fig. 2). SS content followed a similar geographical pattern, in both *Qrob*~~ (*Qrob* $F_{[2, 117]}$ = 17.72, *Qpyr* $F_{[2, 117]}$ = 21.89, $P < 0.001$) ~~and *Qpyr* (F = 21.89, $P < 0.001$)~~. The subhumid site exhibited a higher starch content than the hyperhumid location for *Qpyr* ($F_{[2, 117]}$ = 8.59, $P < 0.001$), whereas no clear ~~geographical~~ pattern was found for *Qrob* ($F_{[2, 117]}$ = 2.52, $P = 0.085$).

Overall, *Qpyr* exhibited a higher D_h than *Qrob* (~~2012~~ $F_{\text{2012}[1, 236]}$ = 7.76, ~~2013~~ $F_{[1, 236]\text{2013}}$ = 8.31, $P < 0.010$) (Fig. 4a). ~~Yet, *Qrob* had larger EVP (F = 30.28, $P < 0.001$) and wider latewood (F = 51.15, $P < 0.001$) than *Qpyr* (Fig. 3a, b).~~ The highest D_h values were found for *Qpyr* at the humid (both years) and subhumid sites (2012), while *Qrob* had a more reduced variation along the gradient ~~In *Qpyr*, D_h was substantially lower at the hyperhumid site in 2012 (F = 7.67, $P < 0.001$) and 2013 (F = 3.72, $P = 0.027$), whereas much less variation was found among sites for *Qrob*~~ (~~2012~~ $F_{[2, 117]\text{2012}}$ = 2.89, ~~2013~~ $F_{[2, 117]\text{2013}}$ = 0.18, $P > 0.050$) (Fig. 4b). EVP and latewood width were higher in *Qrob* than in *Qpyr* at the hyperhumid and subhumid sites, whereas differences were non-significant at the humid location (Fig. 4c, d). Trees at the subhumid site exhibited wider latewood (both species) and higher EVP (*Qrob*) than those at the hyperhumid location (Fig. 4c, d). ~~EVP and latewood width differed along the gradient (F_EVP = 8.45, F_LW = 12.50, $P < 0.001$), with the lowest values at the hyperhumid site (Fig. 3c, d). Conversely, the highest EVP and latewood width values occurred at the subhumid site for *Qrob*, and at the humid site for *Qpyr* (Fig. 3c, d).~~

~~Stem diameter was positively correlated with tree height in *Qrob* (r = 0.60, $P < 0.001$) and *Qpyr* (r = 0.58, $P < 0.001$). At the hyperhumid site,~~ *Qrob* had a larger stem diameter ~~was larger for *Qrob*~~ than ~~for~~ *Qpyr* at the hyperhumid site ~~(Z = 3.29, $P = 0.012$)~~, whereas ~~the studied species showed~~ similar values were found at the humid and subhumid locations (Fig. ~~4a~~5a). Stem diameter was positively correlated with tree height in *Qrob* ($r_{[118]}$ = 0.60, $P < 0.001$) and *Qpyr* ($r_{[118]}$ = 0.58, $P < 0.001$). Trees of both species were taller at the hyperhumid and subhumid sites than at the humid location (*Qrob* $F_{[2, 117]}$ = 22.85, *Qpyr* $F_{[2, 117]}$ = 29.46, $P < 0.001$). ~~Trees at the subhumid site had a larger stem diameter than at the humid (*Qrob* Z = 5.08, *Qpyr* Z = 7.58, $P < 0.001$) and hyperhumid locations (*Qrob* Z = 2.67, $P = 0.021$; *Qpyr* Z = 7.13, $P < 0.001$). *Qpyr*~~ *Qrob* exhibited a~~n~~ earlier ~~later~~ budburst than ~~*Qrob*~~ *Qpyr* ($F_{[1, 236]}$ = 527.83, $P < 0.001$), occurring from early ~~mid to late April~~March to late April for the former, and from mid April to late May for the latter ~~at the subhumid site, and from late April to late May at the hyperhumid and humid locations (Fig. 4b)~~. In both species, budburst occurred earlier at the

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subhumid site than at humid and hyperhumid locations (Fig. 5b)~~Budburst occurred synchronously at the hyperhumid and humid sites ($Qrob$ $t = 1.92$, $Qpyr$ $t = 0.54$, $P > 0.05$), but comparatively earlier ($Qrob$ $F = 128.45$, $Qpyr$ $F = 79.49$, $P < 0.001$) at the subhumid location (Fig. 4b). Trees showing an earlier budburst had a delayed senescence ($Qrob$ $r = 0.36$, $Qpyr$ $r = 0.68$, $P < 0.001$).~~ By contrast, l~~L~~eaf shedding was first recorded at the hyperhumid and humid sites for $Qpyr$ (DOY 312 on average) (Fig. 5c), whereas some green leaves could be perceived until late December at the subhumid site ($Qrob$ DOY 357, $Qpyr$ DOY 354~~; Fig. 4c~~). The leaf period ~~from budburst to leaf shedding in 2013~~ was on average 42 days longer for $Qrob$ than for $Qpyr$ ($F_{[1, 236]} = 450.90$, $P < 0.001$) in 2013. Foliage density was similar along the gradient for $Qrob$, but significantly lower at ~~ALT~~ the hyperhumid site for $Qpyr$ (Fig. 4d5d). It is also relevant to consider that numerous $Qpyr$ trees at this latter location had their leaves infected with powdery mildew in spring 2013.

3.2 Species-specific models on functional relationships affecting wood production

SEM models showed a good fit for both species (~~$df = 1$;~~ $Qrob$, $\chi^2_{[1, N=120]} = 0.202$, $P = 0.653$; $Qpyr$, $\chi^2_{[1, N=120]} = 0.118$, $P = 0.732$), with AGFI > 0.90 and RMSEA < 0.1 (Fig. 5a6a, b). Stem diameter~~Large trees exhibited a higher D_h in 2012, having~~ had a positive indirect effect on SS levels that was mediated by D_h in 2012~~, irrespective of the species~~. Large trees exhibited an earlier budburst date, which was partially related to their higher SS concentrations in winter. ~~In $Qrob$, SS concentration in December showed positive covariation with starch content in both species (Fig. 5). High SS contents were associated to advanced budburst, whereas starch concentration and date of budburst were unrelated. In Qpyr, SS concentrations had a positive direct effect in EVP. By contrast, this relationship was not direct, but~~SS content indirectly affected EVP through budburst date ~~mediated by SS effect on budburst date in $Qrob$ (Fig. 5)~~, although our model explained a low amount of the observed variability in EVP (Fig. 6a). ~~The proportion of variance explained by SEM models was lower for D_h than for budburst date. Similarly, R^2 scores for EVP substantially differed between species, with values of 0.06 and 0.20 in $Qrob$ and $Qpyr$, respectively (Fig. 5a, b).~~ In $Qpyr$, SS concentrations had a positive direct effect in EVP, with an acceptable R^2 value for EVP ($R^2 = 0.20$) (Fig. 6b). Neither EVP nor budburst date responded to winter starch concentration, although our model failed to account for the observed variability in the latter variable.

