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1 **Are differences among forest tree populations in carbon isotope composition**  
2 **an indication for adaptation to drought?**

3

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18 **Population differences in water use efficiency and adaptation to drought**

19 Plants have developed different strategies to cope with a reduced water availability  
20 in the soil (Levitt 1980). Drought resistance of forest trees is mainly a question of  
21 survival and competition within an ecosystem. However, in forestry, it is also a  
22 question of maintaining growth. Functional traits can be termed “adaptive” to drought,  
23 providing that their genetic variation can be linked to an increased fitness under soil  
24 water deficit conditions. The observation of trees grown from seeds of different  
25 populations in one or several common environments (e.g. provenance trials or  
26 common garden experiments) is a means to control for environmental variation, and  
27 therefore to detect genetic differences among these different populations and  
28 potentially genotype x environment interactions, if trials are replicated at different  
29 locations. Populations from different environments may differ in their mean values of  
30 any functional trait in the sense that these mean values relate to the environmental  
31 differences of the original population sites. This can be taken as a first indication that  
32 these traits are involved in the adaptation of populations to the local conditions.  
33 Studying population differences involves measuring the phenotypes of large numbers  
34 of individual plants. In this context, the carbon isotope composition ( $\delta^{13}\text{C}$ ) of plant  
35 organic material has been widely used.

36  $\delta^{13}\text{C}$  variations of plant organic matter reflect variations in intrinsic water use  
37 efficiency ( $W_i$ , the ratio between  $A$ , the net  $\text{CO}_2$  assimilation rate and  $g_s$ , the stomatal

38 conductance to water vapour). This relationship has been explained by Farquhar et al.  
 39 (1989) using a mechanistic model of CO<sub>2</sub> fluxes in the leaf and isotopic fractionation  
 40 factors. Some of the model parameters — listed in Figure 1 — are likely to vary across  
 41 genotypes or populations and could therefore weaken the relationship between δ<sup>13</sup>C  
 42 and W<sub>i</sub>. A number of publications on forest trees have nevertheless shown a strong  
 43 relationship between these two traits, either when comparing provenances  
 44 (Grossnickle et al. 2005, Ducrey et al. 2008, Kaluthota et al. 2015) or within family  
 45 variations (Roussel et al. 2009, Marguerit et al. 2014).

