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Use of physiological traits in tree breeding for improved yield in drought-prone environments. The case of *Eucalyptus globulus*

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Abstract

Selecting for improved growth in drought-prone environments may lead to a trade-off between traits related to both growth and drought resistance. This paper provides a review of the use of physiological traits in breeding for yield improvement in water-limited environments. Plant responses to water stress can be grouped into strategies, which are species-specific. Once a species drought resistance strategy is known, several physiological traits can be selected to be used in the species breeding program. Despite there are multiple physiological traits involved in plant responses to drought, only a few of them have been actually used to improve both growth and drought resistance. This review highlights the relevance of stomatal conductance and water-use efficiency as well as hydraulic traits in breeding for improved growth in drought-prone environments. It is illustrated with unpublished results obtained in several research programmes that share a common objective: improving *Eucalyptus globulus* growth and survival in south-western Spain throughout early selection based on morpho-physiological traits.

Key words: Drought tolerance strategies, stomatal conductance, water use efficiency, hydraulic conductivity, xylem vulnerability, Tasmanian blue gum.

Resumen

Utilización de parámetros fisiológicos en programas de mejora del crecimiento bajo déficit hídrico

La selección de genotipos con el objetivo de mejorar el crecimiento bajo suministro hídrico limitante exige buscar un equilibrio entre aquellos caracteres que permiten optimizar el crecimiento y los que confieren mayor resistencia a la sequía. En el presente artículo se realiza una revisión del uso de parámetros fisiológicos en programas de mejora establecidos para zonas donde el agua es factor limitante. Las plantas muestran un amplio abanico de respuestas frente al déficit hídrico, que se pueden agrupar en estrategias. Una vez conocida la estrategia de respuesta al estrés hídrico en una especie, se puede abordar la selección parámetros fisiológicos a utilizar como herramientas de mejora. Entre estos parámetros destacan por su interés la conductancia estomática, la eficiencia en el uso del agua y parámetros hidráulicos. La revisión del uso de estos parámetros se ha ilustrado con datos bibliográficos y datos obtenidos en el marco de varios proyectos de investigación, establecidos con un objetivo primordial: mejorar la productividad de las plantaciones de *Eucalyptus globulus* en el suroeste español, mediante programas de mejora que incorporen criterios de selección precoz basados en parámetros morfo-fisiológicos.

Palabras clave: Estrategias de tolerancia a la sequía, conductancia estomática, eficiencia en el uso del agua, conductividad hidráulica, vulnerabilidad a la cavitación, eucalipto.

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Introduction

According to Pereira (1995) we may define stress as any environmental factor that makes growth rate lower than maximum. Water stress is thought to be the main cause of forest and agronomical productivity loss (Flexas *et al.* 2002, Pereira and Pallardy 1989). Tree species cannot escape from drought as annual plants and have developed several drought-tolerance mechanisms, which can be classified following Ludlow (1989) as two major strategies. The avoidance strategy includes responses that lead to avoidance of plant water deficits, such as maximizing water uptake by growing deep roots or decreasing water loss by both elastic or plastic responses. Stomatal control and leaf movements are examples of elastic responses, whereas decreasing leaf size or shedding leaves are plastic responses. Responses under the tolerance strategy may enhance the tolerance of dehydration, like osmotic adjustment.

Species with the avoidance strategy can be water savers or water spenders. The first ones have little osmotic and stomatal adjustment, minimize water loss at early stages of drought and keep high values of leaf water potential (Ludlow 1989). On the other hand, water spenders keep high transpiration rates, photosynthesis and growth. Water spenders may as well tolerate the loss of relatively high amounts of xylem hydraulic conductivity by embolism. Responses under the avoidance strategy may allow plants to survive drought periods of three to four months (Ludlow 1989). To survive longer periods, plants may show dehydration tolerance responses. It is worth noting that each species possesses its own drought resistance strategy, which may be closer to the «Extreme avoidance» or the «Extreme tolerance». Knowing the species strategy as well as possible seems crucial to improve drought resistance.