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Our GLMM model had a sufficiently good performance ($R^2_{[conditional]} > 36$ %). The fixed factors explained most of the variability in latewood width ($Qrob$ $R^2_{[marginal]} > 34$ %), while considerably high PCV values confirmed the better fit of the full model with respect to the null one. A similar result was obtained after ranking the models according to their AICc, log likelihood and BIC scores (Table 2). Larger and more numerous earlywood vessels strongly favoured latewood production (Table 2). In fact, EVP and D_h ~~of the current year had a strong positive influence on subsequent latewood growth in both species~~were the most relevant predictors, attaining a relative influence above 85 % (Fig. 67). However, EVP accounted for a 69 (83) % of the variability in latewood width predicted by the fixed part of the model~~.~~ for $Qpyr$ ($Qrob$), whereas D_h only explained a 8–16 % (Table 2). V~~A second group of v~~ariables ~~included in the models was~~ related to tree vigour were less relevant~~,~~ such as ~~such as~~ foliage density~~, with a positive effect and a relative importance (of~~ 40–60 %~~);~~ and length of the growing season ~~, with a stronger influence for $Qrob$~~ (31–40 %), with no significant effects on latewood width (Table 2) ~~than for $Qpyr$ (31 %). As expected, a higher foliage density together with a longer growing season predicted a larger latewood growth.~~ Winter NSC only accounted for a marginal weight in both species, having ~~however~~ a negative ~~impact~~slope ~~on latewood growth for~~for $Qrob$, ~~whereas~~but positive ~~for~~for $Qpyr$ (Table 2, Fig. 67). Problems of collinearity were not detected among the predictors included in the model (Supplement, Table S1).~~Problems of collinearity were not detected among the predictors included in the model (Supplement, Table S1).~~

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4 Discussion

4.1 NSC allocation to xylem growth reflects contrasting stress-tolerance strategies in oaks

According to our expectations, sapwood SS content decreased from the subhumid to the hyperhumid site for both species, and starch content followed a similar pattern in *Qpyr*. More immediate effects of water shortage on stem growth than on photosynthesis likely favoured carbohydrate accumulation in the previous summer (Sala et al., 2012; Lempereur et al., 2015; DeSoto et al., 2016). Such a response would be adaptive in dry environments because sugars contribute to prevent desicattion through osmotic regulation and cavitation repair (Salleo et al., 2009; Brodersen and McElrone, 2013; Pantin et al., 2013; Deslauriers et al., 2014). The fact that *Qpyr* showed larger vessels at the humid and subhumid locations cannot be explained by corresponding differences in tree height, whereby long-distance water transport was probably prompted under drier conditions, which concurrently increased the risk of vessel dysfunction (Urli et al., 2015). Although the prevalence of vessel refilling is still under discussion (Delzon and Cochard, 2014), we hypothesize that enhanced SS concentration might be involved in compensating hydraulic vulnerability in this species.

Wood formation declined along with NSC content from the subhumid toward the hyperhumid site, which contradicts our expectations, as well as a possible trade-off between NSC accumulation and growth. A shorter growing season at the hyperhumid and humid locations could restrict photosynthesis (Morecroft et al., 2003), as well as xylem formation (Rathgeber et al., 2011). Complementarily, a lower tree density at the subhumid site might be associated to a reduced inter-tree competition, which is assumed to favour both carbon uptake and xylem growth (Fernández-de-Uña et al., 2016). However, strong differences between the two Atlantic sites in *Qpyr* cannot be accounted for their similar tree density. Alternatively, soil water excess in winter at the hyperhumid site could exacerbate carbon consumption associated to fermentation processes and root anaerobic stress (Ferner et al., 2012). Moreover, *Qpyr* trees exhibited sparser foliage and more severe powdery mildew infestation at this latter site, which may reduce NSC levels and growth (Améglio et al., 2001; Martínez-Vilalta, 2014; Camarero et al., 2016). Indeed, growth decline and tree dieback were recently reported for oaks suffering from both high competition levels and water excess after extremely rainy periods (Rozas and García-González, 2012).

~~the~~ The sub-Mediterranean *Qpyr* exhibited a higher SS-to-starch ratio at the onset of dormancy than the temperate *Qrob*, even although NSC content was similar in both species. Sugars play a key role in the osmotic protection against freezing damage (Améglio et al., 2004), whereby higher symplastic SS concentrations would reflect stronger cold tolerance (Morin et al., 2007), as is the case for *Qpyr*. ~~Sugars are involved in the osmotic protection against freezing damage (Améglio et al., 2004), whereby cold acclimation requires the accumulation of high symplastic SS concentration in winter (Morin et al., 2007). This process is influenced by the timing of leaf shedding, which occurred earlier for *Qpyr* than for *Qrob*, reflecting the stronger cold tolerance of the former species. Additionally, SS content is maintained over a certain threshold to mitigate detrimental effects of eventual extreme events in long-lived trees (Sala et al., 2012). This may be of high relevance in the Mediterranean area, where fire and drought induced defoliation are frequent (Rosas et al., 2013; Camarero et al., 2015). Under drought, sugars contribute to prevent desicattion through osmotic regulation and cavitation repair (Salleo et al., 2009; Brodersen and McElrone, 2013; Pantin et al., 2013; Deslauriers et al., 2014), although the prevalence of vessel refilling is still under discussion (Delzon and Cochard, 2014). In this regard, it is noteworthy that *Qpyr* exhibited larger vessels at the humid and subhumid locations, being even larger than those of *Qrob*. Trade-offs between efficiency and safety thus suggest that *Qpyr* prompted long-distance water transport under drier conditions, but concurrently increased the risk of vessel dysfunction (Sperry et al., 1994). One posible explanation is that enhanced SS concentration might be involved in compensating hydraulic vulnerability in this species, although further research on SS fractioning and longer records of vessel size mesurements may be required to confirm such hypothesis.~~ On the other hand, EVP and latewood width were generally lower for *Qpyr* than for *Qrob*, particularly under more Mediterranean climatic conditions. This contradictory outcome

suggests that *Qpyr* is more conservative than *Qrob* in allocating NSC to wood production, hence reflecting a stronger drought tolerance (Valladares et al., 2000; Piper, 2011). Saving NSC may allow long-lived trees to mitigate detrimental effects of eventual wildfire and drought episodes (Sala et al., 2012), which are frequent at the Mediterranean area (Rosas et al., 2013; Camarero et al., 2016). However, such strategy might entail a high opportunity cost under favourable conditions (Chapin et al., 1990). Therefore, *Qrob* probably outcompeted *Qpyr* in our study sites, demonstrating that temperate oaks are more competitive than sub-Mediterranean ones (Rodríguez-Calcerrada et al., 2008; Grossiord et al., 2014). But validation of these hypotheses would require further research quantifying the whole-tree NSC pool size and the activity of complementary carbon sinks. In this regard, a recent study evidenced that neighbouring *Qpyr* trees are able to share NSC through the root system, which is an important carbon reservoir within the tree (Salomon et al., 2016).

~~This result supports that storage is an actively competing sink, rather than a passive compartment (Dietze et al., 2014).~~Deslauriers et al. (2014) attributed drought-induced growth decline in black spruce to the increasing demand of NSC for osmotic purposes, together with dehydration effects on cell turgor.

~~Wood formation declined along with NSC from the subhumid toward the hyperhumid site, which is opposed to our expectations. A lower tree density at the subhumid than at the Atlantic sites probably favoured carbon uptake and growth due to more reduced inter-tree competition (Fernández de Uña et al., 2016). Nevertheless, strong differences between the two Atlantic sites in *Qpyr* might be attributed to contrasting moisture, instead to the similar tree density. Indeed, *Qpyr* trees exhibited sparser foliage and more severe powdery mildew infestation at the hyperhumid site, which may reduce carbon uptake and growth (Améglio et al., 2001, Martínez Vilalta, 2014, Camarero et al., 2015). On the other hand, soil water excess in winter could exacerbate carbon consumption associated to fermentation processes and root anaerobic stress (Ferner et al., 2012). Furthermore, the growing season was shorter at the hyperhumid and humid locations, probably restricting the carbon gain (Morecroft et al., 2003), as well as xylem formation (Rathgeber et al., 2011). Interestingly, growth decline and tree dieback were recently reported in oaks suffering from both high competition levels and water excess after extremely rainy periods (Rozas and García González, 2012). In contrast, more immediate effects of water shortage on stem growth than on photosynthesis likely favour carbohydrate accumulation in summer (Sala et al., 2012, Lempereur et al., 2015). This idea is further supported by the higher SS concentrations reported at the subhumid site, which also exhibited higher starch content for *Qpyr*.~~

~~EVP and latewood width were generally lower for *Qpyr* than for *Qrob*, but such differences were striking at the subhumid site in spite of the more Mediterranean climatic conditions. This apparently contradictory result supports that *Qpyr* is more conservative than *Qrob* in allocating NSC to wood production. This is also consistent with results from Rodríguez Calcerrada et al. (2008), who suggested that temperate oaks are more competitive than sub-Mediterranean ones. Hence, the carbon saving strategy here suggested for *Qpyr* could entail a high opportunity cost in favourable environments (Chapin et al., 1990), where coexisting *Qrob* probably outcompetes *Qpyr*. In this regard, Grossiord et al. (2014) reported that temperate sessile oaks exerted a negative effect on coexisting Turkey oaks, which experienced a reduction of their transpiration fluxes as a result of increasing water stress.~~