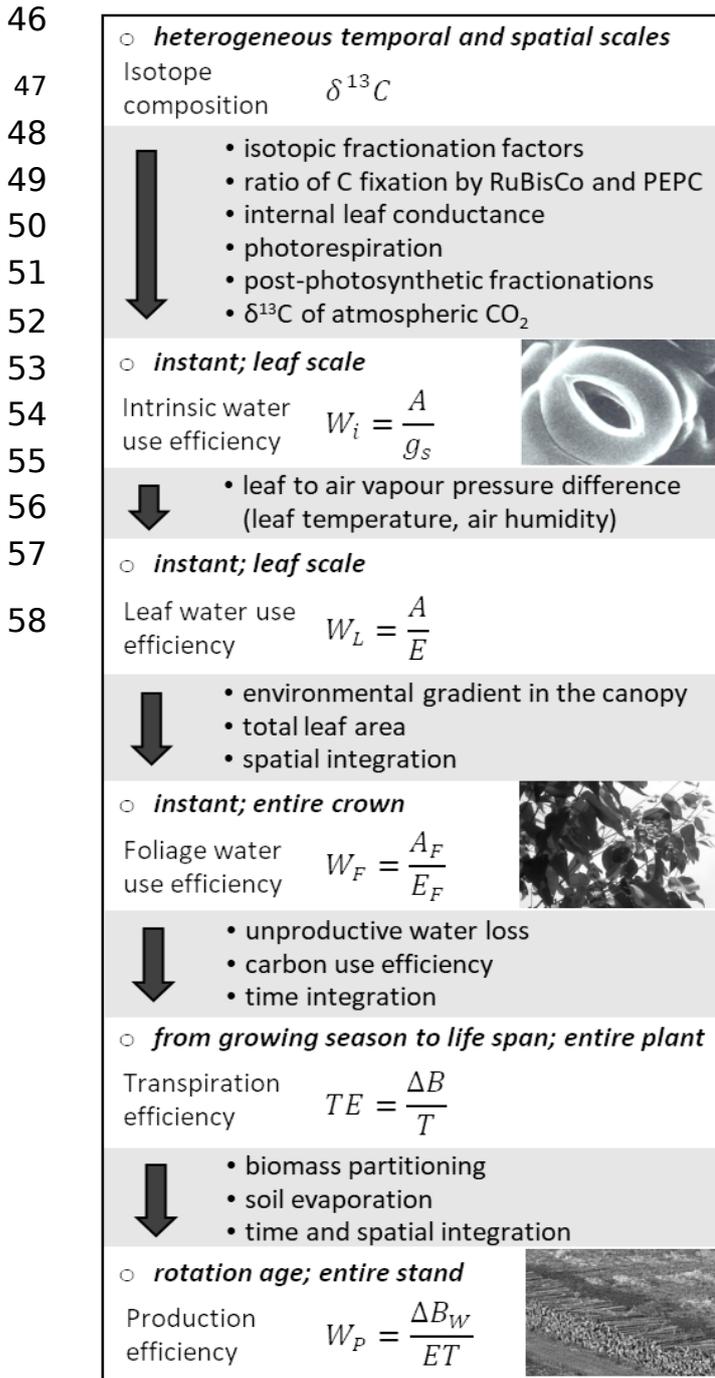


Figure 1: Stable carbon isotope composition (δ<sup>13</sup>C) and water use efficiency at different time and spatial scales. Factors and traits involved at each change of scale are listed on a gray background. ΔB and ΔB<sub>W</sub> are total tree biomass and harvested woody biomass, respectively; and T and ET are tree transpiration (or water use) and stand evapotranspiration, respectively.

59 Hu et al. (2021) examined variations of  $\delta^{13}\text{C}$  in leaves and stems of *Salix eriocephala*  
60 individuals from 34 populations selected from within the large natural range of the  
61 species across eastern and western Canada. They were able to show that  $W_i$   
62 (estimated from  $\delta^{13}\text{C}$ ) varied among populations, and to relate these variations to the  
63 geographical and climatic characteristics of the sites of origin. A large number of  
64 studies have shown population differences in  $W_i$  for forest trees. However, only a few  
65 of these studies have actually related these differences to the variation in  
66 environmental conditions among the original populations, thereby suggesting adaptive  
67 differences.

68 As  $W_i$  generally increases under drought stress, one hypothesis is that this would  
69 also be the case with respect to adaptive differences among populations, so that  
70 populations from dry environments would have a high  $W_i$ . As a first approximation, a  
71 negative correlation between the mean  $W_i$  of different populations and the  
72 precipitation of their original environments would sustain this hypothesis, which has  
73 been substantiated by a number of studies on tree species (e.g. Aitken et al. 1995, Li  
74 et al. 2000, Cregg and Zhang 2001, Bekessy et al. 2002, Zhang et al. 2005, Aleta et al.  
75 2009).

76 However, this hypothesis is not necessarily the only explanation. To elaborate on an  
77 alternative hypothesis, we need to look at water use efficiency at the whole plant  
78 level, where it is defined as the ratio of dry biomass accumulation per unit water  
79 transpired, namely the transpiration efficiency (TE). Maximov (1929) suggested that  
80 there was no direct proportionality between TE and the degree of drought resistance,  
81 but that TE was an indicator for the ecological drought adaptation strategy of a plant.  
82 He found both high and low TE plants among different herbaceous species that were  
83 adapted to dry environments (xerophytes). He then demonstrated that plants with  
84 high TE developed rapidly and had a large leaf area, whereas plants with low TE were  
85 characterised by large root systems. Similarly, Ehleringer (1993) found high and low  
86  $W_i$  individual plants within the species *Encelia farinosa*, a drought-deciduous desert  
87 shrub. He hypothesized that such plants with low  $W_i$  might allocate more carbon to the  
88 root system than those with high  $W_i$ . Recent research on *Arabidopsis thaliana*  
89 ecotypes has shown that different drought adaptation strategies can exist within one  
90 species, where high  $W_i$  was suggested to correspond to drought-sensitive and early  
91 closing stomata and low  $W_i$  to a drought escape strategy due to early flowering (Lovell  
92 et al. 2013, Kenney et al. 2014, Campitelli et al. 2016, Lorts and Lasky 2020). These  
93 works thus substantiate a second hypothesis, where populations from dry  
94 environments would have a low  $W_i$ . The evolution of such a strategy would result in a

