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*Brief Communications*

3 **Differences in xylogenesis between dominant and suppressed trees**

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21 Short title: Xylogenesis in dominant and suppressed trees

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23 **PREMISE OF THE STUDY:** Most dendroecological studies focus on dominant trees, but little is known  
24 about the growing season of trees belonging to different size classes and their sensitivity to biotic factors.  
25 The objective of this study was to compare the dynamics of xylem formation between dominant and  
26 suppressed trees with similar ages in *Abies fabri* (Mast.) Craib growing in the Gongga Mountains,  
27 southeastern Tibetan Plateau, and to identify the association between xylem growth and climate.

28 **METHODS:** The timing and duration of xylogenesis were investigated weekly on histological sections  
29 during the 2013-2015 growing seasons.

30 **KEY RESULTS:** Our investigation found that timing and duration of xylogenesis varied with canopy  
31 position and its associated tree size. Xylogenesis started 6-14 days earlier, and ended 5-11 days later in  
32 dominant trees than in suppressed trees, resulting in a significantly longer growing season. Dominant trees  
33 also exhibited higher temperature sensitivity of tracheid production rate than suppressed trees.

34 **CONCLUSIONS:** The observed differences of xylogenesis among trees suggested that competition affects  
35 tree growth by reducing the growing period in suppressed trees. Representative climate-growth  
36 relationships should involve trees of all size classes when evaluating the effects of the environment on  
37 forest dynamics.

38 **KEY WORDS:** *Abies fabri* (Mast.) Craib; cambial activity; competition; Tibetan Plateau; secondary  
39 growth

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50 Competition, as a major endogenous process, plays a critical role in moderating species' distribution  
51 patterns and responses to climate change (Franklin et al., 1987; Turner, 2010; Zhang et al., 2015).  
52 Neighboring trees compete for limiting resources, resulting in different size classes, such as dominant and  
53 suppressed trees (Chu et al., 2009). There is extensive evidence that tree growth sensitivity to climate  
54 increases with decreasing competition intensity (e.g. Martin-Benito et al., 2011; Rozas and Olano, 2013;  
55 Sánchez-Salguero et al., 2015). Intraspecific and interspecific competition can influence forest dynamics.  
56 As shown by analysis of trees in plots across treeline ecotones, upslope migration rates of alpine treeline  
57 are controlled largely by species interactions (Liang et al., 2016), and increasing competition between  
58 adults and juveniles or seedlings could counteract positive effects of future warming on tree growth (Wang  
59 et al., 2016). However, climatic sensitivity of tree growth according to competition status is variable,  
60 species specific and site dependent (McDonald et al., 2002; Carnwath and Nelson, 2016; Tullus et al.,  
61 2017). Most results on the effects of competition on climate-growth relationships in dendroecology are  
62 derived from year-to-year variations in basal area increment associated with climate variability, but they  
63 lack thorough understanding of the timing and processes of xylem growth (Fraver et al., 2014; Sánchez-  
64 Salguero et al., 2015; Carnwath and Nelson, 2016). Furthermore, trees subjected to contrasting competition  
65 status can differ in their xylem growth pattern, potentially influencing the responses to climate variability  
66 (Linares et al., 2010; Castagneri et al., 2008). However, the mechanism driving intra-annual dynamics of  
67 xylem formation among different competition statuses is still scarcely known.

68 The intra-annual dynamics of xylem formation in various tree species have been investigated  
69 worldwide, contributing to a deeper understanding of the timing and duration of cell production during the  
70 growing seasons (e.g. Oribe et al., 2001; Seo et al., 2011; Cuny et al., 2015; Pérez-de-Lis et al., 2016;  
71 Ren et al., 2018). However, most studies have focused on dominant trees without separating the effect of  
72 size or age. Information regarding the timing of xylogenesis among different tree sizes is rare (Rathgeber et  
73 al., 2011). In particular, there is basically no information about the intra-annual growth of trees of different  
74 sizes in natural forests, although several studies have reported that the reduction of competition through  
75 thinning induces a longer growing season, higher c Gottaell production rate and enhanced xylem growth  
76 (Grotta et al., 2005; Linares et al., 2009; Lemay et al., 2017). More systematic investigation is needed  
77 because variations of timing and duration of xylogenesis with different tree size in natural forests would be

78 important to improved understanding of phenology, carbon and water cycling, informing ecosystem models,  
79 and more accurate assessment and representation of tree-ring growth-climate relationships.

80 The objective of this study is to compare timing and duration of xylogenesis between dominant and  
81 suppressed trees of similar age in a natural *Abies fabri* (Mast.) Craib forest in the Gongga Mountains,  
82 southeastern Tibetan Plateau. Previous studies have found that the radial growth of this species was  
83 correlated to April–June temperature (Liu et al., 2011). Based on the evidence that dominant trees have  
84 larger stems, we hypothesized that 1) the timing and duration of xylogenesis varies with canopy position  
85 and its associated tree size in a natural forest; 2) dominant trees are more sensitive to spring temperature  
86 during growth reactivation.

## 87 MATERIALS AND METHODS

88 ***Study site and tree selection***—The study site (29°34' N, 101°59' E, 3000 m a.s.l.) is located in the  
89 Gongga Mountains, southeastern Tibetan Plateau, a region characterized by a cold-temperate and humid  
90 climate (Chang et al., 2003). According to the weather station installed nearby the site, the annual average  
91 temperature is 3.8 °C, with average temperatures of the coldest (January) and hottest (July) months of -7.6  
92 and 17.5 °C, respectively. Annual precipitation is 1940 mm.