4.2 Dependencies among NSC, phenology, and earlywood vessels

Our SEM model confirmed the hypothesized functional relationships among earlywood anatomy, spring phenology,~~,~~ and NSC ~~content, and date of budburst~~. The growing season started earlier in large trees, which is in line with previous studies analyzing cambial activity (Rathgeber et al., 2011). Stem diameter~~Tree size~~ also had a positive ~~direct~~ effect on ~~on the~~ ~~hydraulic capacity (i.e. larger vessels), and~~ SS content at dormancy, which was mediated by the hydraulic capacity (i.e. vessel size). ~~Wider vessels would be formed at the tree base of large trees to counteract the increasing hydraulic resistance with height (Petit et al., 2008). This was corroborated by the significant correlation between stem diameter and tree height in~~

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both studied species. Enhanced water transport capacity in trees owing large vessels Vessels of large diameter may boost carbohydrate uptake under a high evaporative demand (Meinzer et al., 2005; Fichot et al., 2009), which is a consequence of the enhanced water transport capacity (Meinzer et al., 2005). Alternatively, since large vessels are thought to be more vulnerable to cavitation (Sperry et al., 1994), higher SS concentrations may be required in the sapwood of trees bearing wider vessels to maintain long-distance water transport (Brodersen and McElrone, 2013).

Trees having a higher SS concentration in the stem showed earlier budburst the following spring, as reported in poplar (Park et al., 2009). BThis is related to the fact that ud swelling depends on carbohydrate sugar influx from sapwood vessels may promote bud development (Maurel et al., 2004; Bonhomme et al., 2010), which have been suggested to be responsible for carbohydrate transport during the dormant period (Lacointe et al., 2004). In this regard, Lacointe et al. (2004) suggested that carbon transport during the dormant period relies on xylem vessels. In addition, xylem sap osmolarity plays a role in the generation of the stem pressure , which is needed to reverse winter embolisms in early spring (Améglio et al., 2001). A rIt is noteworthy that vessels of previous years may be responsible for carrying water over quiescence because first formed earlywood vessels are not functional at least until budburst (Pérez de Lis et al., 2016). Thereby, reduced ability to repair winter embolism in trees with low xylem sap SS concentration could thus affect negatively the supply of water to swelling buds in those trees showing lower SS content in the xylem sap (Améglio et al., 2001).

In Qrob, the observed positive effect of SS concentration on EVP was mediated by the timing of budburst. The observation that budburst coincides with the onset of vessel maturation in the stem suggests that early-flushing trees had an advanced onset of earlywood formation (Pérez de Lis et al., 2016). Therefore, larger EVP in early-flushing trees could result from the longer period of earlywood formation, which is underpinned by that greater EVP values measured at the location with earlier budburst. Yet, the impact of SS concentration on EVP was more pronounced for Qpyr, as demonstrated the fact that EVP was in tune with SS concentration for Qpyr, whereas this effect was irrelevant for Qrob. Feedbacks between SS content and EVP differed between species, which may be attributed to their contrasting stress tolerance (Guillemot et al., 2015). Such discrepancy in the effect of stored carbohydrates on growth is consistent with the aforesaid carbon use strategies, and could reflect the contrasting stress tolerance of the study species (Guillemot et al., 2015). Our results thus suggest that Qpyr was able to limit construction costs in spring according to SS levels. Presumably, high overwintering sugar SS levels in sapwood somehow increased energy and materials as well as water supplied to growing tissues in spring, even though starch mobilization may be initiated at that time (Améglio et al., 2001). Furthermore, sugars are elicitors of auxin biosynthesis and distribution (Lilley et al., 2012; Sairanen et al., 2012), as well as growth promoters (Stewart et al., 2011). Although relations between carbon allocation to storageaccumulation and growth are complex, and mainly related to the activity of carbon sinks (Lempereur et al., 2015), a growing body of literature suggests that NSC availability is involved in growth regulation (Pantin et al., 2013; Dietze et al., 2014; Guillemot et al., 2015). This might be particularly true for earlywood given its reliance on stored carbohydrates winter NSC reserves (Skomarkova et al., 2006). This idea agrees with the direct association between tree vigour, NSC pool, and growth found in multiple species (Sundberg et al., 1993; Deslauriers et al., 2009; Carbone et al., 2013), but also with the observed positive effect of CO_2 fertilization on tree growth (Nissinen et al., 2016). EVP did not respond to sapwood starch content, which hints that In Qrob, the observed positive effect of SS concentration on EVP was mediated by the timing of budburst.

thermal-induced changes in starch breakdown during cold hardening could be more decisive than total amount of reserves. This is consistent with the connection between earlywood anatomy and autumn-winter temperature reported by dendrochronological studies (Gea-Izquierdo et al., 2012). However, the actual starch availability could be overestimated if starch contained in sapwood is partially inaccessible (Sala et al., 2012). Feedbacks between SS content and EVP differed between species, which may be attributed to their contrasting stress tolerance (Guillemot et al., 2015). Our results therefore suggest that the more drought-resistant Qpyr limits construction costs under favourable conditions in spring if NSC levels decrease, which conveys its more conservative carbon use strategy. This result supports that storage is an actively

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~~competing sink, rather than a passive compartment (Dietze et al., 2014). Deslauriers et al. (2014) attributed drought-induced growth decline in black spruce to the increasing demand of NSC for osmotic purposes, together with dehydration effects on cell turgor. In the same line, Anderegg et al. (2013) suggested that reduced carbon uptake under drought can impair growth in subsequent years. Yet, we noted increasing NSC concentrations and higher EVP under drier conditions, whilst sapwood starch concentrations scarcely affected growth. EVP was probably affected by the starch breakdown rate at the onset of dormancy, rather than by drought-induced changes in the reserve pool the previous summer. Our results hint that earlywood vessel anatomy and winter temperature connections reported by dendrochronological studies (Gea-Izquierdo et al., 2012) could be attributed to thermal-induced changes in carbon partitioning during cold hardening (Améglio et al., 2004; Morin et al., 2007). However, not all the starch that is contained in sapwood is readily accessible (Sala et al., 2012). Thereby, the assessment of mean starch concentrations in sapwood probably failed to reflect their actual availability.~~

4.3 Earlywood anatomy is a predictor of latewood growth

The most influential predictors driving latewood growth did not differ between *Qrob* and *Qpyr*, suggesting common underlying mechanisms for both species. Latewood width was considerably influenced by earlywood properties within the same tree ring, ~~and, to a lesser extent, by~~ whereas the effects of foliage density, length of the growing season, and winter NSC content were secondary ~~and phenology~~. This result confirms the positive impact of enhanced water transport capacity on xylem formation (Fichot et al., 2009), which is largely related to both conduit size (Sperry et al., 1994), and total conductive area (Meinzer et al., 2005). A more efficient water supply to growing tissues probably allows trees to protect cambial activity against water shortage in summer (Wang and Ruan, 2013). ~~This confirms the positive impact of enhanced water transport capacity on xylem growth (Fichot et al., 2009), which is largely related to both conduit size (Sperry et al., 1994), and total conductive area (Meinzer et al., 2005).This confirms the positive impact of enhanced water transport capacity on xylem growth (Fichot et al., 2009), which is largely related to both conduit size (Sperry et al., 1994), and total conductive area (Meinzer et al., 2005).~~ Despite the higher construction costs, abundant earlywood vessels of distinct size could be useful to ~~mitigate~~avoid hydraulic failure ~~the physiological effects of drought,~~ because ~~still~~ functioning small conduits would serve as local water reservoirs to recover neighbouring collapsed ones (Brodersen and McElrone, 2013). Moreover, an~~This is consistent with the higher EVP observed in Qrob at the subhumid site. In addition, an~~ efficient hydraulic network may enhance~~enable~~ carbon gain ~~to be maximized~~ under favourable conditions (Fichot et al., 2009), hence ~~protecting~~ensuring key processes in which sugars are involved, such as osmotic regulation (Sala et al., 2012; Deslauriers et al., 2014) and embolism repair (Salleo et al., 2009). Our results suggested that changes in cell division and differentiation rates are more relevant for wood production than the duration of the growing period, as it was previously reported for conifers (Rathgeber et al., 2011).

