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

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Population differences in water use efficiency and adaptation to drought

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

$\delta^{13}C$ variations of plant organic matter reflect variations in intrinsic water use efficiency (W_i, the ratio between A, the net CO_2 assimilation rate and g_s, the stomatal conductance to water vapour). This relationship has been explained by Farquhar et al. (1989) using a mecanistic model of CO_2 fluxes in the leaf and isotopic fractionation factors. Some of the model parameters — listed in Figure 1 — are likely to vary across genotypes or populations and could therefore weaken the relationship between $\delta^{13}C$ and W_i. A number of publications on forest trees have nevertheless shown a strong relationship between these two traits, either when comparing provenances (Grossnickle et al. 2005, Ducrey et al. 2008, Kaluthota et al. 2015) or within family variations (Roussel et al. 2009, Marguerit et al. 2014).

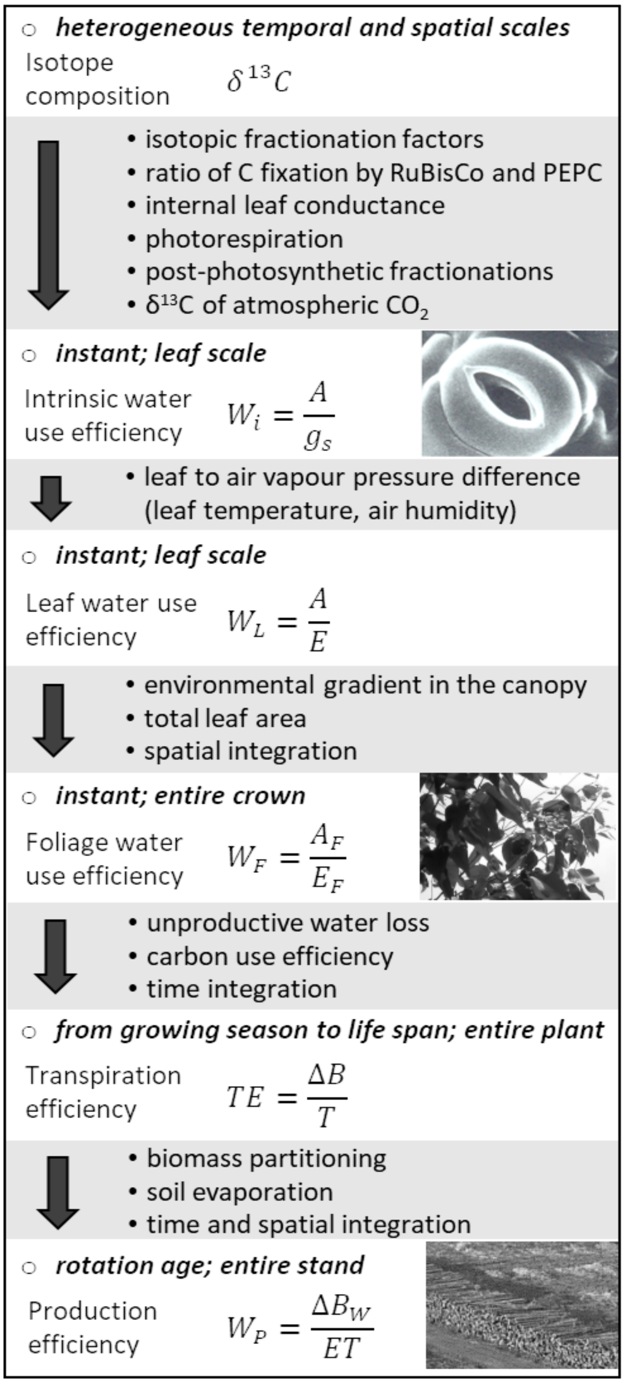

Figure 1: Stable carbon isotope composition ($\delta^{13}C$) and water use efficiency at different time and spatial scales. Factors and traits involved at each change of scale are listed on a gray background. ΔB and ΔB_W are total tree biomass and harvested woody biomass, respectively; and T and ET are tree transpiration (or water use) and stand evapotranspiration, respectively.