93 *Abies fabri* (Mast.) Craib grows in natural forests mixed with *Picea brachytyla*, *Picea likiangensis* var.  
94 *balfouriana*, *Rhododendron* spp., *Populus purdomii* Rehd, and *Salix magnifica* Hemsl. Pure natural *Abies*  
95 *fabri* forests occur between 2800 m and 3800 m a.s.l.

96 Trees belonging to two size classes of *Abies fabri* (Mast.) Craib were selected based on canopy position  
97 and the diameter at breast height (DBH). Paired suppressed and dominant trees within a distance of 3 m  
98 were selected for weekly microcore sampling. Suppressed trees have smaller DBH and lower canopy than  
99 dominant trees. To avoid age effects, dominant and suppressed trees with similar age were finally selected  
100 after establishing tree age by taking tree-ring cores at DBH. Dominant and suppressed trees had a mean  
101 DBH of 64.6±13.6 and 38.4±2.9 cm, and a mean height of 23.9±2.1m and 21.7±2.3m, and a mean crown  
102 projected area of 63.0±23.9 and 34.4±14.0 m<sup>2</sup>, respectively (Appendix S1, S2, see Supplement Data with  
103 this article). Five trees per class with upright stem, healthy overall appearance, and similar growth patterns  
104 were selected. Trees with polycormic stems, partially dead crowns, reaction wood or evident damage were  
105 avoided. Tree-ring cores from each sampled tree at DBH were taken and tree ages at DBH were determined

106 by counting the rings. The ages of dominant and suppressed trees in DBH were  $187.4 \pm 18.9$  and  $177.6 \pm 20.4$   
107 years, respectively (Appendix S1). The differences in age between two classes were  $9.8 \pm 5.2$  years ( $t =$   
108  $4.202$ ,  $df = 4$ ,  $P = 0.014$ ), being much less than the variation among individual within class.

109

110 ***Sample collection and preparation***—In 2013-2015, microcores (2 mm in diameter and 15-mm long) were  
111 collected weekly between April and October at breast height using a Trephor device (Rossi et al., 2006a).  
112 Before sampling, the outer bark was partly removed to just above the living tissues. The microcores were  
113 stored in 50% ethanol to avoid deterioration of the tissues. In the laboratory, the microcores were marked  
114 with a pencil on the transverse section, dehydrated in a series of ethanol and limonene solutions, and  
115 embedded in paraffin. The transverse sections were cut with a rotary microtome, stained with safranin and  
116 astra blue, and permanently fixed on glass slides (Gričar et al., 2006). The sections were observed under  
117 visible and polarized light to detect cambial activity and to differentiate the developing xylem.

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119 ***Analysis of xylem development***—The developing xylem was divided into zones of enlarging tracheids,  
120 secondary-wall formation, and mature tracheids (Deslauriers et al., 2014). For each sample, the radial  
121 number of cells in the cambial zone, radial enlargement, cell-wall thickening and the mature cells were  
122 counted along three radial files (Rossi et al., 2006b, Huang et al., 2014). Cambial cells are characterized by  
123 thin cell walls and small radial diameters. Enlarging cells have thin primary cell walls, but a diameter twice  
124 that of cambial cells (Camarero et al., 2010). Unlike cells with secondary walls, cambial and enlarging  
125 cells are not illuminated under polarized light. Hence, observations under polarized light enable  
126 discrimination between enlarging and wall-thickening tracheids. When no cytoplasm is observed in the cell,  
127 and the color of whole cell wall changes from blue to red, lignification is complete and tracheids are mature.  
128 In spring, when at least one row of enlarging cells was observed, xylogenesis was considered to have begun  
129 (Li et al., 2013, 2017); in late summer-early fall, when no cells were observed in wall thickening and  
130 lignification stages, xylogenesis was considered finished (Rossi et al., 2008). The period between the  
131 initiation of cell enlargement and the presence of the first mature cells was calculated (Jacobsen et al.  
132 2018). The dates of xylem phenology were computed as days of the year (DOY).

133

134 **Data analysis and statistics**—Timing and duration of xylogenesis were compared between dominant and  
135 suppressed trees using paired *t*-tests after checking the assumptions of normality.

136 The dynamics of total tracheids number were fitted using the Gompertz function defined as:

137 
$$y = A \exp [- e^{(\beta - kt)}]$$

138 where *y* is the weekly cumulative sum of tracheids, *t* is the time of the year computed as day of the year, *A*  
139 is an asymptote (constant) and  $\beta$  and *k* are constants reflecting the x-intercept placement and rate of change,  
140 respectively (Deslauriers et al., 2003; Gruber et al., 2009).

141 From the estimated parameters of the Gompertz function, the date of the inflection point (*t<sub>p</sub>*), the  
142 corresponding maximum tracheid production rate (*r<sub>max</sub>*) and the average tracheid production rate (*r<sub>m</sub>*) were  
143 computed according to Rathgeber et al. (2011) as:

144

145 
$$t_p = \beta/k$$

146 
$$r_{max} = kA/e$$

147 
$$r_m \approx 9/40 e r_{max}$$

148 The sensitivity of tree growth to temperature was calculated as the slope of the regression between  
149 average tracheid production rate (*N<sub>cell</sub>/day*) and the mean temperature of April-June, where *N<sub>cell</sub>* is number  
150 of cells. A General Linear Model was applied to compare the differences in the sensitivity of tree growth to  
151 temperature in the two classes.