~~Latewood growth was also higher in trees exhibiting high foliage density,~~ Although defoliation ~~which is consistent with the~~is assumed to impair ~~reduced~~ carbon ~~reserves~~gain and radial growth ~~found in defoliated trees for evergreen oaks~~in evergreen (Rosas et al., 2013; Camarero et al., 201~~5~~6) and deciduous species (Améglio et al., 2001)~~(Rosas et al., 2013; Camarero et al., 2015)~~, we found that foliage density had ~~, or walnut trees (Améglio et al., 2001). The lower importance of this factor~~a minor effect on latewood growth, which ~~could~~may ~~also be related to~~reflect the high overall foliage density levels at the study sites.

~~Trees having earlier budburst showed delayed leaf shedding and thus longer growing season, as found in previous studies on cambial activity (Deslauriers et al., 2009; Rathgeber et al., 2011). Duration of the growing season had limited influence on latewood width, suggesting that cambial activity rates were more influential on xylem production than phenology (Deslauriers et al., 2009; Rathgeber et al., 2011).~~

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5 Conclusions

In this study, non-structural carbohydrates in sapwood, wood anatomy, and leaf phenology were comprehensively addressed in two ring-porous species during one year, along a broad geographical range in NW Iberian Peninsula. Our results reveal that feedbacks between earlywood vessels and soluble sugars involve changes in wood production. Earlywood vessel formation in *Q. pyrenaica* showed a tighter control by soluble sugar content than in *Q. robur*, suggesting a more conservative carbon use strategy in the former species. These lines of evidence support that non-structural carbohydrates play a role in the acquisition of resistance to cope with harsh environmental conditions in the sub-Mediterranean area. ~~This study~~It is a first attempt to unravel the interactions between non-structural carbohydrates, wood anatomy, and phenology in ring-porous oaks. We acknowledge the need for further research comprising a longer time span, soluble sugar fractioning, additional tree compartments such as branches and roots, and a comprehensive dataset on cambial phenology instead of isolated leaf phenophases. However, this study hints the existence of stable functional interactions between sapwood carbohydrate levels, xylem anatomy, and phenology in ring-porous oaks. In the light of ~~these~~ our results, we suggest that *Q. pyrenaica*, and to a lesser extent *Q. robur*, ~~might~~ could mitigate increasing hydraulic vulnerability under climate warming by prioritizing carbon accumulation over growth. Nevertheless, such mechanism would impose additional limitations for secondary growth if adverse climate episodes become more frequent in future decades.

Author contribution IGG, JMO, VR conceived and designed the experiment. IGG, VR, GP conducted fieldwork. GP performed sample processing and data collection. JMO and GP executed model calculation. GP prepared the manuscript. IGG, JMO, VR provided editorial advice.

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Table 1. Climatic information of the study sites in 2012 and 2013.

Site	P (mm)	Rainy days	Tm (ºC)	Tmax (ºC)	Tmin (ºC)
2012					
Hyperhumid	1346.8	210	11.7	16.4	7.8
Humid	858.3	169	10.4	14.9	7.1
Subhumid	555.0	172	12.4	16.8	8.5
2013					
Hyperhumid	1979.0	225	11.6	15.8	8.0
Humid	1351.6	190	10.2	14.2	7.2
Subhumid	856.3	168	12.3	16.4	8.8

P, mean precipitation; *Tm*, mean temperature; *Tmax*, mean maximum temperature; *Tmin*, mean minimum temperature.

Table 2. Statistics of the null and full generalized linear models for *Quercus robur* (left) and *Q.pyrenaica* (right).

	Q. robur (N = 120)			*Q. pyrenaica* (N = 120)		
	Null Model	Full Model	PVE (%)	Null Model	Full Model	PVE (%)
Fixed effects						
Intercept	7.209***	4.348***		6.404***	2.696**	
GS_{13}		0.003	4.84		0.003	5.22
NSC_{12}		−0.022	1.06		0.003	5.81
D_{h13}		0.004*	8.26		0.005**	16.64
EVP_{13}		0.050***	83.37		0.092***	69.03
FD_{13}		0.006	2.47		0.008	3.31
Variance components						
Site	0.033	0.013		0.183	0.060	
Residuals	0.380	0.332		0.829	0.605	
Fixed effects		0.181			0.363	
$PCV_{[Site]}$		83.79 %			89.18 %	
$PCV_{[Residuals]}$		26.81 %			28.30 %	
$R^2_{GLMM\,(m)}$		34.42 %			35.28 %	
$R^2_{GLMM\,(c)}$		36.95 %			41.14 %	
− log likelihood	968.20	946.44		889.84	865.13	
AIC	1942.41	1908.89		1785.67	1746.25	
AICc	1942.62	1910.19		1785.88	1747.55	
BIC	1950.77	1931.19		1794.03	1768.55	