95 negative relationship between  $\delta^{13}\text{C}$  and the drought index of the populations, as  
96 reported by Hu et al. (2021). Similar results have been found for other tree species,  
97 where populations from low precipitation environments had low  $W_i$  (Nguyen-Queyrens  
98 et al. 1998) or low TE (Fan et al. 2008). But for trees, unlike annual plants, escaping  
99 drought is not an option. Therefore, drought adapted trees with a low  $W_i$ , due to more  
100 open stomata, could either correspond to a drought tolerance strategy, for example by  
101 anatomical adaptations reducing vulnerability to cavitation, or to a drought  
102 avoidance/water spender strategy through a wide soil exploration by roots. Both  
103 strategies would allow stomata to remain open to some extent during drought.  
104 Eriksson et al. (2005) demonstrated that European *Castanea sativa* populations from  
105 the driest sites showed the lowest  $W_i$ , but also had the deepest rooting pattern  
106 (Lauteri et al. (2004) and M. Lauteri, personal comm.). This response was similar to  
107 that of low TE xerophytes in Maximov's study, and consistent with Ehleringer's  
108 hypothesis. On the other hand, drought adapted trees with a high  $W_i$  (the first  
109 hypothesis above) could correspond to a drought avoidance/water saving strategy,  
110 through drought-sensitive, early closing stomata.

111 Hu et al. (2021) included two drought indices in a canonical correlation analysis to  
112 show that  $W_i$  was more related to the duration and the temperature of the growing  
113 seasons than water availability. The use of drought indices to characterise the dryness  
114 of an environment is an improvement over the use of precipitation only, as these  
115 indices take in account other atmospheric variables. However, drought indices often  
116 do not directly reflect seasonal variation in precipitation and temperature. A generally  
117 dry climate with low but regular precipitation does not correspond to the same  
118 selection pressure as a highly seasonal climate with a strong drought (even if, the  
119 overall net precipitation might be the same). The few studies that have taken into  
120 account seasonality (Voltas et al. (2008) for *Pinus halepensis*; Soolanayakanahally et  
121 al. (2009) for *Populus balsamifera*) could relate populations with a higher  $W_i$  to sites  
122 with a stronger seasonality of drought, compared with climates with less seasonal  
123 variability. In addition, the variation of soil types between environments is only rarely  
124 taken into account, even though the soil type has a strong impact on the long-term  
125 soil water availability. Raddad and Luukkanen (2006) found a higher  $W_i$  for *Acacia*  
126 *senegal* populations from sandy soils with a low water holding capacity, compared  
127 with soils with a higher clay content.

128 There is thus substantial evidence in the literature on forest trees which suggests  
129 that population differences in  $\delta^{13}\text{C}$ , observed in a common environment, are linked to

130 environmental differences in their original locations. In many cases, a higher  $W_i$  is  
131 observed for populations from drier sites, but a few examples also show a lower  $W_i$  at  
132 drier sites, supporting the interpretation of population differences in  $W_i$  as an indicator  
133 of differences in ecological strategies. To facilitate the interpretation of variations in  $W_i$   
134 among populations in terms of adaptive strategies, a comprehensive characterisation  
135 of the strength and timing of the soil water deficit seems necessary. Moreover,  
136 adaptive strategies should also be explored by analysing the underlying functional  
137 causes of the observed diversity in  $W_i$ .

### 138 **How to interpret variations in $W_i$ in terms of underlying traits?**

139 Hu et al. (2021) found significant population differences for  $\delta^{13}\text{C}$  and leaf nitrogen  
140 related traits in *Salix eriocephala*. They found higher mean  $W_i$  for populations with a  
141 cooler, shorter growing season and suggested that  $W_i$  differences were driven by  
142 photosynthetic capacity. This has also been found for *Alnus sinuata* and *Populus*  
143 *balsamifera* populations (Benowicz et al. 2000, Soolanayakanahally et al. 2009,  
144 respectively), whether using  $W_i$  or through using  $W_L$  (the ratio of A to leaf  
145 transpiration).