152

## 153 **RESULTS**

154 Similar patterns of variation in the number of cambial cells were observed in dominant and suppressed  
155 trees. The dormant cambium consisted of 4-6 cells in both classes in all years (example in Fig. 1c, f for  
156 2015). In later spring, the cambial cells started to divide and the cambial zone widened rapidly. The  
157 number of cambial cells reached its maximum between June and July, with 8-9 cells. Cambial cell division  
158 ended in late August.

159 Dominant and suppressed trees had the same trend but with different timing of xylem formation. The  
160 number of cambial cells, enlargement and wall-thickening cells represented bell-shaped curves, whereas  
161 mature cells exhibited a sigmoid pattern. One or two layers of enlarging cells were detected in dominant

162 trees on 29 May 2015 (Fig. 1a), while no differentiating cells occurred in suppressed trees (Fig. 1d). On 5  
163 June, three or four layers of enlarging cells were observed in dominant trees (Fig.1b) and one layer of  
164 enlarging cells was observed in suppressed trees (Fig. 1e). In dominant trees in 2014, at the beginning of  
165 xylogenesis (DOY 147, Fig. 2), the number of enlarging cells increased. Once wall thickening was  
166 observed (DOY 181, Fig. 2), the number of enlarging cells gradually declined while the number of wall-  
167 thickening cells increased. The number of mature cells gradually increased.

168 Significant differences were observed in the onset of growth ( $t=-3.083$ ,  $df=14$ ,  $P=0.008$ , Appendix S3)  
169 between dominant and suppressed trees. The dominant trees produced the first enlarging cells on DOY 143-  
170 147, about 6-14 days earlier than suppressed trees (Table 1). The period between the initiation of cell  
171 enlargement and the presence of the first mature cells took  $38.1\pm 5.4$  and  $37.7\pm 6.9$  days, respectively, for  
172 dominant trees and suppressed trees, showing no significant differences ( $t=0.182$ ,  $df=7$ ,  $P=0.901$ ).  
173 Significant differences were detected in the ending of cell wall thickening between the two classes ( $t=4.443$ ,  
174  $df=9$ ,  $P=0.002$ , Appendix S3). The cessation of cell wall thickening in dominant trees occurred on DOY  
175 248-261, about 5-11 days later than suppressed trees (Fig 2, Appendix S3). In three years, the duration of  
176 xylogenesis was significantly different between classes ( $t=7.529$ ,  $df=9$ ,  $P=0.000$ ). Overall, dominant trees  
177 had longer growing season and hence produced more mature tracheids than their suppressed counterparts  
178 (Table 1). No significant difference was found among years in the onset, ending and duration of  
179 xylogenesis (ANOVA,  $P>0.05$ ).

180 Temperature and interactions between temperature and classes showed significant effects on growth  
181 rate of *Abies fabri* (Mast.) Craib trees ( $P<0.05$ , Appendix S4). Significant differences were observed in the  
182 slope coefficient of the linear regression equation between dominant and suppressed trees (GLM,  $F_{1,3}=4.76$ ,  
183  $P<0.05$ ). The temperature sensitivity of tracheid production rate in dominant trees was higher than  
184 suppressed trees (Fig. 3). For every 1°C increase in the mean temperature during early growing seasons, the  
185 temperature sensitivities of tracheid production rate rose by 0.07 and 0.04  $N_{\text{cell}}/\text{day}^{\circ}\text{C}^{-1}$ , respectively.

186

## 187 **DISCUSSION**

188 Our results clearly showed that dominant trees had earlier onset and later cessation of xylem growth and  
189 hence a longer duration of xylogenesis than suppressed trees. This is in agreement with the findings based

190 on controlled experiments. As shown by Grotta et al. (2005) and Linares et al. (2009), the reduction of  
191 competition through thinning induced a longer growing season and enhanced xylem growth, indicating that  
192 the dominant trees have a longer duration of xylogenesis and produced more xylem. The timing of  
193 xylogenesis is related to tree age and size. Tree age was considered to be one of the major internal factors  
194 controlling the onset of cell production (Deslauriers et al., 2003; Rossi et al., 2008; Li et al., 2013, 2016).  
195 However, disentangling the influence of tree age and size on xylem growth remains a challenge. Previous  
196 studies suggested that at least 100-year differences in tree age could affect the timing and duration of xylem  
197 growth significantly (Rossi et al., 2008; Li et al., 2013, 2016). In our case, an average age difference of ~  
198 10 years between two classes is much less than the age variation among individuals within the class. As  
199 shown, young trees were characterized by an earlier onset of xylogenesis and a longer growing season than  
200 old trees (Rossi et al., 2008; Li et al., 2013). In spite of a bit younger in suppressed trees, a later onset of  
201 Xylogenesis and a shorter growing season in suppressed trees than in dominant trees mainly reflect  
202 competitive status rather than age effect on xylem growth. In an even-aged silver-fir and maritime pine  
203 plantation, Rathgeber et al. (2011) and Vieira et al. (2014) also observed that cambial activity started 3/1  
204 weeks earlier and lasted longer in dominant/fast-growing trees than suppressed/slow-growing ones. The  
205 timing and duration of xylogenesis varied with size class in natural forests, supporting our hypothesis.