N, sample size for each species; PVE, relative proportion of variance explained by each fixed factor; NSC_{12}, total non-structural carbohydrates in December 2012; D_{h13}, hydraulic diameter in 2013; EVP_{13}, earlywood vessel production in 2013; GS_{13}, length of the growing season in 2013 and FD_{13}, foliage density in 2013; PCV, proportion change in variance; $R^2_{GLMM\,(m)}$, marginal coefficient of determination; $R^2_{GLMM\,(c)}$, conditional coefficient of determination; AIC, Akaike's information criterion; AICc, corrected Akaike's information criterion; BIC, Sawa Bayesian information criterion; ***, $P \leq 0.001$; **; $P \leq 0.01$; *, $P \leq 0.05$.
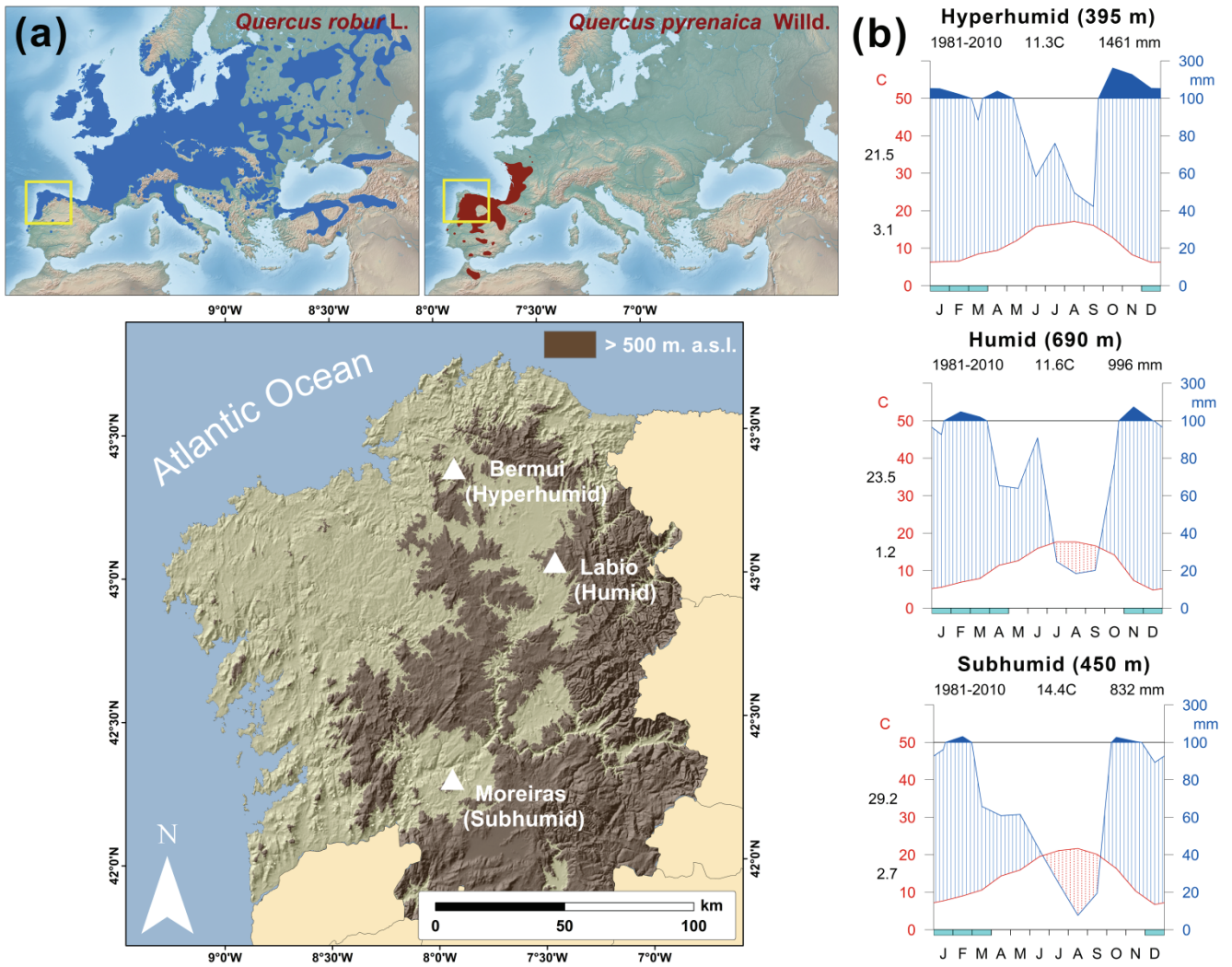
Figure 1: (a) Location of the study sites in NW Iberian Peninsula and distribution range of *Quercus robur* and ~~*Quercus*~~ *Q. pyrenaica* (base map: http://www.euforgen.org). **(b)** Climatic diagrams of the sites including site altitude in m a.s.l, mean annual temperature, and total annual precipitation for the specified period.