Unfortunately, most drought tolerance mechanisms tend to lower yield potential. It seems likely that a successful adaptation to drought is related to traits that enhance survival rather than growth (Pereira y Pallardy 1989). This is the case of decreasing water loss through stomatal closure, which also decreases carbon gain. Similarly, increasing water uptake by an enhanced root growth will decrease shoot growth. Interestingly, fast-growing pioneers such as *Populus, Salix* or *Eucalyptus* are characterized by the accumulation of relatively high amounts of shoot biomass, at least in the early stages of life (Pereira and Pallardy 1989). According to this, pioneers should be classified as low drought resistant species. However, drought resistance is quite different in riparian trees such as *Salix* or *Populus* and some *Eucalypt* species, that grow successfully in drought environments around the world (Eldridge *et al.* 1993). These findings highlight once more the challenge of improving growth when water is scarce.

Almost every response to water deficit has a metabolic cost. That is the case of osmotic adjustment, which is defined as the accumulation of solutes that occurs as a result of exposure to water shortage (Turner 1997). Most of these ions interfere with cytosolic enzymes, and are kept in the vacuole. Other solutes, called compatible solutes, must be synthesized to maintain water potential equilibrium within the cell (Taiz and Zeiger 2002). Similarly, osmotic stress regulates the biosynthesis of several proteins that enhance dehydration tolerance. The hydraulic conductivity of shoots has also been found to decrease under water shortage (Pita *et al.* 2003, Tognetti *et al.* 1997, Vander Willigen and Pammenter 1998), probably due to a decrease in the number and/or size of vascular conduits in the xylem (Corcuera *et al.* 2004). This may lead to a more conservative use of soil water and may decrease water use even after drought is released (Eamus *et al.* 2000).

Finally, most trees shed leaves when water is scarce and stomatal closure is not enough to prevent further water loss from plant tissues. Early leaf shedding also implies an important and long-term cost for growth. Investment in leaf area is by far the most important factor in promoting growth during establishment (Pereira 1995), but it is at the expense of investment in other structures, for example wood density and roots. Wood density has been reported to increase resistance to xylem cavitation (Hacke *et al.* 2001, Wikberg and Ögren 2004). Consistent with this, Meinzer (2003) collected data from 27 species showing a tight and positive relationship between diel variation in leaf water potential and wood density.

These observations have led some authors to question the possibility of improving drought resistance without decreasing growth (Wikberg and Ögren 2004). But even if drought-adapted genotypes grow less than others when water is non-limiting, the point is if they do actually grow more when water is scarce.

Despite the existence of many traits related to drought resistance that could be used for yield improvement in water-limited environments, only a few of them have been tested, mainly on agricultural crops. The best suited traits may accomplish with the following characteristics: (1) They have to be easy to measure on large amounts of plants, (2) Genotypic variation must be possible to identify in these traits, (3) They must show an adequate heritability and (4) They must allow tree breeders to identify consistently the best and worst genotypes.

The following will review major results of some physiological traits commonly proposed to be used in breeding for improved drought resistance, such as stomatal conductance, water use efficiency and hydraulic traits. Preliminary results from several research programmes led to investigating the use of morpho-physiological traits in early selection of *Eucalyptus globulus* Labill. drought-resistant clones are included. *E. globulus* clones used in this programmes can be classified into two categories: commercial clones, currently used in field plantations in SW Spain, characterized by a high rooting success, such as clone C14, and clones obtained from crosses between C14 and other commercial clones (such as clones h231, h491, h354, h463) or C14 and plants from the highly inbred Wilson's Promontory provenance (such as w4, w349 and w562).

Though osmotic adjustment (OA) has been considered worthy when searching for improved yield under water limiting conditions, it is not included in the present review for several reasons. Firstly, because osmotic adjustment is a time dependent response, and this makes particularly difficult to arrange an experimental design in such a way that all plants from a large number of clones display an adequate degree of osmotic adjustment at the time of measuring. Besides, OA measurements are highly time consuming. Secondly, there are not still concluding results about the ability of OA to enhance plant growth under water deficits (Taiz and Zeiger 2002).