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

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

However, this hypothesis is not necessarily the only explanation. To elaborate on an alternative hypothesis, we need to look at water use efficiency at the whole plant level, where it is defined as the ratio of dry biomass accumulation per unit water transpired, namely the transpiration efficiency (TE). Maximov (1929) suggested that there was no direct proportionality between TE and the degree of drought resistance, but that TE was an indicator for the ecological drought adaptation strategy of a plant. He found both high and low TE plants among different herbaceous species that were adapted to dry environments (xerophytes). He then demonstrated that plants with high TE developed rapidly and had a large leaf area, whereas plants with low TE were characterised by large root systems. Similarly, Ehleringer (1993) found high and low W_i individual plants within the species *Encelia farinosa*, a drought-deciduous desert shrub. He hypothesized that such plants with low W_i might allocate more carbon to the root system than those with high W_i. Recent research on *Arabidopsis thaliana* ecotypes has shown that different drought adaptation strategies can exist within one species, where high W_i was suggested to correspond to drought-sensitive and early closing stomata and low W_i to a drought escape strategy due to early flowering (Lovell et al. 2013, Kenney et al. 2014, Campitelli et al. 2016, Lorts and Lasky 2020). These works thus substantiate a second hypothesis, where populations from dry environments would have a low W_i. The evolution of such a strategy would result in a negative relationship between $\delta^{13}C$ and the drought index of the populations, as reported by Hu et al. (2021). Similar results have been found for other tree species, where populations from low precipitation environments had low W_i (Nguyen-Queyrens et al. 1998) or low TE (Fan et al. 2008). But for trees, unlike annual plants, escaping drought is not an option. Therefore, drought adapted trees with a low W_i, due to more open stomata, could either correspond to a drought tolerance strategy, for example by anatomical adaptations reducing vulnerability to cavitation, or to a drought avoidance/water spender strategy through a wide soil exploration by roots. Both strategies would allow stomata to remain open to some extent during drought. Eriksson et al. (2005) demonstrated that European *Castanea sativa* populations from the driest sites showed the lowest W_i, but also had the deepest rooting pattern (Lauteri et al. (2004) and M. Lauteri, personal comm.). This response was similar to that of low TE xerophytes in Maximov's study, and consistent with Ehleringer's hypothesis. On the other hand, drought adapted trees with a high W_i (the first hypothesis above) could correspond to a drought avoidance/water saving strategy, through drought-sensitive, early closing stomata.

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

There is thus substantial evidence in the literature on forest trees which suggests that population differences in $\delta^{13}C$, observed in a common environment, are linked to environmental differences in their original locations. In many cases, a higher W_i is observed for populations from drier sites, but a few examples also show a lower W_i at drier sites, supporting the interpretation of population differences in W_i as an indicator of differences in ecological strategies. To facilitate the interpretation of variations in W_i among populations in terms of adaptive strategies, a comprehensive characterisation of the strength and timing of the soil water deficit seems necessary. Moreover, adaptive strategies should also be explored by analysing the underlying functional causes of the observed diversity in W_i.

How to interpret variations in W_i in terms of underlying traits?

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

Photosynthetic capacity is one of the major drivers of variation in W_i; however, the resulting net CO_2 assimilation (A) is closely linked to stomatal conductance (g_s). During an ongoing, increasing soil water deficit, under most environmental circumstances and for most plants, W_i increases due to the non-linear nature of the relationship between A and g_s (e.g. Epron and Dreyer 1993). That is to say, during an increasing drought, A is reduced proportionally less than g_s, until respiration becomes the dominant component of A (Figure S1 available as Supplementary Data at Tree Physiology Online; Valladares and Sanchez-Gomez 2006). Because W_i is the ratio of A/g_s, an observed genetic diversity in W_i might be driven by a diversity in A, or in g_s. Even if a genetic diversity exists for photosynthetic capacity, it will be less expressed in an observable diversity of W_i if A is constrained by a low g_s. However, the variation in A that is due to a variation in photosynthetic capacity increases with increasing g_s (Figure S1; e.g. Marguerit et al. 2014). The resulting positive correlations between A and W_i have been confirmed within species (e.g. Aranda et al. 2017). Under certain environmental conditions, a genetic diversity in photosynthetic capacity can therefore clearly play a role in observed differences in W_i among populations.