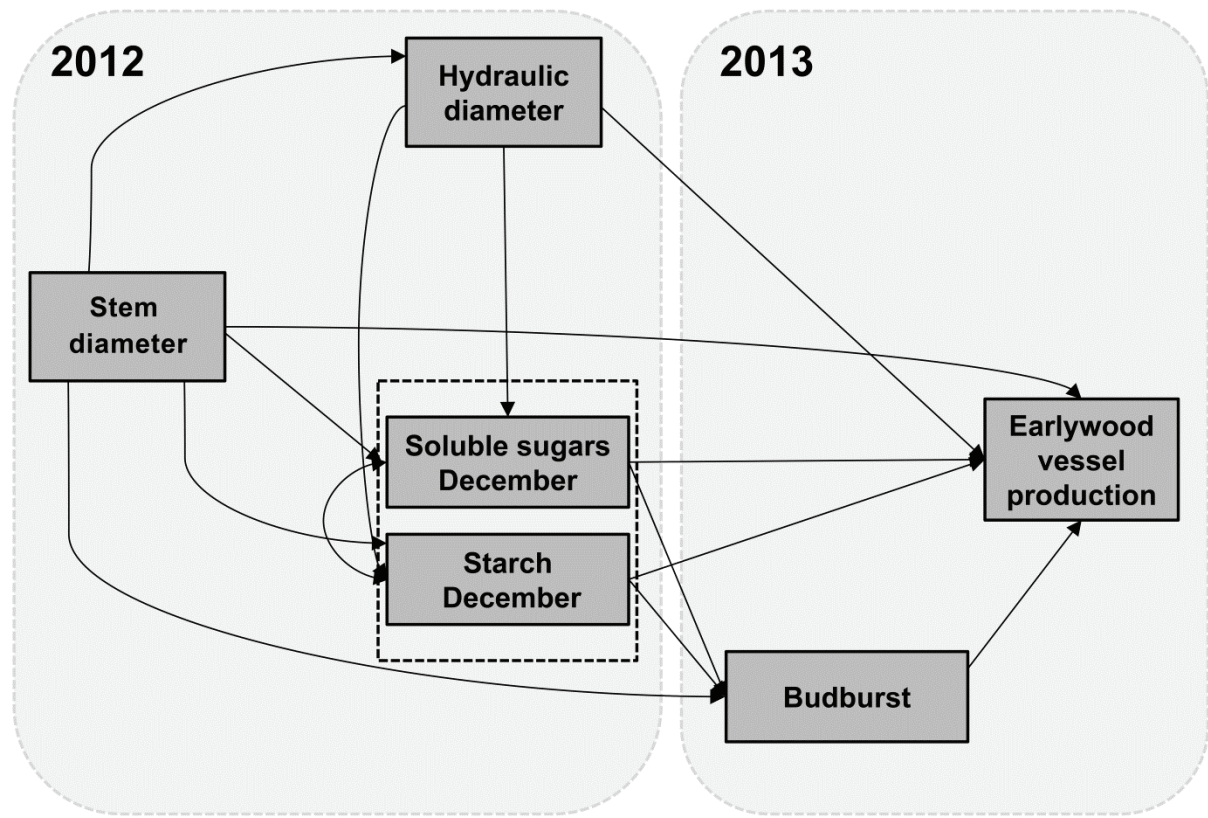
Figure 2: Structure of the hypothetical conceptual model showing interactions among stem diameter, hydraulic diameter in 2012, soluble sugars and starch concentrations in December 2012, and budburst date and earlywood vessel production in 2013.
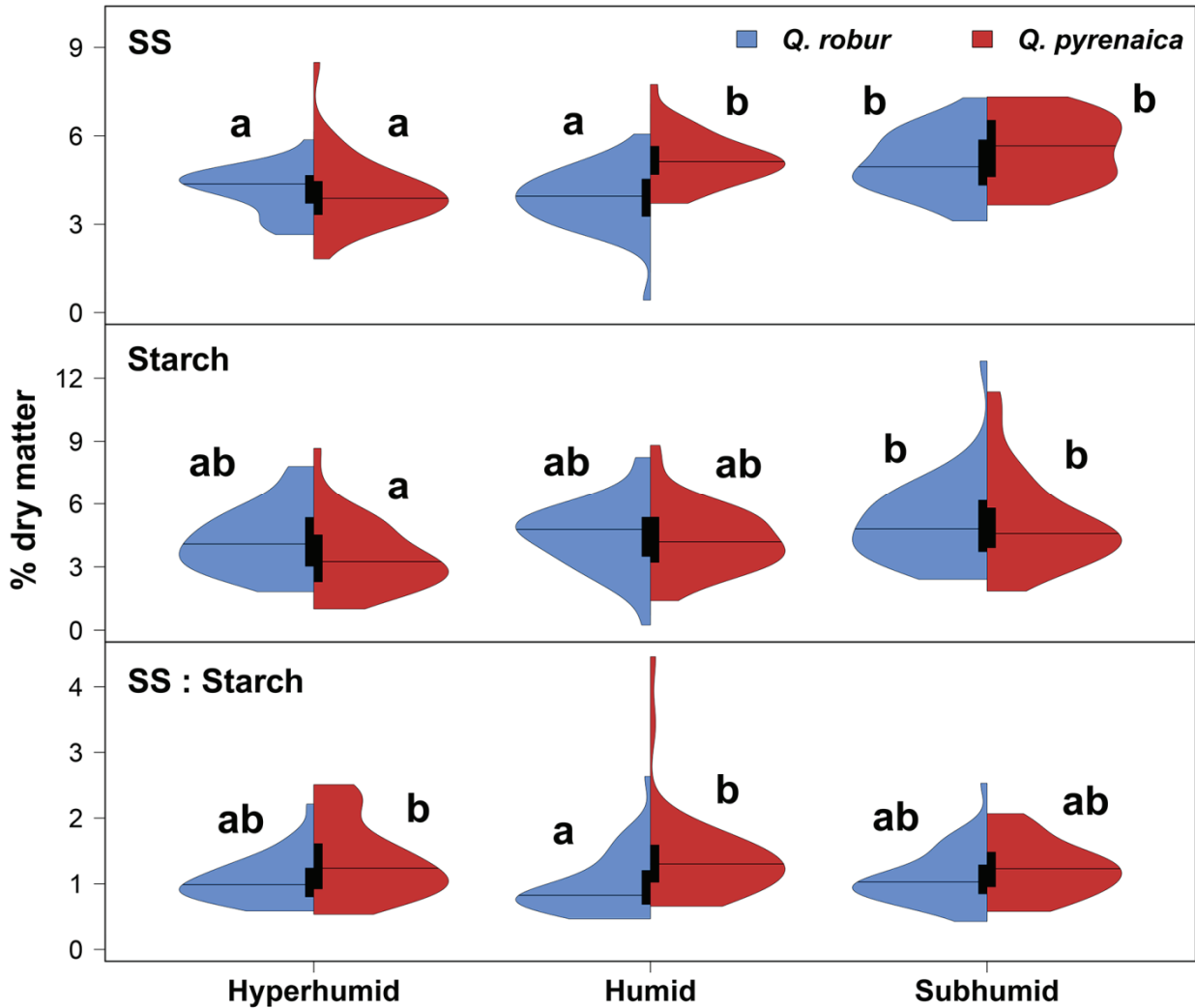
Figure 23: Distribution of soluble sugars (SS), starch concentrations, and SS-to-starch ratio, for *Quercus robur* (*N* = 120) and *Q. pyrenaica* (*N* = 120) at the three study sites. Horizontal lines represent the median, and black boxplots show the extent of 25th and 75th percentiles. Lower case letters indicate statistically significant differences along the gradient according to multiple pairwise comparisons.
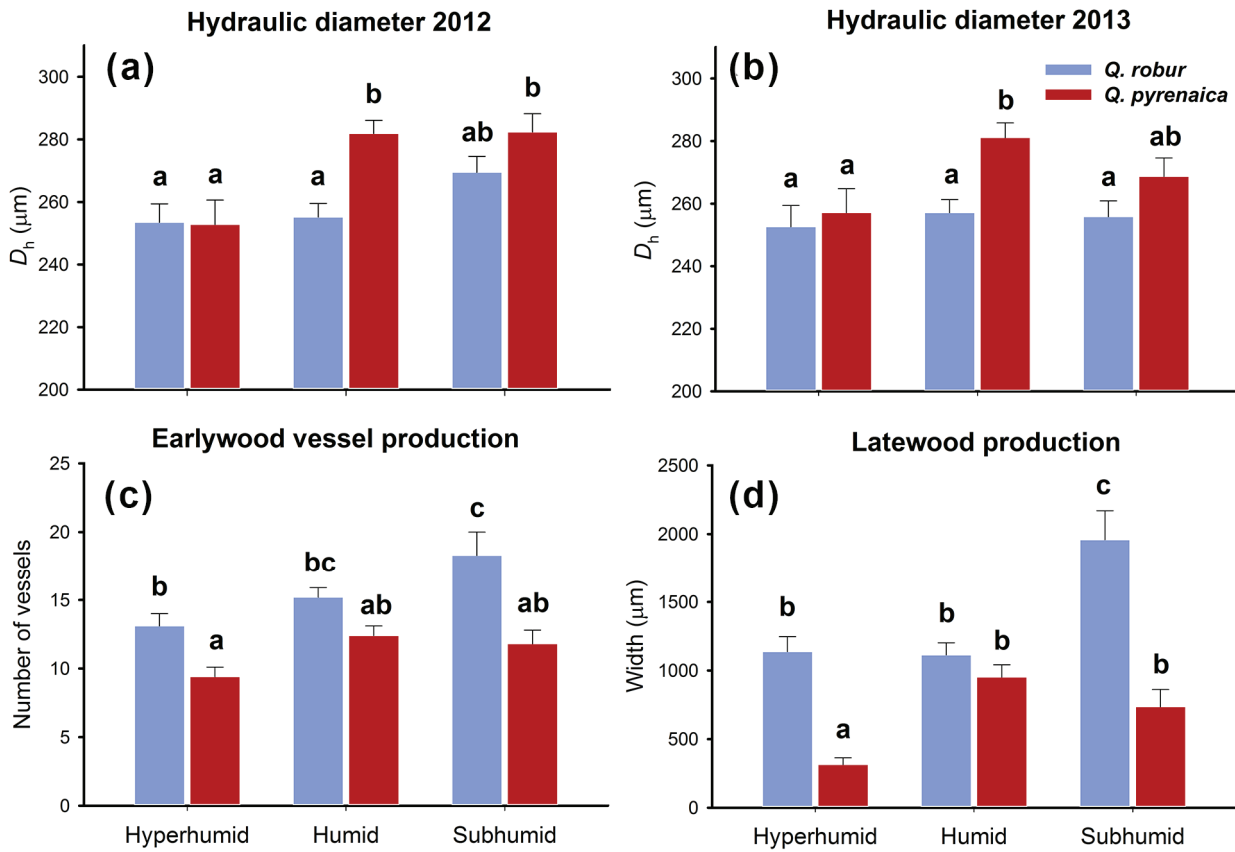