206 The differences of xylogenesis between the two classes suggest that intraspecific competition could  
207 affect tree growth and potentially the responses to climate. In fact, both natural studies and control  
208 experiments have demonstrated that competition directly or indirectly modulates climate-growth  
209 relationships (Sánchez-Salguero et al., 2015; Wang et al., 2016). At the individual level, we found that  
210 growth sensitivity to temperature is greater in dominant trees than suppressed trees, which is in line with  
211 other dendroecological studies (Martin-Benito et al., 2011; Rozas and Olano, 2013). Compared with  
212 suppressed trees, dominant trees have longer growing seasons, which is influenced by climate directly, but  
213 the earlier onset of growth also increases their risk from extreme climatic events (Begum et al., 2013). As a  
214 result, the dominant trees are more vulnerable to climatic stresses than suppressed individuals (Thomas and  
215 Winner, 2002; Niinemets, 2010). This supports findings that climate sensitivity of tree growth decreases  
216 with increasing competition intensity (Martin-Benito et al., 2011; Rozas and Olano, 2013), since the  
217 proportion of suppressed trees increases. As shown by dendroecological analysis, after the selective logging

218 in the Mongolian forest–steppe a *Larix sibirica* forest was associated with a high sensitivity of stemwood  
219 formation to high summer temperatures (Khansaritoreh et al., 2017). Several authors also reported that tree  
220 growth sensitivity to climate change is lower in a mixed-species stand than in monoculture (Kozovits et al.,  
221 2005; Thurm et al., 2016). Such an effect might be magnified in the vegetation transition zones such as the  
222 treeline, and offers a physiological explanation for why increased competition diminishes the positive  
223 effects of warming at the alpine treeline (Wang et al., 2016).

224 In conclusion, the timing and duration of xylem growth varied according to competitive status. This  
225 case study showed that xylogenesis started earlier and stopped later in dominant trees than in suppressed  
226 trees, resulting in a longer xylogenesis period. Furthermore, the sensitivity of tracheid production to  
227 temperature variation early in the growing season was greater in dominant trees than in suppressed trees.  
228 The comprehensive xylogenesis findings demonstrate that biotic competition can affect tree growth, forest  
229 dynamics, and ecosystems. Dominant trees are inferred to be using water, carbon, and light resources for  
230 growth earlier and later than the growth period of suppressed trees. The timing window for correlations of  
231 climate to tree-ring formation is therefore likewise expected to be wider for dominant than for suppressed  
232 trees. Xylogenesis in suppressed trees of *Abies fabri* at our site takes place over a shorter interval than that  
233 of the dominant trees, but we do not know how universal this response is. It will be important to conduct  
234 similar studies with other species at different locations.

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## 241 **CONTRIBUTIONS**

242 EL and LW designed study and started the microcore sampling in 2013. SL and XL did laboratory work.  
243 All authors contributed to data analyses, interpretation and writing.

244 **DATA ACCESSIBILITY STATEMENT**

245 All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary  
246 Materials. Additional data related to this paper may be requested from the authors.

247

248 **LITERATURE CITED**

249 Begum, S., S. Nakaba, Y. Yamagishi, Y. Oribe, and R. Funada. 2013. Regulation of cambial activity in  
250 relation to environmental conditions: understanding the role of temperature in wood formation of trees.

251 *Physiologia Plantarum* 147: 46–54.

252 Camarero, J. J., J. M. Olano, and A. Parras. 2010. Plastic bimodal xylogenesis in conifers from continental  
253 Mediterranean climates. *New Phytologist* 185:471–480.

254 Carnwath, G. C., and C. R. Nelson. 2016. The effect of competition on responses to drought and  
255 interannual climate variability of a dominant conifer tree of western North America. *Journal of Ecology*  
256 104: 1421–1431.

257 Castagneri, D., G. Vacchiano, E. Lingua, and R. Motta. 2008. Analysis of intraspecific competition in two  
258 subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). *Forest Ecology*  
259 *and Management* 255: 651–659.

260 Chang, Z., Z. Lu, and W. Guan. 2003. Water holding effect of subalpine dark coniferous forest soil in  
261 Gongga Mountain, China. *Journal of Forestry Research* 14: 205–209.

262 Chu, C., J. Weiner, F. Maestre, S. Xiao, Y. Wang, Q. Li, J. Yuan, et al. 2009. Positive interactions can  
263 increase size inequality in plant populations. *Journal of Ecology* 97: 1401–1407.

264 Cuny, H. E., C. B. K. Rathgeber, D. Frank, P. Fonti, H. Mäkinen, P. Prislan, S. Rossi, et al. 2015. Woody  
265 biomass production lags stem-girth increase by over one month in coniferous forests. *Nature Plants* 1:  
266 15160.

267 Deslauriers, A., M. Beaulieu, L. Balducci, A. Giovannelli, M. J. Gagnon, and S. Rossi. 2014. Impact of  
268 warming and drought on carbon balance related to wood formation in black spruce. *Annals of Botany*  
269 114: 335-345.

270 Deslauriers, A., H. Morin, and Y. Begin. 2003. Cellular phenology of annual ring formation of *Abies*  
271 *balsamea* in the Quebec boreal forest (Canada). *Canadian Journal of Forest Research* 33: 190-200.

272 Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as ecological process. *Biosciences* 37:  
273 550–556.