Stomatal conductance

Stomatal closure

Stomatal closure may be considered as the third line of defense against drought, after decreased leaf expansion and enhanced root growth (Taiz and Zeiger 2002). Stomata close during water deficit in response to changes in leaf water potential and/or changes in soil water status. The evidence of the existence of root to shoot chemical signalling has been widely documented using split root culture, where individual plants are grown with roots trained into several soil volumes with different moisture contents (Comstock 2002, Taiz and Zeiger, 2002).

In fact, stomatal closure has been reported to occur during soil drying before any mensurable change in bulk leaf water potential is recorded (Salleo *et al.* 2000). This result may be related to patchy stomatal closure or long-distance chemical signalling between roots and shoots. Abscisic acid (ABA), inorganic ion redistribution and changes in xylem sap pH may act as chemical signals (Taiz and Zeiger 2002). Redistribution and/or biosynthesis of ABA in roots and leaves is very effective in causing stomatal closure. Dehydration of the mesophyll cells triggers the release of ABA stored in the chloroplast and increases the rate of ABA biosynthesis in mesophyll cells. Numerous studies show that ABA synthesis in roots increases in response to soil water deficits (Sauter *et al.* 2001, Davies *et al.* 2002, Comstock 2002). As a result, ABA concentrations in leaves can increase 50-fold. Mutants that lack the ability to produce ABA exhibit permanent wilting under rather moderate levels of water deficit (Taiz and Zeiger 2002).

Species originating from wet environments often lack the ability to close stomata far enough to prevent wilting. In this sense, Sparks and Black (1999) found that *Populus trichocarpa* Torr. & A. Gray populations originating from dry environments were able to close stomata completely (< 1 mmol m^{-2} s^{-1}) and avoided leaf water potential to fall below -1.5 MPa until the 6^{th}–7^{th} day of drought, whereas trees from wet populations wilted by the second day of drought, at higher water potentials. Similarly, Wikberg and Ögren (2004) found that stomatal conductance in plants from the most drought sensitive *Salix* sp clone only decreased when wilting had already started.

In a study carried out under controlled conditions, we measured the steepest decrease in stomatal conductance as hydraulic conductivity decreased in the clone that reached the highest survival in field trials (clone h231, Figure 1). The shallowest decrease in stomatal conductance was measured in the clone with the lowest survival and growth (h491). Plants from this clone showed both a limited ability to use soil water (the maximum values of stomatal conductance were not as high as those measured on clone h231) and a

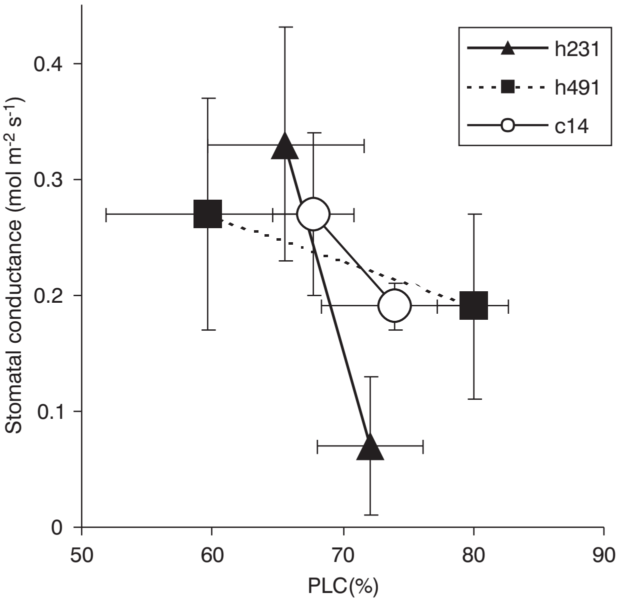

Figure 1. Relationship between stomatal conductance and the average percentage loss of hydraulic conductivity (PLC, see later in this chapter for more details about this trait). Each data is the mean of 5-10 measurements, from a greenhouse experiment carried out on three *E. globulus* clones. At age three years, the percentage of survival was 95%, 80% and 50% and mean height was 14 m, 12.4 m and 8.4 m for clones h231, c14 and h491 respectively.

limited capacity to avoid hydraulic conductivity loss throughout stomatal closure.