146 Photosynthetic capacity is one of the major drivers of variation in  $W_i$ ; however, the  
147 resulting net  $\text{CO}_2$  assimilation (A) is closely linked to stomatal conductance ( $g_s$ ). During  
148 an ongoing, increasing soil water deficit, under most environmental circumstances and  
149 for most plants,  $W_i$  increases due to the non-linear nature of the relationship between  
150 A and  $g_s$  (e.g. Epron and Dreyer 1993). That is to say, during an increasing drought, A  
151 is reduced proportionally less than  $g_s$ , until respiration becomes the dominant  
152 component of A (Figure S1 available as Supplementary Data at Tree Physiology  
153 Online; Valladares and Sanchez-Gomez 2006). Because  $W_i$  is the ratio of  $A/g_s$ , an  
154 observed genetic diversity in  $W_i$  might be driven by a diversity in A, or in  $g_s$ . Even if a  
155 genetic diversity exists for photosynthetic capacity, it will be less expressed in an  
156 observable diversity of  $W_i$  if A is constrained by a low  $g_s$ . However, the variation in A  
157 that is due to a variation in photosynthetic capacity increases with increasing  $g_s$   
158 (Figure S1; e.g. Marguerit et al. 2014). The resulting positive correlations between A  
159 and  $W_i$  have been confirmed within species (e.g. Aranda et al. 2017). Under certain  
160 environmental conditions, a genetic diversity in photosynthetic capacity can therefore  
161 clearly play a role in observed differences in  $W_i$  among populations.

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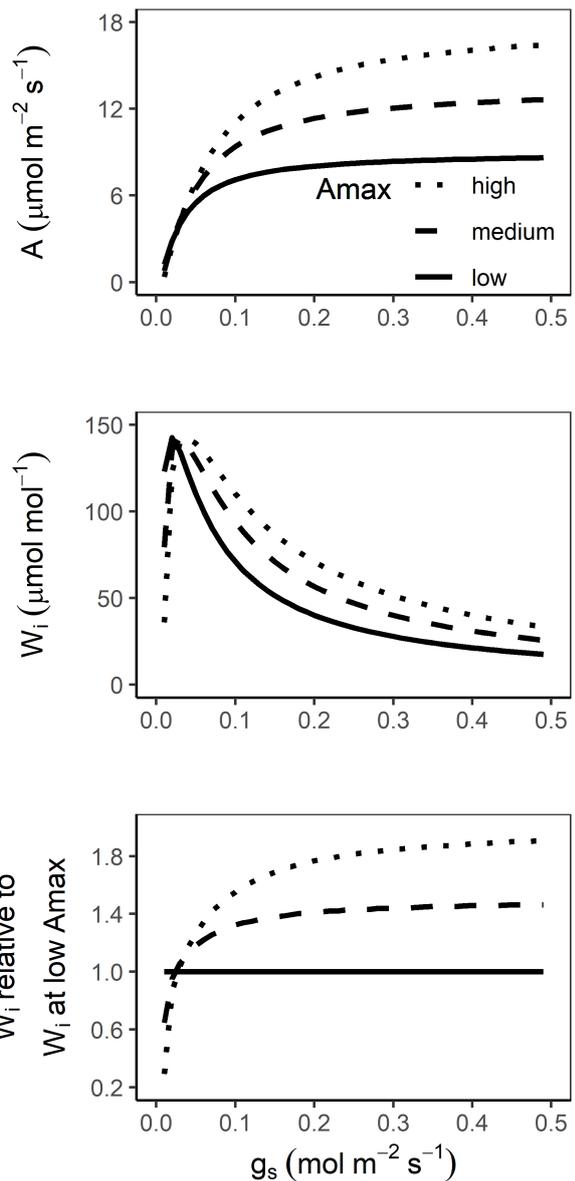


Figure S1: Relationship between stomatal conductance to water vapour ( $g_s$ ) and net CO<sub>2</sub> assimilation (A) and leaf intrinsic water use efficiency ( $W_i$ ) for three different levels of photosynthetic capacity ( $A_{\text{max}}$ ), and  $W_i$  relative to its value at low  $A_{\text{max}}$ . We used a simple Michaelis-Menten kinetics equation with a competitive effect of O<sub>2</sub> with three different values of  $A_{\text{max}}$  (20, 30 and 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The Michaelis constant of the RuBisCO for CO<sub>2</sub> and the inhibition constant for O<sub>2</sub> were set to 270 ppm and 42% respectively. The ambient concentration of CO<sub>2</sub> and O<sub>2</sub>, and the leaf to air vapour pressure difference were set to 400 ppm, 20% and 1 kPa respectively. In this calculation, the photon flux density was assumed not to limit A.

Hu et al. (2021) used leaf nitrogen content as a proxy for photosynthetic capacity. Theoretical considerations demonstrate that compounds involved in photosynthesis could account for well over three-quarters of total leaf nitrogen (Field and Mooney 1986) and for several plant species, photosynthetic capacity was found to correlate with total leaf nitrogen (Evans 1989, Takashima et al. 2004). This is however not always the case, especially at the within species level, when soil nitrogen does not vary and is not limiting (Roussel et al. 2009). One reason for this might be that changes in leaf structure, such as an increased leaf mass per area (LMA), can be linked to a higher investment of nitrogen into cell walls (Takashima et al. 2004). This results in lower photosynthetic capacity for a similar bulk leaf nitrogen content.