274 Fraver, S., A. W. D'Amato, J. B. Bradford, B. G. Jonsson, M. Jönsson, and P-A. Esseen. 2014. Tree growth  
275 and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial  
276 patterning. *Journal of Vegetation Science* 25: 374-385.

277 Gričar J, M. Zupančič, K. Čufar, G. Koch, U. Schmitt, and P. Oven. 2006. Effect of local heating and  
278 cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). *Annals*  
279 *of Botany* 97: 943-951.

280 Grotta, A. T., B. L. Gartner, S. R. Radosevich, and M. Huso. 2005. Influence of red alder competition on  
281 cambial phenology and latewood formation in Douglas-fir. *IAWA Journal* 26: 309-324.

282 Gruber, A., D. Baumgartner, J. Zimmermann, and W. Oberhuber. 2009. Temporal dynamic of wood  
283 formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. *Trees*  
284 23: 623-635.

285 Huang, J-G., A. Deslauriers, and S. Rossi. 2014. Xylem formation can be modeled statistically as a  
286 function of primary growth and cambium activity. *New Phytologist* 203: 831-841.

287 Jacobsen, A. L., J. Valdovinos-Ayala, and R. B. Pratt. 2018. Functional lifespans of xylem vessels:  
288 Development, hydraulic function, and post-function of vessels in several species of woody plants.  
289 *American Journal of Botany*, in press

290 Khansaritoreh, E., M. Eldarov, K. Ganbaatar, D. Saindovdon, C. Leuschner, M. Hauck, and C.  
291 Dulamsuren. 2017. Age structure and trends in annual stem increment of *Larix sibirica* in two  
292 neighboring Mongolian forest–steppe regions differing in land use history. *Trees* 31: 1973-1986.

293 Kozovits, A. R., R. Matyssek, H. Blaschke, A. Göttlein, and T. E. E. Grams. 2005. Competition  
294 increasingly dominates the responsiveness of juvenile beech and spruce to elevated CO<sub>2</sub> and/or O<sub>3</sub>  
295 concentrations throughout two subsequent growing seasons. *Global Change Biology* 11: 1387-1401.

296 Lemay, A., C. Krause, S. Rossi, and A. Achim. 2017. Xylogenesis in stems and roots after thinning in the  
297 boreal forest of Quebec, Canada. *Tree Physiology* 37: 1554–1563,.

298 Li, X., J. J. Camarero, B. Case, E. Liang, and S. Rossi. 2016. The onset of xylogenesis is not related to  
299 distance from the crown. *Canadian Journal of Forest Research* 46: 885–889.

300 Li, X., E. Liang, J. Gričar, P. Prislan, S. Rossi, and K. Čufar. 2013. Age dependence of xylogenesis and its  
301 climatic sensitivity in Smith fir on the south-eastern Tibetan Plateau. *Tree Physiology* 33: 48–56.

302 Li, X., E. Liang, J. Gričar, S. Rossi, K. Čufar, and A. M. Ellison. 2017. Critical minimum temperature  
303 limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau. *Science Bulletin* 62:  
304 804–812.

305 Liang, E., Y. Wang, S. Piao, X. Lu, J. J. Camarero, H. Zhu, L. Zhu, et al. 2016. Species interactions slow  
306 warming-induced upward shifts of treelines on the Tibetan Plateau. *Proceedings of the National*  
307 *Academy of Sciences, USA*, 113: 4380–4385.

308 Linares, J. C., J. J. Camarero, and J. A. Carreira. 2009. Plastic responses of *Abies pinsapo* xylogenesis to  
309 drought and competition. *Tree Physiology* 29: 1525–1536.

310 Linares, J. C., J. J. Camarero, and J. A. Carreira. 2010. Competition modulates the adaptation capacity of  
311 forests to climatic stress: insights from recent growth decline and death in relict stands of the  
312 Mediterranean fir *Abies pinsapo*. *Journal of Ecology* 98: 592–603.

313 Liu, X., L. Zhao, T. Chen, X. Shao, Q. Liu, S. Hou, D. Qin, and W. An. 2011. Combined tree-ring width  
314 and  $\delta^{13}\text{C}$  to reconstruct snowpack depth: a pilot study in the Gongga Mountain, west China. *Theoretical*  
315 *and Applied Climatology* 103: 133–144.

316 Martin-Benito, D., V. Kint, M. del Río, B. Muys, and I. Cañellas. 2011. Growth responses of West-  
317 Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: Past  
318 trends and future perspectives. *Forest Ecology and Management* 262: 1030–1040.

319 McDonald, E. P., E. L. Kruger., D. E. Riemenschmeifer, and J. G. Isebrands. 2002. Competitive status  
320 influences tree-growth responses to elevated  $\text{CO}_2$  and  $\text{O}_3$  in aggrading aspen stands. *Functional Ecology*  
321 16: 792–801.

322 Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings  
323 to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and*  
324 *Management* 260: 1623–1639.

325 Oribe, Y., R. Funada, M. Shibagaki, and T. Kubo. 2001. Cambial reactivation in locally heated stems of the  
326 evergreen conifer *Abies sachalinensis* (Schmidt) Masters. *Planta* 212: 684–691.

327 Pérez-de-Lis, G., S. Rossi, R. A. Vázquez-Ruiz, V. Rozas, and I. García-González. 2016. Do changes in

328 spring phenology affect earlywood vessels? Perspective from the xylogenesis monitoring of two  
329 sympatric ring-porous oaks. *New Phytologist* 209: 521–530.