Stomata must operate to maximize assimilation while minimizing damage from dehydration. However, we lack a clear understanding of how water stress signals, perceived at root and leaf locations, are integrated to control stomatal conductance and how they differ between plants of different drought tolerance strategies (Sperry, 2000).

Water stress limits photosynthesis both through stomatal limitations to gas exchange and metabolic impairment (Flexas *et al.* 2002). Under mild to moderate drought, stomatal conductance seems to be the main cause of decreased photosynthesis (Medrano *et al.* 2002). A tight relationship between net photosynthetic rate and stomatal conductance has been obtained both in C_4 (Meinzer 2003) and C_3 species (Medrano *et al.*2002). For C_3 species, it is worth noting that there is a low degree of scatter around the regression line, fitted to grapevine data, and data from other species (Medrano *et al.* 2002) or *Eucalyptus globulus* (Fig. 2).

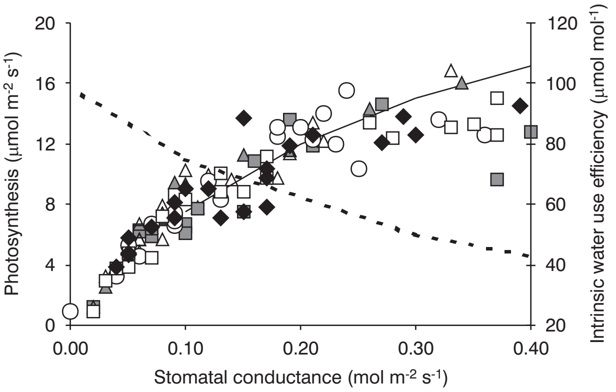

Figure 2. Relationship between stomatal conductance, net photosynthetic rate (unbroken line) and intrinsic water use efficiency (dashed line) in glasshouse-grown *Eucalyptus globulus* (Pita, unpublished). The regression line was calculated for field-grown grapevines by Flexas (2000).

The strong relationship between stomatal conductance and several photosynthetic parameters lead Medrano *et al.* (2002) to suggest the use of stomatal conductance as a reference parameter to assess the degree of water stress. Besides these results, stomatal conductance may be a useful tool in breeding for improved yield in drought-prone environments because stomatal conductance provides a crucial link between (1) water loss by transpiration and carbon gain (and thus growth) and (2) water saving by stomatal closure and increased heat stress. Moreover, stomatal conductance has been reported to be under genetic control in Pima cotton *(Gossypium barbadense* L.) (Percy *et al.* 1996, Lu *et al.* 2000), and a useful tool to predict higher yields in hot environments (Lu *et al.* 1998). According to this, stomatal conductance has been used to assess the effects of breeding for improved drought resistance on growth (Wikberg and Ögren 2004) and the impact of selection for growth and wood quality on drought resistance (Wang *et al.* 2003).

Water Use Efficiency

Following Turner (1997), we define water use efficiency as the dry matter produced per unit evapotranspiration. When dry matter production is related to the amount of water lost by transpiration, we shall talk of transpiration efficiency. Finally, instantaneous water use efficiency and intrinsic water use efficiency will be used to define the ratio of net photosynthetic rate to the rate of transpiration and stomatal conductance respectively.

As drought progresses, the proportional decrease in net photosynthetic rate is less than the decline in stomatal conductance, leading to an increase in intrinsic water use efficiency (Fig. 2). A higher water use efficiency (WUE) may be related to either higher growth and photosynthesis or to lower growth rates due to stomatal closure. Unfortunately, the tendency for instantaneous WUE to increase as stomata close (Fig. 2) means that selecting for improved WUE may often be the same as selecting for low productivity. However, maximizing long-term water use efficiency does not necessarily imply continuous maximization of the instantaneous WUE (Jones 1993). Plants display a continuum of responses to drought ranging from predominantly leaf gas exchange to whole plant morphological adjustments; and it is the long-term expression of all these responses that determines productivity.

