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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 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 CO₂ 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 δ¹³C
 42 and W_i. 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).

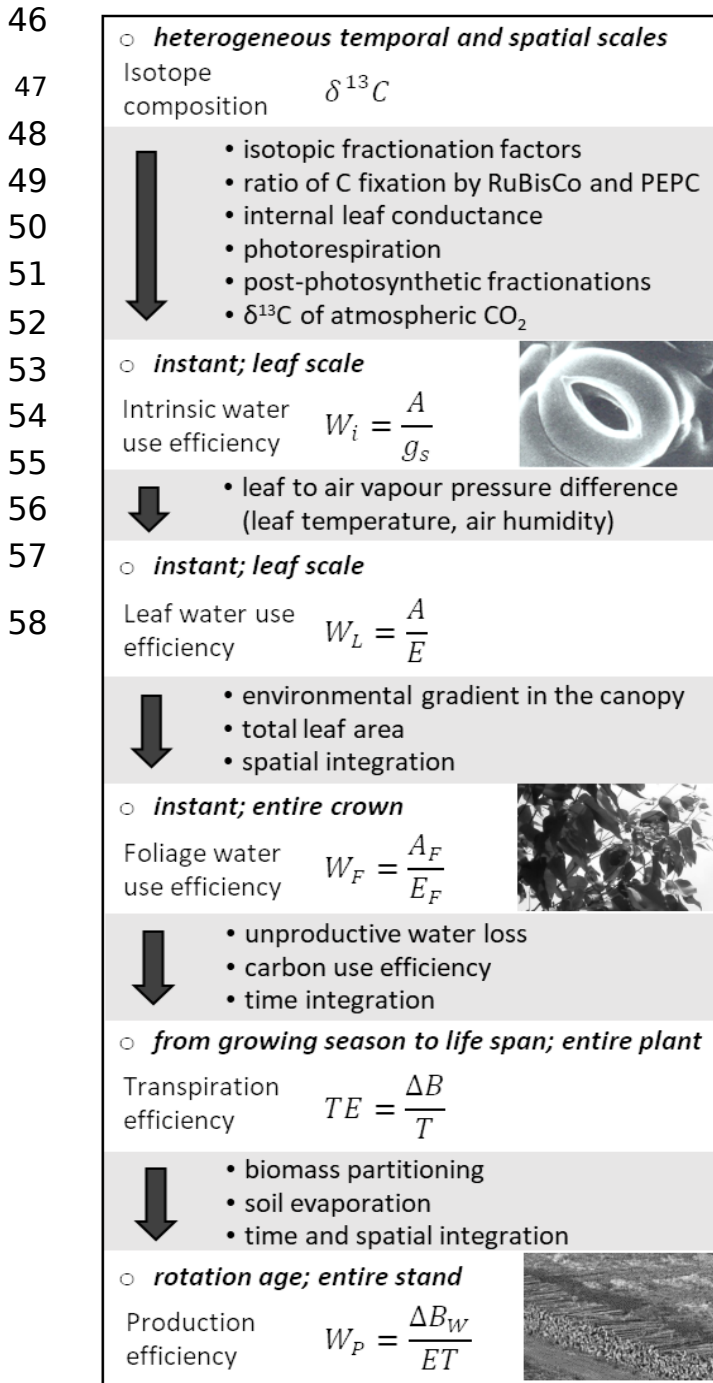


Figure 1: Stable carbon isotope composition (δ¹³C) and water use efficiency at different time and spatial scales. Factors and traits involved at each change of scale are listed on a gray background. ΔB and ΔB_W are total tree biomass and harvested woody biomass, respectively; and T and ET are tree transpiration (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 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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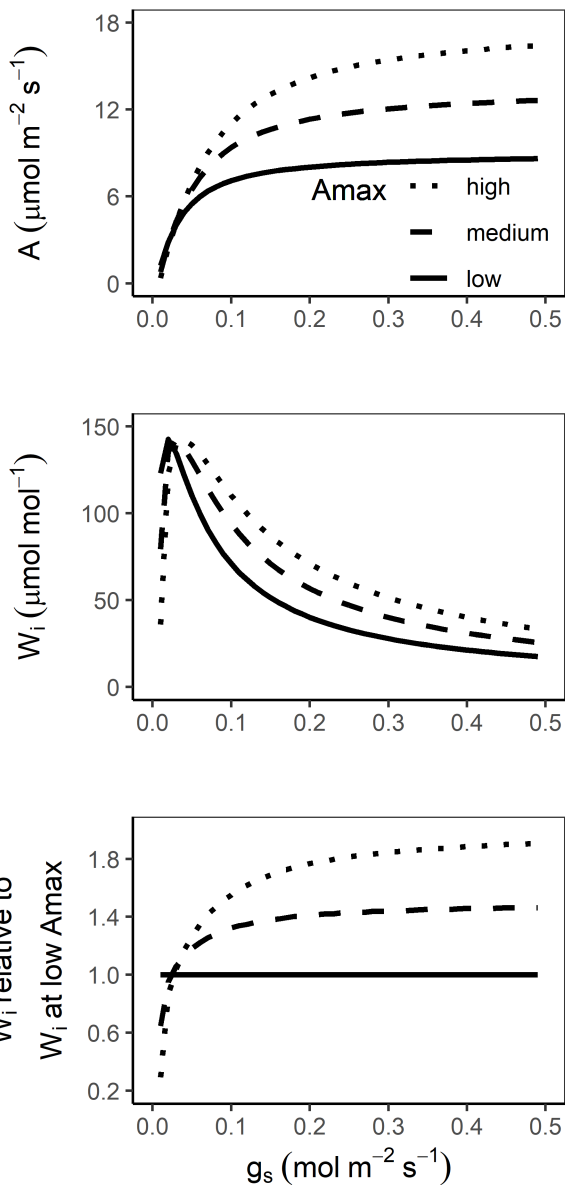


Figure S1: Relationship between stomatal conductance to water vapour (g_s) and net CO₂ assimilation (A) and leaf intrinsic water use efficiency (W_i) for three different levels of photosynthetic capacity (A_{max}), and W_i relative to its value at low A_{max} . We used a simple Michaelis-Menten kinetics equation with a competitive effect of O₂ with three different values of A_{max} (20, 30 and 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The Michaelis constant of the RuBisCO for CO₂ and the inhibition constant for O₂ were set to 270 ppm and 42% respectively. The ambient concentration of CO₂ and O₂, 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 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 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 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.