330 Rathgeber, C. B. K., S. Rossi, and J. D. Bontemps. 2011. Cambial activity related to tree size in a mature  
331 silver-fir plantation. *Annals of Botany* 108: 429–438.

332 Ren, P., S. Rossi, J. J. Camarero, A. M. Ellison, E. Liang, and J. Peñuelas. 2018. Critical temperature and  
333 precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the  
334 northeastern Tibetan Plateau. *Annals of Botany*, doi: 10.1093/aob/mcx188.

335 Rossi, S., T. Anfodillo and R. Menardi. 2006a. Trephor: A new tool for sampling microcores from tree  
336 stems. *IAWA Journal* 27: 89–97.

337 Rossi, S., A. Deslauriers, and T. Anfodillo. 2006b. Assessment of cambial activity and xylogenesis by  
338 microsampling tree species: an example at the Alpine timberline. *IAWA Journal* 27: 383–394.

339 Rossi, S., A. Deslauriers, T. Anfodillo, and M. Carrer. 2008. Age-dependent xylogenesis in timberline  
340 conifers. *New Phytologist* 177: 199–208.

341 Rozas, V., and J. M. Olano. 2013. Environmental heterogeneity and neighbourhood interference modulate  
342 the individual response of *Juniperus thurifera* tree-ring growth to climate. *Dendrochronologia* 31: 105–  
343 113.

344 Sánchez-Salguero, R., J. C. Linares, J. J. Camarero, J. Madrigal-González, A. Hevia, Á. Sánchez-Miranda ,  
345 J. A. Ballesteros-Cánovas, et al. 2015. Disentangling the effects of competition and climate on  
346 individual tree growth: A retrospective and dynamic approach in Scots pine. *Forest Ecology and*  
347 *Management* 358: 12–25.

348 Seo, J-W., D. Eckstein, R. Jalkanen, and U. Schmitt. 2011. Climatic control of intra- and inter-annual  
349 wood-formation dynamics of Scots pine in northern Finland. *Environmental and Experimental Botany*  
350 72: 422–431.

351 Thomas, S. C., and W. E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an  
352 integration of field results by meta-analysis. *Tree Physiology* 22: 117–127.

353 Thurm, E. A., E. Uhl, and H. Pretzsch. 2016. Mixture reduces climate sensitivity of Douglas-fir stem  
354 growth. *Forest Ecology and Management* 376: 205–220.

355 Tullus, A., P. Kupper, A. Kassik, H. Tullus, K. Lõhmus, A. Sober, and A. Sellin. 2017. The competitive

356 status of trees determines their responsiveness to increasing atmospheric humidity - a climate trend  
357 predicted for northern latitudes. *Global Change Biology* 23: 1961–1974.

358 Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849.

359 Vieira, J., S. Rossi, F. Campelo, and C. Nabais. 2014. Are neighboring trees in tune? Wood formation in  
360 *Pinus pinaster*. *European Journal of Forest Research* 133: 41–50.

361 Wang, Y., N. Pederson, A. M. Ellison, H. L. Buckley, B. S. Case, E. Liang, and J. J. Camarero. 2016.  
362 Increased stem density and competition may diminish the positive effects of warming at alpine treeline.  
363 *Ecology* 97: 1668–1679.

364 Zhang, J., S. Huang, and F. He. 2015. Half-century evidence from western Canada shows forest dynamics  
365 are primarily driven by competition followed by climate. *Proceedings of the National Academy of*  
366 *Sciences* 112: 4009–4014.

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369 TABLE 1. Timing and duration of xylogenesis and number of xylem cells in dominant and suppressed *Abies fabri* (Mast.)  
 370 Craib trees in 2013-2015 (n=5 trees per diameter class); onset and end of xylem differentiation phase are given as day of  
 371 year (DOY).

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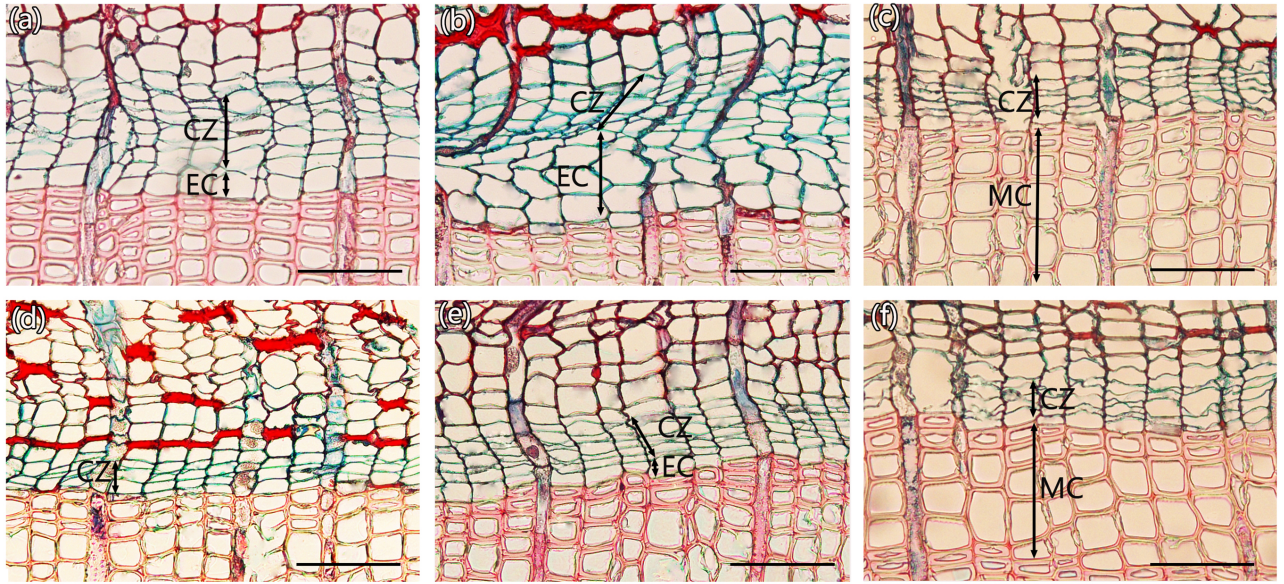
Tree class	Enlargement					Wall thickening		Xylem differentiation				
	Onset (DOY)			End (DOY)		End (DOY)		Duration (days)		Xylem cells (n)		
	2013	2014	2015	2014	2015	2014	2015	2014	2015	2013	2014	2015
Dominant	143±4	147±3	147±4	222±0	220±4	253±4	261±6	106±1	113±3	17±4	10±2	22±10
Suppressed	149±9	157±4	161±3	222±6	215±3	248±5	250±5	93±5	93±13	11±6	8±3	10±3