Long-term water use efficiency can be estimated from the analysis of carbon isotope discrimination in plant tissues. Photosynthesis tends to discriminate against the heaviest isotope of carbon (^{13}C) and thus the ratio of ^{13}C / ^{12}C in plant tissues is usually lower than the corresponding ratio for the air. The isotopic composition of plant tissues (δ) is calculated as:

$$\delta\ (‰) = ((Rp/Rs) - 1)\ 1000$$

and carbon isotope discrimination (Δ) is defined as:

$$\Delta\ (‰) = ((Ra/Rp) - 1)\ 1000$$

Where Ra, Rp and Rs are the molar abundance ratios ^{13}C / ^{12}C of the air, the plant and a standard, respectively. Traditionally, a fossil belemnite from the PeeDee Formation (PDB) has been used as a standard.

Δ and δ are interrelated:

$$\Delta\ (‰) = ((\delta a - \delta p) / (1000 + \delta p))\ 1000$$

Where δa and δp are the isotopic composition of the air and the plant, respectively.

Both transpiration efficiency and carbon isotope discrimination are related to the ratio of internal (mesophyll) to external (air) CO_2 concentration. The experimental confirmation of the relationship between transpiration efficiency and Δ (Sun *et al.* 1996, Wright *et al.* 1993) as well as a substantial genetic variation in Δ values (Turner 1997) focused a great interest on screening the possibility of using Δ in breeding programmes.

Working with three *Eucalyptus camaldulensis* Dehnh. provenances under controlled conditions, Hubick and Gibson (1993) measured the highest carbon isotope discrimination (Δ) and the lowest transpiration efficiency in the provenance originating from the driest environment. Pita *et al.* (2001) reported similar results in field-grown *E. globulus* provenances: the highest Δ was measured in plants from the provenance that achieved the highest growth and survival under a xeric Mediterranean climate. Similarly, Bond and Stock (1990) and Le Roux *et al.* (1996) reported higher productivity in the less transpiration-efficient genotypes of *Eucalyptus grandis* W. Hill *ex* Maiden.

These results suggest that the best adapted genotypes have an enhanced ability to utilize water when available, maximizing short-term carbon gain. It has been suggested that an early stomatal closure may lead to a more gradual use of soil water (Sperry 2000). However, this seems likely to be no advantage in natural environments, where competitors could use the available soil water (Jones 1993). In a study carried out in *E globulus* plantations established in South-western Spain, Pita *et al.* (2001) found that Δ increases with increasing failures in neighbouring trees and Δ decreases with stand age. Both results show the effect of competition for water on Δ and further explain the success of less water-efficient genotypes in South-western Spain. Moreover, when Δ is measured in wood cores (Pita *et al.* 2001), Δ is an index of water availability during the time of the year when the plant is actively growing, ie, Springtime. When water is scarce, both photosynthesis and growth decline (Figure 3) and thus only a small fraction of carbon is fixed under severe drought conditions.

Hydraulic traits

Definitions

Hydraulic conductance (k) is a measure of the amount of water flow driven by a given pressure ($g\ s^{-1}\ MPa^{-1}$). It can be estimated at the whole plant level (K_{plant}), using a high-pressure flow meter (Tyree *et al.*