198 Furthermore, other leaf anatomical traits may influence photosynthetic capacity  
199 (Niinemets 1999) and modulate the photosynthesis-nitrogen relationship (Reich et al.  
200 1998). Therefore, an interpretation of bulk leaf nitrogen content as a proxy for  
201 photosynthetic capacity could be improved if LMA, leaf thickness, and leaf tissue  
202 density were measured simultaneously, on the same leaves. In addition,  
203 measurements of stomatal density, size and depth as well as vein density would allow  
204 for the calculation of a theoretical stomatal conductance (McElwain et al. 2016). Such  
205 a comprehensive set of leaf traits improves the understanding of the evolution of  
206 functional trait syndromes (Chapin III et al. 1993, Arntz and Delph 2001), and  
207 therefore the interpretation in terms of ecological strategies.

208 Hu et al (2021) used the ratio of carbon to nitrogen in leaves (C/N) as an easily  
209 accessible, time integrated estimator of nitrogen use efficiency (NUE; based on  
210 Patterson et al. 1997). A more process-based version of this trait is the photosynthetic  
211 nitrogen use efficiency (PNUE) - the ratio between photosynthetic capacity and leaf  
212 nitrogen content (Chapin 1980). Because both efficiencies (water and nitrogen)  
213 depend on photosynthesis, a relationship is expected. Field et al. (1983) observed a  
214 trade-off between PNUE and  $W_L$  among evergreen species from the central coast of  
215 California. They concluded that species native to the driest sites tended to conserve  
216 water, but showed a lower photosynthetic carbon gain per unit of leaf nitrogen,  
217 whereas species native to wetter sites used more water but showed a greater carbon  
218 gain per unit of leaf nitrogen. Reich et al. (1989) hypothesized, that plants would  
219 maximize the use efficiency of the most limiting resource, resulting in the suggested  
220 trade-off. Their data and others (Wang et al. 1998) support this hypothesis and show  
221 that when water is limiting,  $W_L$  increases and when nitrogen is limiting, PNUE  
222 increases. Hu et al (2021) also found a negative correlation between  $\delta^{13}\text{C}$  and C/N  
223 across all their individual measurements of heart-leaved willow, but not among  
224 populations, even though both traits demonstrated significant population effects. This  
225 could suggest that the trade-off between water and nitrogen use efficiency,  
226 respectively approximated by  $\delta^{13}\text{C}$  and C/N, might not be associated with local  
227 adaptation in heart-leaved willow, but rather with plant intrinsic functioning. However,  
228 there are also examples in the literature where a significant correlation between  $W_i$   
229 and PNUE was found at the population level (Gornall and Guy 2007).

### 230 **Does diversity in $\delta^{13}\text{C}$ reflect variation in whole plant water use efficiency?**

231  $\delta^{13}\text{C}$  reflects  $W_i$  at the leaf level. However, in the context of adaptation to drought,  
232 some thoughts are necessary on the relationship between whole plant TE, which

233 reflects whole plant carbon gain and water losses, and leaf bulk  $\delta^{13}\text{C}$  (Figure 1), which  
234 is used in the majority of diversity studies. Whole plant TE, which has been studied for  
235 a long time (Brendel 2021), is highly relevant in agriculture (e.g. Tallec et al. 2013,  
236 Vadez et al. 2014) and in forest ecology (e.g. Bates 1923, Zhang and Marshall 1994, Li  
237 et al. 2000, Cernusak et al. 2007a).

238 A first aspect for consideration is the relationship between processes expressed per  
239 leaf area ( $A$ ,  $g_s$ ), and the whole plant leaf area. The total leaf area is a major driver for  
240 cumulative water loss through transpiration; however, it has been shown for *Populus*  
241 *nigra* genotypes that a high total leaf area can be overcompensated by a low per leaf  
242 area transpiration rate (Bogeat-Triboulot et al. 2019). Carbon allocation to different  
243 plant organs matters for plant adaptive strategies, not only in terms of total leaf area,  
244 but also in terms of carbon allocation to the root system. Moreover, from a forestry  
245 point of view, the relationship between the carbon invested into roots and in the above  
246 ground biomass is important, and the latter has been used to calculate an above-  
247 ground TE ( $W_p$  in Figure 1). Significant differences have been observed for the biomass  
248 allocation to the roots compared with the shoots among *Pinus pinaster* families  
249 (Fernandez et al. 2006) and also among *Cedrus libani* provenances (Ducrey et al.  
250 2008), where provenances from dry sites had larger root systems than those from wet  
251 sites. Allocating more biomass to the root system will reduce the available amount of  
252 carbon for stem growth, but a larger root system could be a drought avoidance trait.  
253 As highlighted by Blum (2009) for crop yield improvement under drought, an effective  
254 use of water, even at the expense of a high water use efficiency, could be more  
255 relevant for tree growth in dry areas.