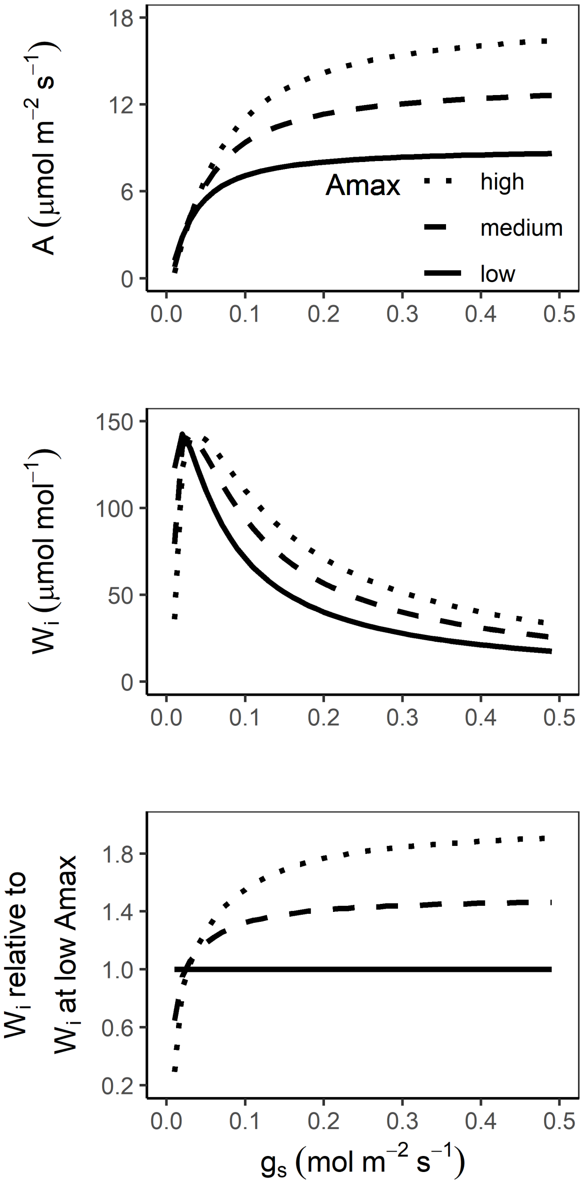

Figure S1: Relationship between stomatal conductance to water vapour (g_s) and net CO_2 assimilation (A) and leaf intrinsic water use efficiency (W_i) for three different levels of photosynthetic capacity (Amax), and W_i relative to its value at low Amax. We used a simple Michaelis-Menten kinetics equation with a competitive effect of O_2 with three different values of Amax (20, 30 and 40 $\mu mol\ m^{-2}\ s^{-1}$). The Michaelis constant of the RuBisCO for CO_2 and the inhibition constant for O_2 were set to 270 ppm and 42% respectively. The ambient concentration of CO_2 and O_2, 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.

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

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

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

$\delta^{13}C$ reflects W_i at the leaf level. However, in the context of adaptation to drought, some thoughts are necessary on the relationship between whole plant TE, which reflects whole plant carbon gain and water losses, and leaf bulk $\delta^{13}C$ (Figure 1), which is used in the majority of diversity studies. Whole plant TE, which has been studied for a long time (Brendel 2021), is highly relevant in agriculture (e.g. Tallec et al. 2013, Vadez et al. 2014) and in forest ecology (e.g. Bates 1923, Zhang and Marshall 1994, Li et al. 2000, Cernusak et al. 2007a).

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

Further, TE integrates whole plant functioning, whereas leaf bulk $\delta^{13}C$ represents the functioning of one or only a few, often fully sunlit, leaves. But even though fully sunlit leaves make up only a fraction of the photosynthesising and transpiring total leaf area of a tree, they are likely a major contributor to the whole plant CO_2 assimilation or transpiration, and therefore are, up to a certain point, representative of the total plant functioning. In addition, it is clear that this aspect is even less crucial for young seedlings grown hydroponically in a greenhouse, as in Hu et al. (2021), compared with stands with closed canopies.

A second aspect are the traits that are involved in TE but not in leaf level W_i, such as unproductive water losses, and carbon losses during the night and from non-photosynthetic organs (Farquhar et al. 1989, Cernusak et al. 2008). For example, leaf $\delta^{13}C$ captured well the variability of W_i among several *Acacia* species, whereas differences in carbon use efficiency or the relative unproductive water losses disrupted the relationship between TE and $\delta^{13}C$ (Konate et al. 2016). Even though all of these traits can also vary genetically among genotypes or populations, strong correlations have nevertheless been observed between TE and W_i (or W_L) within tree species, either driven by environmental variations, such as different drought levels or soil fertility (Osorio and Pereira 1994, Cernusak et al. 2007, respectively), or by within species genetic diversity (Zhang et al. 1994, Sun et al. 1996, Roupsard et al. 1998, Li 2000). However, it is clear that more research is needed on the genetic co-variation of the traits underlying TE and their relationship to the plant's ecological strategy.

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

Hu et al. (2021) reported an absence of a trade-off between water and nitrogen use efficiencies and suggested that it is therefore possible to capture additive genetic variation of both. Because $\delta^{13}C$ can be easily measured on a large number of samples, it is tempting to use $\delta^{13}C$ for tree breeding to select genotypes with high water use efficiency, especially when positive genetic gains can be achieved without compromising growth, wood quality and other adaptive and economic traits (Cumbie et al. 2011, Marguerit et al. 2014, Bartholomé et al. 2015, Bouvet et al. 2020). Furthermore, $\delta^{13}C$ is a promising trait for the characterisation of within population functional diversity to foster forest resilience (Messier et al. 2019), especially for the Mediterranean area, where the introduction of less water demanding ecotypes, in the frame of an assisted migration program, could increase resilience (Bussotti et al. 2015). It is however important to ensure that variation in $\delta^{13}C$ corresponds to variation in TE, and therefore accounts for an adaptive strategy. Other than the possibility of increasing drought, also the rising CO_2 concentration in the decades to come would need to be taken into account to predict the water use efficiency of different genetic backgrounds. Up to now, the rising CO_2 concentration has increased water use efficiency at a global level (Cernusak et al. 2019), because of its impact on photosynthesis and stomatal conductance. However this trend might slow in future due to saturation of photosynthesis. Also, the introduction of high TE and high growth genotypes, which might use more water overall, into existing ecosystems or plantations needs to be regarded with caution. This is because it has important economic and political implications, especially in areas where water resources are critical.

Supplementary Data

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

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