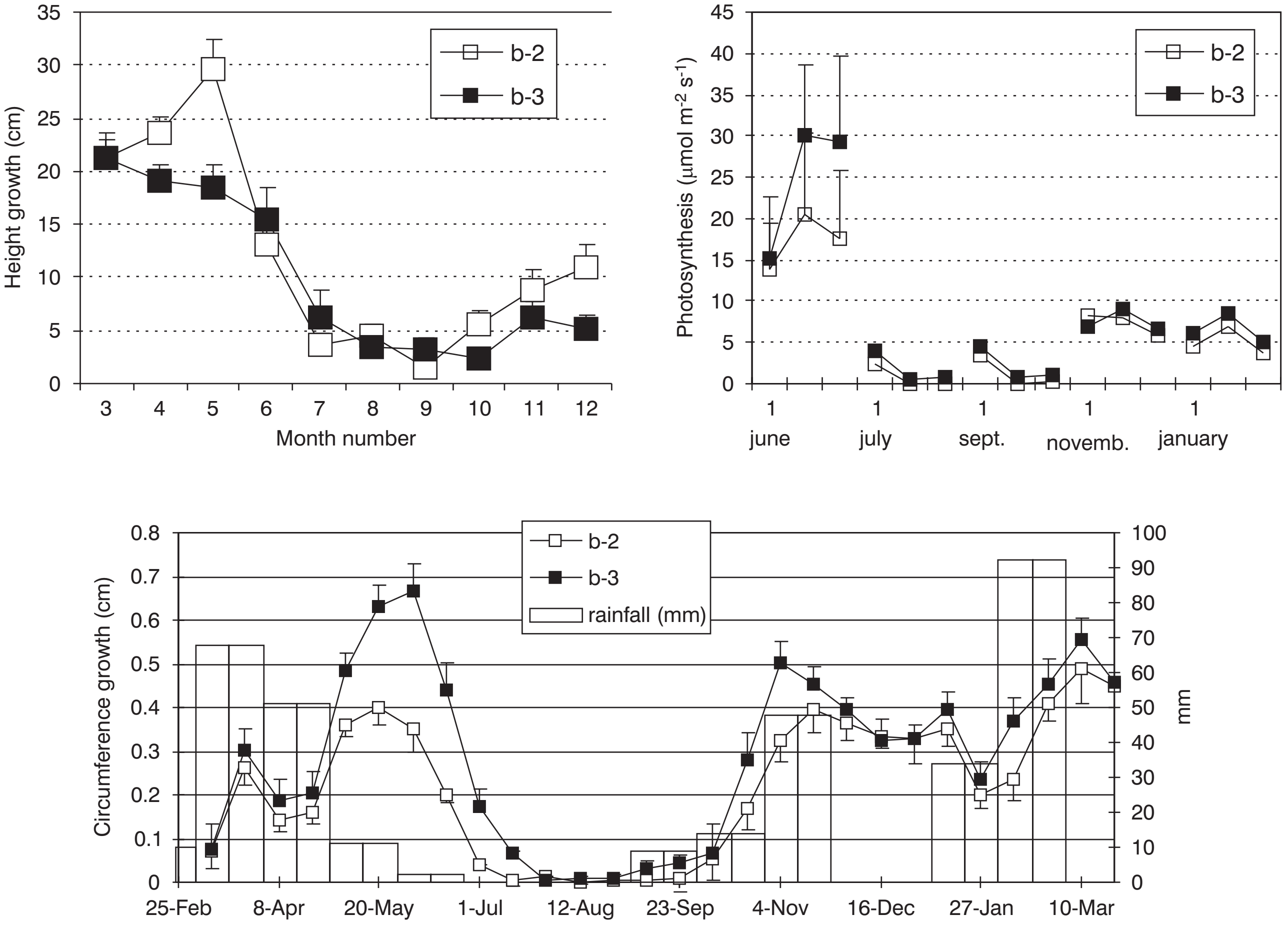

Figure 3. Height growth, circumference growth and photosynthesis measured over one year in a plantation established with two provenances (b-2 and b-3) of *Eucalyptus globulus* ssp bicostata in South-western Spain. Photosynthesis was measured in the early morning (1), at midday (2) and late afternoon (3). Photosynthesis and height: n = 25 data per date and provenance, circumference: n = 17 data per date and provenance. Initial height: 7.9 and 7.2 m for b-3 and b-2 respectively. (Pita 1998).