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377 Figure Legends  
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379 FIGURE 1 Phases of wood formation observed in (a-c) dominant and (d-e) suppressed *Abies fabri* (Mast.) Craib trees on  
380 the following dates: a and d, 29 May, 2015; b and e, 5 June; c and f, 9 September. CZ, cambium zone; EC, enlarging cells;  
381 MC, mature cells. Bars are equivalent to 100  $\mu$ m.  
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383 FIGURE 2 Numbers of cells in the cambial zone, radial enlargement, wall thickening and lignification, and mature cells  
384 in dominant and suppressed *Abies fabri* (Mast.) Craib. Error bars indicate mean  $\pm$  SD between five trees per sampling  
385 date.  
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387 FIGURE 3 Temperature sensitivities of the tracheid production in dominant and suppressed trees during early growing  
388 season (April-June) in 2013-2015. *p* denotes the significance of the regression equation.  
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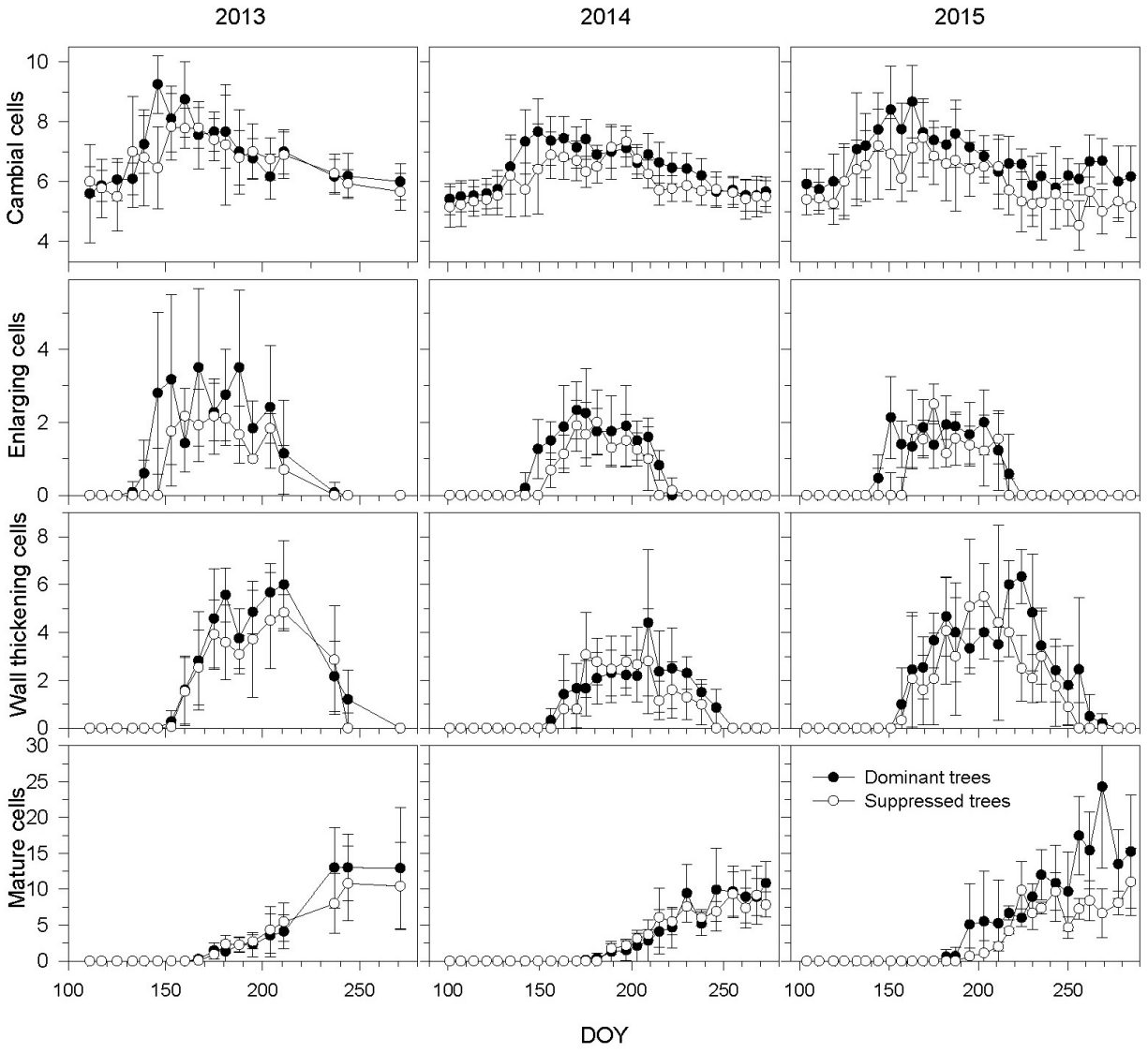