Figure 3̶4: Mean values and SE of (a) hydraulic diameter in 2012, (b) hydraulic diameter in 2013, (c) earlywood vessel production, and (d) latewood production in 2013 for *Quercus robur* (*N* = 120) and *Q. pyrenaica* (*N* = 120). Lower case letters indicate statistically significant differences along the gradient according to ~~multiple~~ Multiple ~~pairwise~~ Pairwise ~~comparisons~~Comparisons.
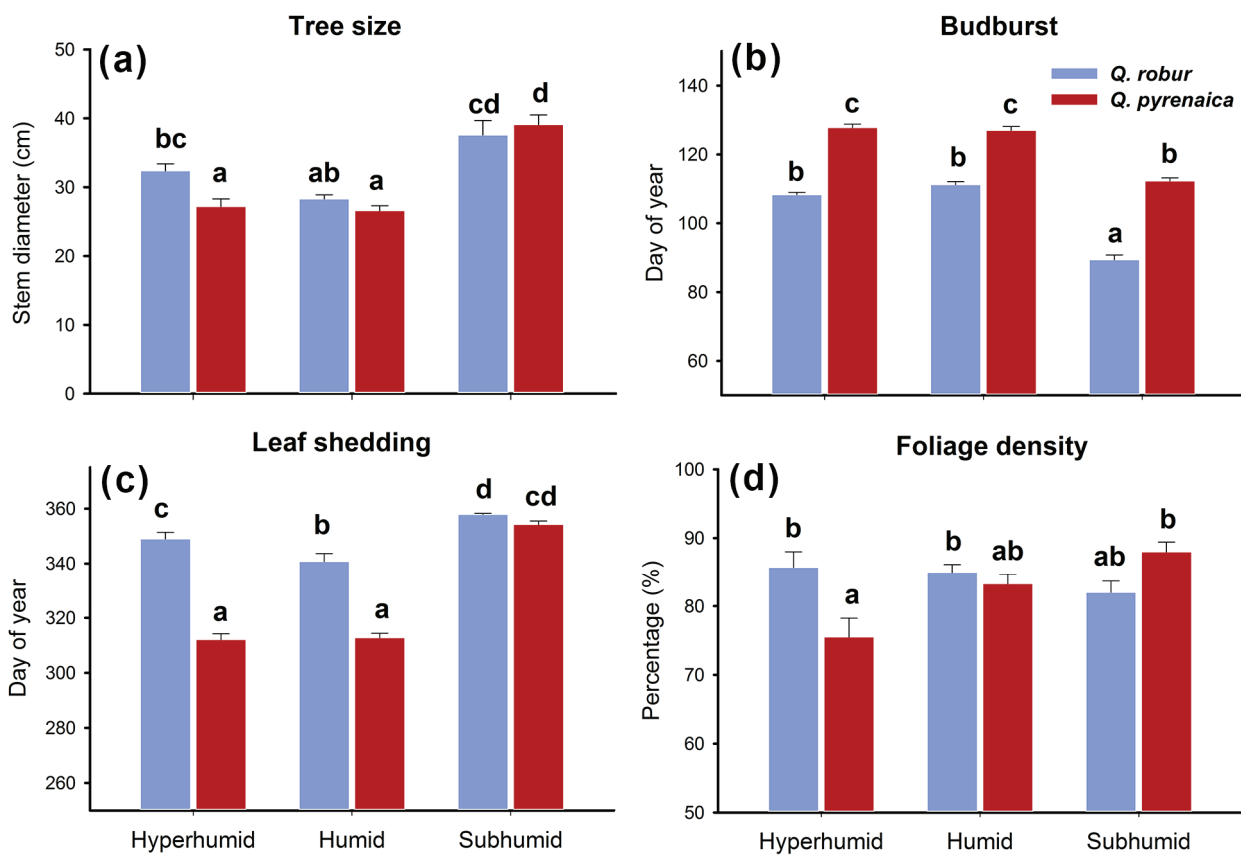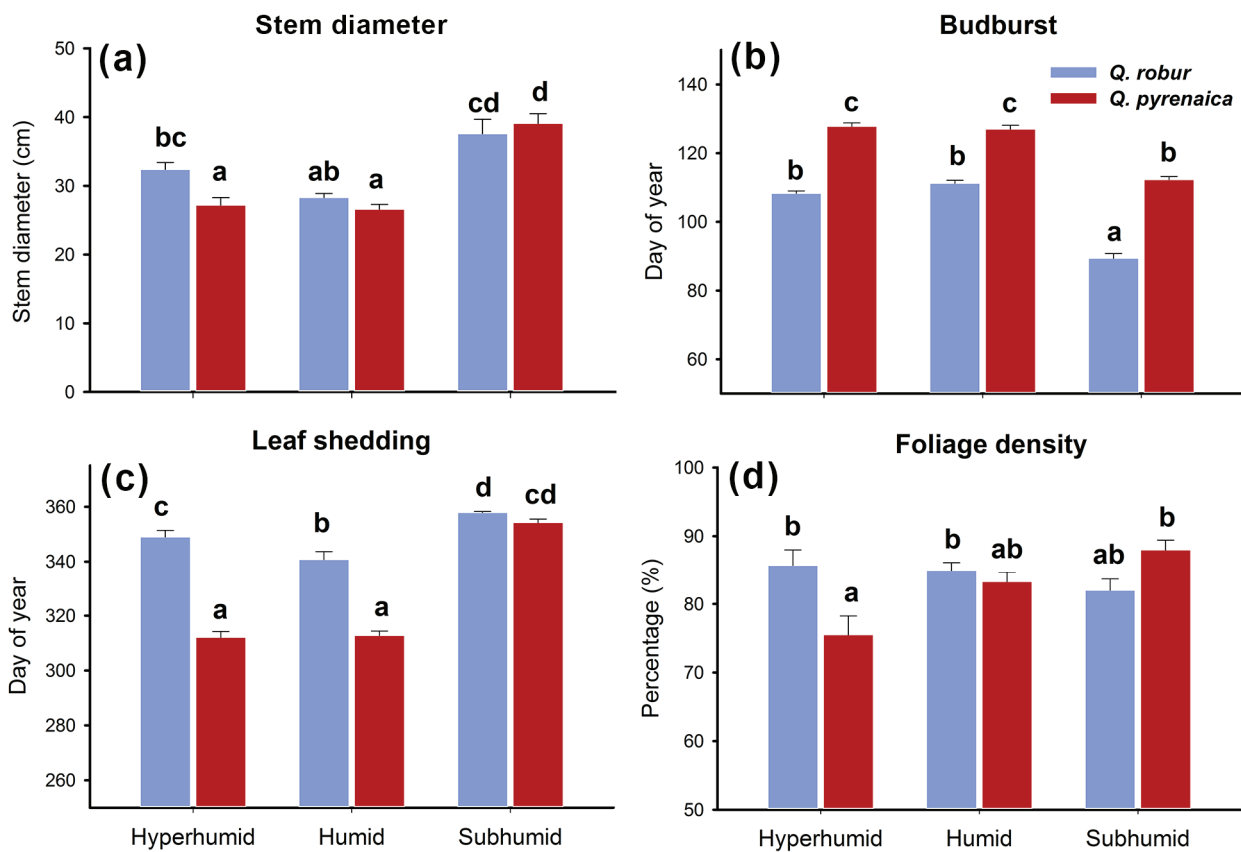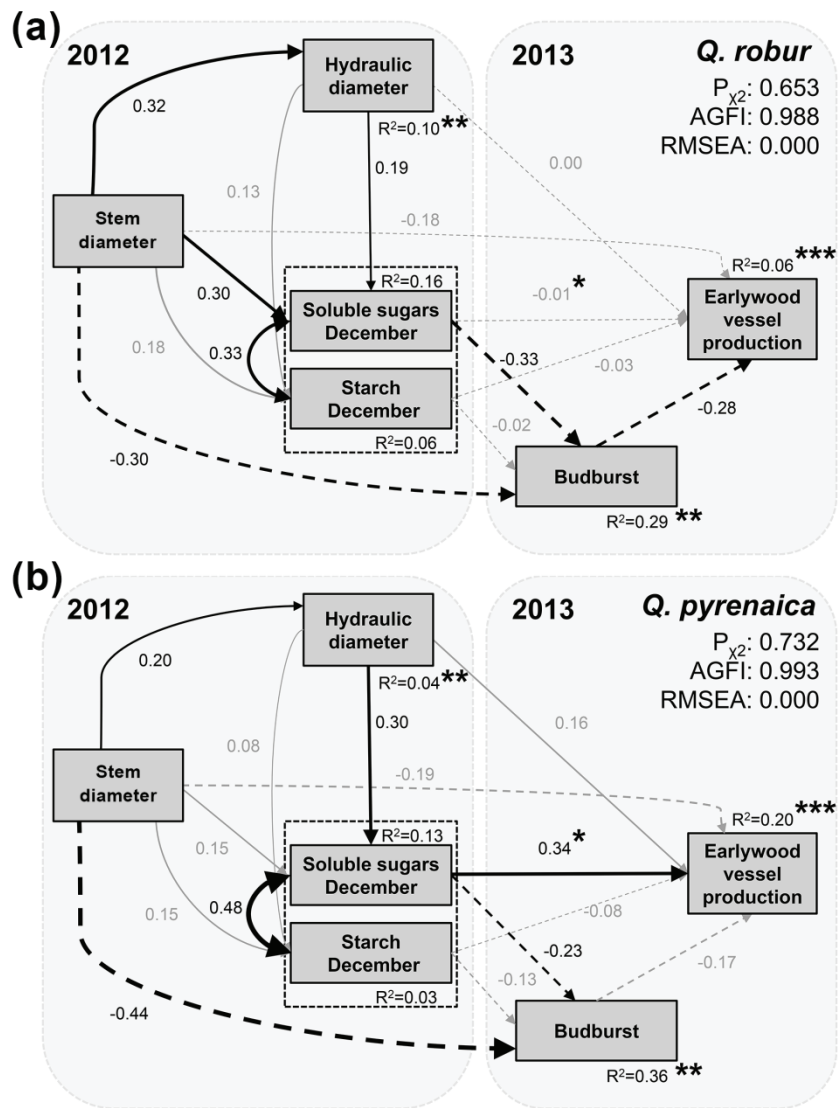
Figure 45: Mean values and SE of (a) stem diameter, (b) ~~date of~~ **budburst _date_, (c) date of leaf shedding, and (d) foliage density in 2013 for** *Quercus robur* _(N = 120)_ **and** *Q. pyrenaica* _(N = 120)_**. Lower case letters indicate statistically significant differences along the gradient according to Multiple Pairwise Comparisons.**
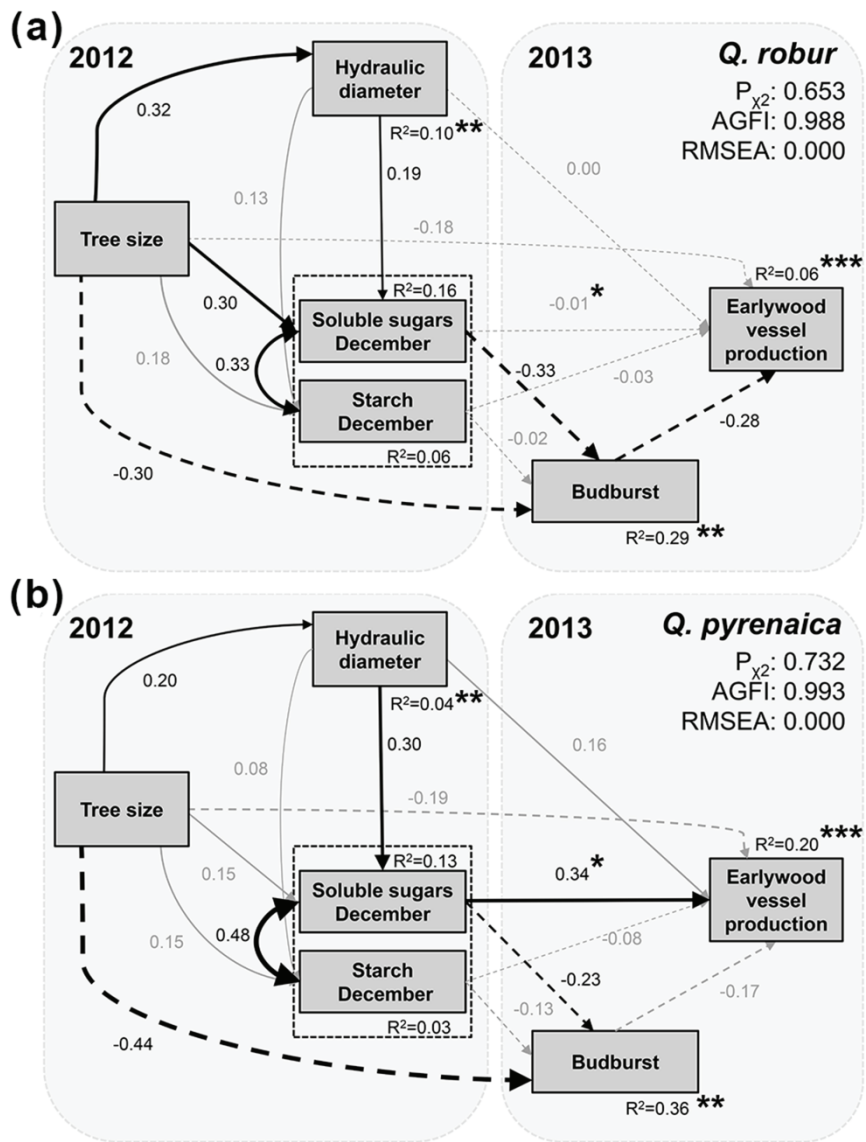
(a) 2012 — Hydraulic diameter — 2013 — *Q. robur*