1995). It can be also measured in different organs such as shoots, stem segments, roots, petioles or leaf midribs, using several techniques (Tyree and Dixon 1983, Sperry *et al.* 1988, Cochard *et al.* 1992, Salleo *et al.* 1992, Van Lepren *et al.* 2001, Hubbard *et al.* 2001, Sack *et al.* 2002). Hydraulic conductivity differs from hydraulic conductance in being a length-specific measure. Hydraulic conductivity can be normalized by the amount of leaf area supplied by the stem (leaf conductivity k_L), the xylem functional area (specific conductivity *ks*) or the cross-sectional area of the stem used for measurements (permeability, *P*). Under soil water deficit and/or high vapour pressure deficits, water loss may exceed water supply and some xylem conduits may become embolized (air filled), leading to a loss of hydraulic conductance. A vulnerability curve defines the relationship between the percentage loss of hydraulic conductance and xylem water potential.

Hydraulic conductance and Stomatal conductance

According to the Ohm's law analogy for water flux, stomatal conductance (*gs*) and whole plant hydraulic conductance (K_{plant}) are interrelated:

$$gs = K_{plant}\,(\Psi s - \Psi \ell)\ D^{-1},$$

where D is the leaf to air vapour pressure gradient, Ψ*s* and Ψℓ the soil and leaf water potentials respectively and (Ψ*s* – Ψℓ) = ΔΨ is the driving force for water movement from roots to leaves. Thus, plants can maximize stomatal conductance, and therefore also CO_2 fixation and productivity, either by developing high hydraulic conductances or generating large $\Delta\Psi s$. Several studies have shown a correlation between stem segment hydraulic conductivity and tree growth rates (Tyree 2003).

In a study carried out with eleven woody species from contrasting habitats growing in the same place, Nardini and Salleo (2000) found a positive relationship between maximum shoot hydraulic conductance and maximum stomatal conductance. Similarly, Hubbard *et al.* (2001) found a tight linear relationship (R^2 = 0.9) between whole-plant leaf specific hydraulic conductance and both stomatal conductance and net photosynthetic rate in *Pinus ponderosa* Dougl. *ex* Laws.

In a greenhouse study, *E. globulus* clones showed different responses to decreasing *k* (Fig. 4). Plants from clone w562 reached high values of stomatal conductance under moderate water deficit and were very responsive to low values of *k*, whereas clone w349 was relatively unresponsive to decreasing *k*. Clone w4 showed an intermediate response (Fig. 4).

Hydraulic conductance and carbon-isotope discrimination

Carbon isotope discrimination can be related to hydraulic conductivity (Fig. 5). Both Δ and hydraulic conductivity increase under irrigation (Williams and Ehleringer 1996). Moreover, conifers tend to have a greater $\delta^{13}C$ than deciduous trees, suggesting that the narrower conducting elements in conifers result in a greater stomatal constraint (Panek 1996).

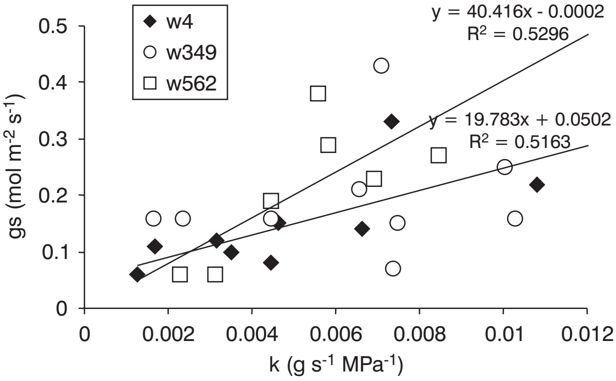

Figure 4. Relationship between hydraulic conductance (k) and stomatal conductance (gs). Stomatal conductance was measured on the first leaf over the stem segment used for k measurements and just before k was measured. Each data was measured on a single plant from three *E. globulus* clones in a greenhouse experiment. For simplicity, the regression line fitted to data from clone w349 (R^2 = 0.03) is omitted (Pita, unpublished).