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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

312 **Bibliography**

Aitken SN, Kavanagh KL, Yoder BJ (1995) Genetic variation in seedling water-use efficiency as estimated by carbon isotope ratios and its relationship to sapling growth in Douglas-fir. *For Genet* 2:199–206.

Aleta N, Vilanova A, Diaz R, Voltas J (2009) Genetic variation for carbon isotope composition in *Juglans regia* L.: relationships with growth, phenology and climate of origin. *Ann For Sci* 66:1–11.

Aranda I, Bahamonde HA, Sánchez-Gómez D (2017) Intra-population variability in the drought response of a beech (*Fagus sylvatica* L.) population in the southwest of Europe. *Tree Physiol* 37:938–949.

Arntz AM, Delph LF (2001) Pattern and process: evidence for the evolution of photosynthetic traits in natural populations. *Oecologia* 127:455–467.

Bartholomé J, Mabilia A, Savelli B, Bert D, Brendel O, Plomion C, Gion J (2015) Genetic architecture of carbon isotope composition and growth in Eucalyptus across multiple environments. *New Phytol* 206:1437–1449.

Bates CG (1923) Physiological requirements of Rocky Mountain trees. *J Agri Res* 24:97–164.

Bekessy SA, Sleep D, Stott A, Menuccini M, Thomas P, Ennos RA, Burgman MA, Gardner MF, Newton AC (2002) Adaptation of monkey puzzle to arid environments reflected by regional differences in stable carbon isotope ratio and allocation to root biomass. *For Genet* 9:63–70.

Benowicz A, Guy RD, El-Kassaby YA (2000) Geographic pattern of genetic variation in photosynthetic capacity and growth in two hardwood species from British Columbia. *Oecologia* 123:168–174.

Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Res* 112:119–123.

Bogeat-Triboulot MB, Buré C, Gerardin T, Chuste PA, Le Thiec D, Hummel I, Durand M, Wildhagen H, Douthe C, Molins A, Galmés J, Smith HK, Flexas J, Polle A, Taylor G, Brendel O (2019) Additive effects of high growth rate and low transpiration rate drive differences in whole plant transpiration efficiency among black poplar genotypes. *Environ Exp Bot* 166:103784.

- Bouvet J-M, Ekomono CGM, Brendel O, Laclau J-P, Bouillet J-P, Epron D (2020) Selecting for water use efficiency , wood chemical traits and biomass with genomic selection in a Eucalyptus breeding program. *For Ecol Manag* 465:118092.
- Brendel O (2021) The relationship between plant growth and water consumption: a history from the classical four elements to modern stable isotopes. *Ann For Sci* 78:47.
- Bussotti F, Pollastrini M, Holland V, Brüggemann W (2015) Functional traits and adaptive capacity of European forests to climate change. *Environ Exp Bot* 111:91-113.
- Campitelli BE, Des Marais DL, Juenger TE (2016) Ecological interactions and the fitness effect of water-use efficiency: Competition and drought alter the impact of natural MPK12 alleles in *Arabidopsis*. *Ecol Lett* 19:424-434.
- Cernusak LA, Winter K, Aranda J, Turner BL (2008) Conifers, Angiosperm Trees, and Lianas: Growth, Whole-Plant Water and Nitrogen Use Efficiency, and Stable Isotope Composition ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of Seedlings Grown in a Tropical Environment. *Plant Physiol* 148:642-659.
- Cernusak LA, Winter K, Aranda J, Turner BL, Marshall JD (2007) Transpiration efficiency of a tropical pioneer tree (*Ficus insipida*) in relation to soil fertility. *J Exp Bot* 58:3549-3566.
- Cernusak LA, Haverd V, Brendel O, Thiec DL, Guehl J, Cuntz M (2019) Robust response of terrestrial plants to rising CO₂. *Trends in Plant Science* 24:578-586.
- Chapin FS (1980) The Mineral Nutrition of Wild Plants. *Annu Rev Ecol Syst* 11:233-260.
- Chapin III FS, Autumn K, Pugnaire F (1993) Evolution of suites of traits in response to environmental stress. *Am Nat* 142:S78-S92.
- Cregg BM, Zhang JW (2001) Physiology and morphology of *Pinus sylvestris* seedlings from diverse sources under cyclic drought stress. *For Ecol Manag* 154:131-139.
- Cumbie WP, Eckert A, Wegrzyn J, Whetten R, Neale D, Goldfarb B (2011) Association genetics of carbon isotope discrimination, height and foliar nitrogen in a natural population of *Pinus taeda* L. *Heredity* 107:105-114.
- Ducrey M, Huc R, Ladjal M, Guehl JM (2008) Variability in growth, carbon isotope composition, leaf gas exchange and hydraulic traits in the eastern Mediterranean cedars *Cedrus libani* and *C. brevifolia*. *Tree Physiol* 28:689-701.
- Ehleringer JR (1993) Variation in Leaf Carbon-Isotope Discrimination in *Encelia farinosa* : Implications for Growth Competition and Drought Survival. *Oecologia* 95:340-346.
- Epron D, Dreyer E (1993) Long-term effects of drought on photosynthesis of adult oak trees [*Quercus petraea* (Matt.) Liebl and *Quercus robur* L.] in a natural stand. *New Phytol* 125:381-389.
- Eriksson G, Jonsson A, Lauteri M, Pliura A (2005) Genetic variation in drought response of *Castanea sativa* Mill. seedlings. *ISHS Acta Hortic Proc Third Int Chestnut Congr* 693:247-254.

- Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* 78:9–19.
- Fan S, Grossnickle SC, Russell JH (2008) Morphological and physiological variation in western redcedar (*Thuja plicata*) populations under contrasting soil water conditions. *Trees - Struct Funct* 22:671–683.
- Farquhar GD, Hubick KT, Condon AG, Richards RA (1989) Carbon isotope fractionation and plant water-use efficiency. In: Rundel P, Ehleringer J, Nagy K (eds) *Stable Isotopes in Ecological Research*. Springer-Verlag, New York, pp 21–40.
- Fernandez M, Novillo C, Pardos JA (2006) Effects of water and nutrient availability in *Pinus pinaster* Ait. Open pollinated families at an early age: Growth, gas exchange and water relations. *New For* 31:321–342.
- Field C, Merino J, Mooney HA (1983) Compromises between water-use efficiency and nitroge-use efficiency in five species of California evergreens. *Oecologia* 60:384–389.
- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: *On the Economy of Plant Form and Function*. In: Givnish TJ (ed). Cambridge University Press, Cambridge, pp 25–55.
- Gornall JL, Guy RD (2007) Geographic variation in ecophysiological traits of black cottonwood (*Populus trichocarpa*). *Can J Bot - Rev Can Bot* 85:1202–1213.
- Grossnickle SC, Fan S, Russell JH (2005) Variation in gas exchange and water use efficiency patterns among populations of western redcedar. *Trees - Struct Funct* 19:32–42.
- Hu Y, Guy RD, Soolanayakanahally RY (2021) Genotypic Variation in C and N Isotope Discrimination Suggests Local Adaptation of Heart-Leaved Willow. *Tree Physiol*. <https://doi.org/10.1093/treephys/tpab010> (12 February 2021, date last accessed).
- Kaluthota S, Pearce DW, Evans LM, Letts MG, Whitham TG, Rood SB (2015) Higher photosynthetic capacity from higher latitude: foliar characteristics and gas exchange of southern, central and northern populations of *Populus angustifolia*. *Tree Physiol* 35:936–948.
- Kenney AM, McKay JK, Richards JH, Juenger TE (2014) Direct and indirect selection on flowering time, water-use efficiency (WUE, $\delta^{13}\text{C}$), and WUE plasticity to drought in *Arabidopsis thaliana*. *Ecol Evol* 4:4505–4521.
- Konate NM, Dreyer E, Epron D (2016) Differences in carbon isotope discrimination and whole-plant transpiration efficiency among nine Australian and Sahelian *Acacia* species. *Ann For Sci* 73:995–1003.
- Lauteri M, Pliura A, Monteverdi MC, Brugnoli E, Villani F, Eriksson G (2004) Genetic variation in carbon isotope discrimination in six European populations of *Castanea sativa* Mill. originating from contrasting localities. *J Evol Biol* 17:1286–1296.
- Levitt J (1980) Responses of plants to environmental stresses, Vol.2. Water, radiation, salt and other stresses. Academic Press, New York.