256 Further, TE integrates whole plant functioning, whereas leaf bulk  $\delta^{13}\text{C}$  represents the  
257 functioning of one or only a few, often fully sunlit, leaves. But even though fully sunlit  
258 leaves make up only a fraction of the photosynthesising and transpiring total leaf area  
259 of a tree, they are likely a major contributor to the whole plant  $\text{CO}_2$  assimilation or  
260 transpiration, and therefore are, up to a certain point, representative of the total plant  
261 functioning. In addition, it is clear that this aspect is even less crucial for young  
262 seedlings grown hydroponically in a greenhouse, as in Hu et al. (2021), compared with  
263 stands with closed canopies.

264 A second aspect are the traits that are involved in TE but not in leaf level  $W_i$ , such  
265 as unproductive water losses, and carbon losses during the night and from non-  
266 photosynthetic organs (Farquhar et al. 1989, Cernusak et al. 2008). For example, leaf  
267  $\delta^{13}\text{C}$  captured well the variability of  $W_i$  among several *Acacia* species, whereas

268 differences in carbon use efficiency or the relative unproductive water losses disrupted  
269 the relationship between TE and  $\delta^{13}\text{C}$  (Konate et al. 2016). Even though all of these  
270 traits can also vary genetically among genotypes or populations, strong correlations  
271 have nevertheless been observed between TE and  $W_i$  (or  $W_L$ ) within tree species,  
272 either driven by environmental variations, such as different drought levels or soil  
273 fertility (Osorio and Pereira 1994, Cernusak et al. 2007, respectively), or by within  
274 species genetic diversity (Zhang et al. 1994, Sun et al. 1996, Roupsard et al. 1998, Li  
275 2000). However, it is clear that more research is needed on the genetic co-variation of  
276 the traits underlying TE and their relationship to the plant's ecological strategy.

### 277 **Is $\delta^{13}\text{C}$ a promising physiological proxy to improve forest genetic resources?**

278 Hu et al. (2021) reported an absence of a trade-off between water and nitrogen use  
279 efficiencies and suggested that it is therefore possible to capture additive genetic  
280 variation of both. Because  $\delta^{13}\text{C}$  can be easily measured on a large number of samples,  
281 it is tempting to use  $\delta^{13}\text{C}$  for tree breeding to select genotypes with high water use  
282 efficiency, especially when positive genetic gains can be achieved without  
283 compromising growth, wood quality and other adaptive and economic traits (Cumbie  
284 et al. 2011, Marguerit et al. 2014, Bartholomé et al. 2015, Bouvet et al. 2020).  
285 Furthermore,  $\delta^{13}\text{C}$  is a promising trait for the characterisation of within population  
286 functional diversity to foster forest resilience (Messier et al. 2019), especially for the  
287 Mediterranean area, where the introduction of less water demanding ecotypes, in the  
288 frame of an assisted migration program, could increase resilience (Bussotti et al.  
289 2015). It is however important to ensure that variation in  $\delta^{13}\text{C}$  corresponds to variation  
290 in TE, and therefore accounts for an adaptive strategy. Other than the possibility of  
291 increasing drought, also the rising  $\text{CO}_2$  concentration in the decades to come would  
292 need to be taken into account to predict the water use efficiency of different genetic  
293 backgrounds. Up to now, the rising  $\text{CO}_2$  concentration has increased water use  
294 efficiency at a global level (Cernusak et al. 2019), because of its impact on  
295 photosynthesis and stomatal conductance. However this trend might slow in future  
296 due to saturation of photosynthesis. Also, the introduction of high TE and high growth  
297 genotypes, which might use more water overall, into existing ecosystems or  
298 plantations needs to be regarded with caution. This is because it has important  
299 economic and political implications, especially in areas where water resources are  
300 critical.

301  
302 **Supplementary Data**

303 Supplementary Data for this article are available at Tree Physiology Online.

304

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307

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311

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