$P_{\chi2}$: 0.653
AGFI: 0.988
RMSEA: 0.000

0.32
0.13
0.00
$R^2=0.10$ **
0.19
-0.18
$R^2=0.06$ ***

Stem diameter

0.30
0.18
0.33
$R^2=0.16$
Soluble sugars December
-0.01 *
Earlywood vessel production
-0.33
-0.03
Starch December
$R^2=0.06$
-0.02
-0.28
Budburst
-0.30
$R^2=0.29$ **

(b) 2012 — Hydraulic diameter — 2013 — *Q. pyrenaica*

$P_{\chi2}$: 0.732
AGFI: 0.993
RMSEA: 0.000

0.20
0.08
$R^2=0.04$ **
0.16
0.30
-0.19

Stem diameter

0.15
0.15
0.48
$R^2=0.13$
Soluble sugars December
0.34 *
Earlywood vessel production
$R^2=0.20$ ***
-0.08
Starch December
$R^2=0.03$
-0.23
-0.17
-0.13
Budburst
-0.44
$R^2=0.36$ **

25

Figure 5̶6̶: Structural equation models fitted for (a) *Quercus robur* (*N = 120*) and (b) *Q. pyrenaica* (*N = 120*). Variables of the conceptual model are ~~tree size (~~stem diameter~~)~~, hydraulic diameter in 2012, soluble sugars and starch concentrations in December 2012, ~~date of~~ budburst _date_, and earlywood ~~growth~~ _vessel production_ (number of vessels) in 2013. Explained deviances of endogenous variables are shown near the boxes. Black solid (positive effects) and dashed (negative effects) arrows denote significant relations, while non-significant relations are shown as grey coefficients and arrows. The Chi-square test, the adjusted goodness of model fit index (AGFI), and the root mean square error of approximation (RMSEA) are shown for each model. Asterisks indicate paths or error values significantly different between the models of both species. *** $P \leq 0.001$, ** $P \leq 0.01$, and * $P \leq 0.05$.
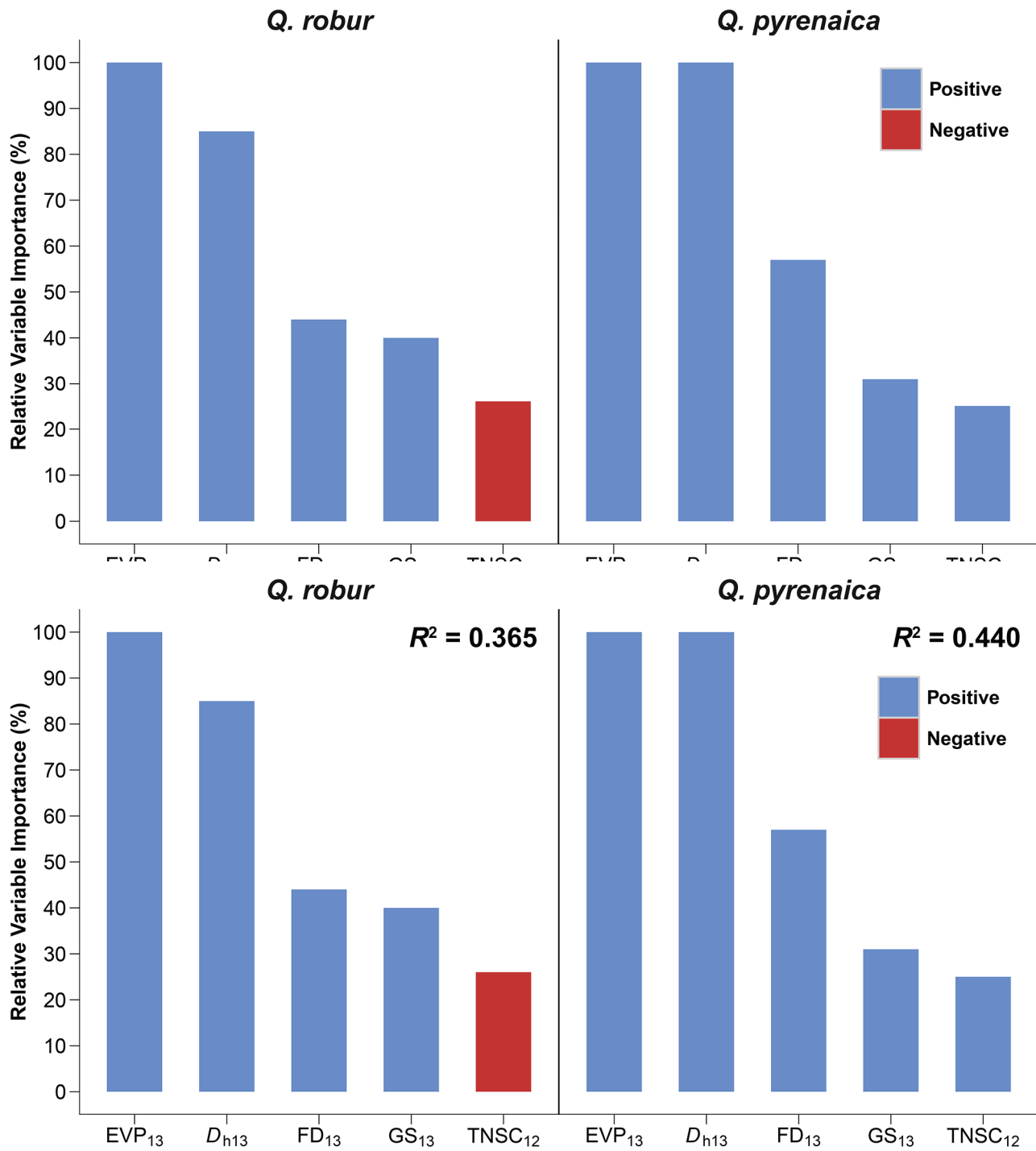
Figure 67: Relative importance of the variables driving latewood production in 2013, expressed as percentage, for *Quercus robur* (*N* = 120) and *O. pyrenaica* (*N* = 120). ~~Location~~ Site effect was included as random factor in the model. NSC_{12} is total non-structural carbohydrates in December 2012, D_{h13} is hydraulic diameter in 2013, EVP_{13} is earlywood vessel production in 2013, GS_{13} is length of the growing season in 2013, and FD_{13} is foliage density in 2013. Different colours of bars denote variables with either a positive or negative effect. ~~We provide the coefficient of determination (R^2) of the full model.~~