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410 FIGURE 2

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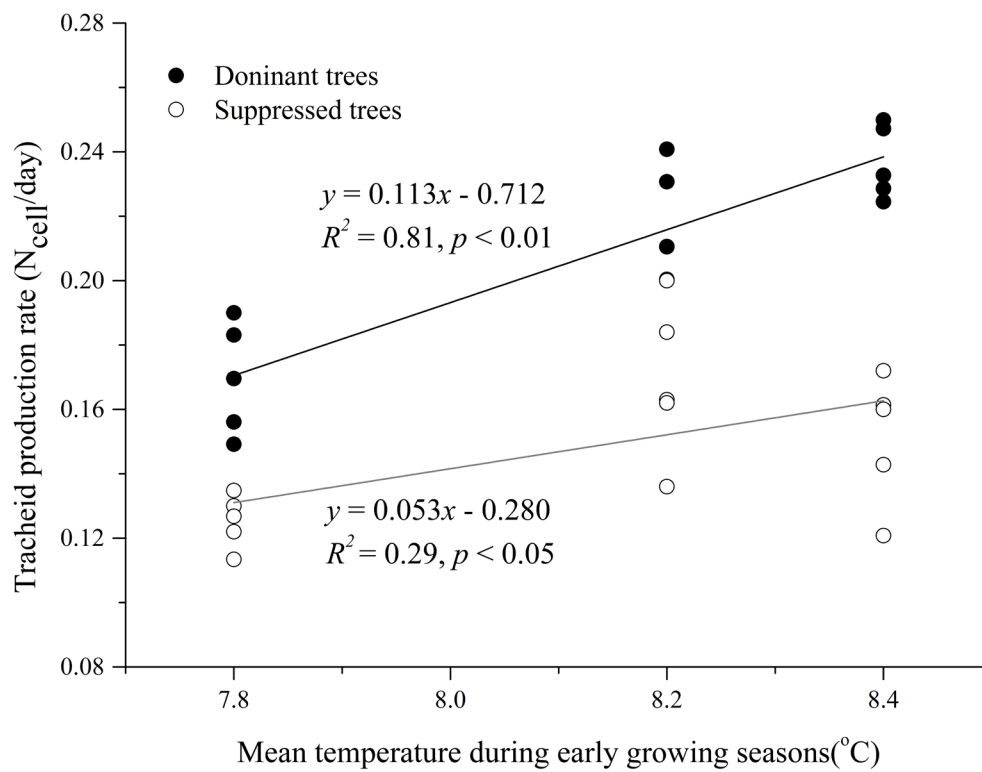
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420 FIGURE 3

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Appendix S1. DBH, height, age and projected crown area for dominant (D) and suppressed (S) trees. Tree height was

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measured using a clinometer. Crown projection area was calculated by an average crown spread from 4 cross directions.

Tree No.	DBH (cm)		Height (m)		Age (y)		Crown area (m <sup>2</sup> )	
	D	S	D	S	D	S	D	S
1	81	42	26	23.8	194	186	89.2	38.5
2	49	35	20.5	19	169	153	29.8	23.4
3	74	40	25	24	217	206	72	24.5
4	66	36	23.8	19.5	181	179	76.4	57.2
5	53	39	24.3	22	176	164	47.6	28.6
Average	64.6	38.4	23.9	21.7	187.4	177.6	63.0	34.4
Standard Deviation	13.6	2.9	2.1	2.3	18.9	20.4	23.9	14.0

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448 Appendix S2. Image of the paired dominant (D) and suppressed (S) *Abies fabri* (Mast.) Craib trees. Paired suppressed and  
449 dominant trees within a distance of 3 m were selected. Suppressed trees have smaller DBH and lower canopy than  
450 dominant trees. To avoid age effects, dominant and suppressed trees with similar age were finally selected after  
451 establishing tree age by taking tree-ring cores at DBH.



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Appendix S3. Paired *t*-tests performed on the phenophase collected from dominant and suppressed *Abies fabri* (Mast.)  
Craib trees.

	Dominant*suppressed		
	<i>t</i>	df	<i>P</i>
Onset of cell enlargement	-3.083	14	0.008
End of cell enlargement	1.478	9	0.171
End of cellwall-thickening	4.443	9	0.002
Durations of xylogenesis	7.529	9	0.000
Final numbers of cell	3.554	13	0.004

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477 Appendix S4. Comparison of general linear models (GLM) assessing the effect of temperature, classes and their

478 interactions on growth rate of *Abies fabri* (Mast.) Craib trees.

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	Growth rate	
	<i>F</i>	<i>P</i>
Temperature	35.81	0.00
Classes	3.39	0.08
Temperatur×Classes	4.76	0.03

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