- Li C (2000) Population differences in water-use efficiency of *Eucalyptus microtheca* seedlings under different watering regimes. *Physiol Plant* 108:134–139.
- Li CY, Berninger F, Koskela J, Sonninen E (2000) Drought responses of *Eucalyptus microtheca* provenances depend on seasonality of rainfall in their place of origin. *Aust J Plant Physiol* 27:231–238.
- Lorts CM, Lasky JR (2020) Competition x drought interactions change phenotypic plasticity and the direction of selection on Arabidopsis traits. *New Phytol* 227:1060–1072.
- Lovell JT, Juenger TE, Michaels SD, Lasky JR, Platt A, Richards JH, Yu X, Easlon HM, Sen S, McKay JK (2013) Pleiotropy of *FRIGIDA* enhances the potential for multivariate adaptation. *Proc R Soc B Biol Sci* 280:20131043.
- Marguerit E, Bouffier L, Chancerel E, Costa P, Lagane F, Guehl J-M, Plomion C, Brendel O (2014) The genetics of water-use efficiency and its relation to growth in maritime pine. *J Exp Bot* 65:4757–4768.
- Maximov NA (1929) The plant in relation to water. George Allen & Unwin LTD London.
- McElwain JC, Yiotis C, Lawson T (2016) Using modern plant trait relationships between observed and theoretical maximum stomatal conductance and vein density to examine patterns of plant macroevolution. *New Phytol* 209:94–103.
- Messier C, Bauhus J, Doyon F, Maure F, Sousa-Silva R, Nolet P, Mina M, Aquilué N, Fortin M-J, Puettmann K (2019) The functional complex network approach to foster forest resilience to global changes. *For Ecosyst* 6:21.
- Nguyen-Queyrens A, Ferhi A, Loustau D, Guehl J-M (1998) Within-ring $\delta^{13}\text{C}$ spatial variability and interannual variation in wood cellulose of two contrasting provenances of *Pinus pinaster*. *Can J For Res* 28:766–773.
- Niinemets Ü (1999) Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol* 144:35–47.
- Osorio J, Pereira JS (1994) Genotypic differences in water-use efficiency and C-13 discrimination in *Eucalyptus globulus*. *Tree Physiol* 14:871–882.
- Patterson TB, Guy RD, Dang QL (1997) Whole-plant nitrogen- and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. *Oecologia* 110:160–168.
- Raddad EY, Luukkanen O (2006) Adaptive genetic variation in water-use efficiency and gum yield in *Acacia senegal* provenances grown on clay soil in the Blue Nile region, Sudan. *For Ecol Manag* 226:219–229.
- Reich P, Ellsworth D, Walters M (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Funct Ecol* 12:948–958.
- Reich PB, Walters MB, Tabone TJ (1989) Response of *Ulmus americana* seedlings to varying nitrogen and water status. 2 Water and nitrogen use efficiency in photosynthesis. *Tree Physiol* 5:173–184.

- Roupsard O, Joly HI, Dreyer E (1998) Variability of initial growth, water-use efficiency and carbon isotope discrimination in seedlings of *Faidherbia albida* (Del.) A. Chev., a multipurpose tree of semi-arid Africa. Provenance and drought effects. *Ann Sci For* 55:329–348.
- Roussel M, Le Thiec D, Montpied P, Ningre N, Guehl J-M, Brendel O (2009) Diversity of water use efficiency among *Quercus robur* genotypes: contribution of related leaf traits. *Ann For Sci* 66:408.
- Soolanayakanahally RY, Guy RD, Silim SN, Drewes EC, Schroeder WR (2009) Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). *Plant Cell Environ* 32:1821–1832.
- Sun ZJ, Livingston NJ, Guy RD, Ethier GJ (1996) Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce (*Picea glauca* (Moench) Voss) seedlings. *Plant Cell Environ* 19:887–894.
- Takashima T, Hikosaka K, Hirose T (2004) Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant Cell Environ* 27:1047–1054.
- Tallec T, Béziat P, Jarosz N, Rivalland V, Ceschia E (2013) Crops' water use efficiencies in temperate climate: Comparison of stand, ecosystem and agronomical approaches. *Agri For Met* 168:69–81.
- Vadez V, Kholova J, Medina S, Kakkera A, Anderberg H (2014) Transpiration efficiency: New insights into an old story. *J Ex Bot* 65:6141–6153.
- Valladares F, Sanchez-Gomez D (2006) Ecophysiological traits associated with drought in Mediterranean tree seedlings: Individual responses versus interspecific trends in eleven species. *Plant Biol* 8:688–697.
- Voltas J, Chambel M, Prada M, Ferrio J (2008) Climate-related variability in carbon and oxygen stable isotopes among populations of Aleppo pine grown in common-garden tests. *Trees - Struct Funct* 22:759–769.
- Wang JR, Hawkins CDB, Letchford T (1998) Photosynthesis, water and nitrogen use efficiencies of four paper birch (*Betula papyrifera*) populations grown under different soil moisture and nutrient regimes. *For Ecol Manag* 112:233–244.
- Zhang JW, Fins L, Marshall JD (1994) Stable carbon-isotope discrimination, photosynthetic gas-exchange, and growth differences among western Larch seedlings. *Tree Physiol* 14:531–539.
- Zhang X, Wu N, Li C (2005) Physiological and growth responses of *Populus davidiana* ecotypes to different soil water contents. *J Arid Environ* 60:567–579.

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