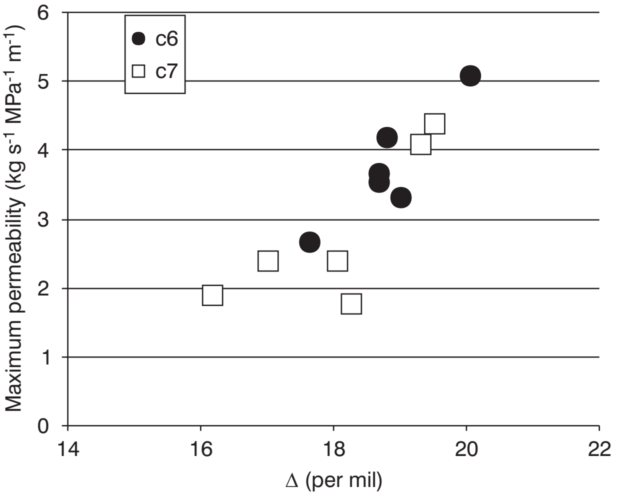

Figure 5. Relationship between xylem carbon isotopic discrimination (Δ) and maximum permeability in two greenhouse-grown *E. globulus* clones. $\delta^{13}C_{air}$ was assumed to be –8‰. Each point is a different plant. (Pita, unpublished).

Δ has been considered a good index of long-term water availability to the plant (Pita *et al.* 2001). Thus, the relationship between Δ and hydraulic traits may be useful to analyze the importance of hydraulic constraints on stomatal conductance as drought progresses.

Stomata closure: Sensing or preventing xylem embolism?

Lemoine *et al.* (2002) found that stomatal conductance decreased sharply under drought in *Fagus sylvatica* L., keeping xylem water potential above the cavitation threshold, and xylem embolism below 20% even at the end of summer. Similar results have been reported in *Betula occidentalis* Hook. (Saliendra *et al.* 1995), *Quercus petraea* Liebl. *ex* Matts. (Cochard *et al.* 1996), *Juglans nigra* L. (Cochard *et al.* 2002) and *Pinus sylvestris* L. (Irvine *et al.* 1998). On the other hand, some tree species can tolerate the loss of relatively high amounts of hydraulic conductivity during the day, without adversely affecting transpiration rates (Vander Willigen *et al.* 2000). Zwieniecki and Holbrook (1998) suggested that a high resistance to water flow in the leaf may limit the ability of stomata to sense changes in xylem hydraulic conductance. Stomatal control of xylem embolism must be important mainly in species that cannot reverse embolism during the growing season. Embolism removal (refilling) has been widely documented in several species (Stiller and Sperry 2002, Tyree *et al.* 1999, Holbrook *et al.* 2001, Zwieniecki and Holbrook 1998).

Loss of hydraulic conductance: Vulnerability to cavitation

Several studies show that adaptation to drought is related to higher resistance to xylem embolism. For example, Lemoine *et al.* (2002) found that *Fagus sylvatica* sun branches were more water efficient and less vulnerable to xylem embolism than the shaded ones. Plants that are more drought-tolerant reach and withstand lower values of xylem water potential. Collecting data from 73 species, Sperry (2000) found a significant and positive relationship between minimum xylem water potential based on field observations and the water potential required to cause 100% loss of xylem conductivity. However, resistance to embolism is not necessarily linked to higher survival in drought-prone environments. In this sense, Vilagrosa *et al.* (2003) reported that *Quercus coccifera* L. showed higher mortality than *Pistacia lentiscus* L. during the first summer after plantation, despite its wider safety margins (Fig. 6). Similarly, Piñol and Sala (2000) found a higher vulnerability to embolism in the more drought-tolerant *Pinus ponderosa* related to the more mesic *Pseudotseuga menziesii* Franco *ex* Mirb. In agreement with these results, high vulnerability to embolism can be found both in fast growing pioneer species (Brodrib and Hill 2000), riparian trees (Wikberg and Ógren 2004) and drought resistant species (Pockman and Sperry 2000).

Fig. 6 shows the vulnerability curves drawn for several tree species of contrasting drought tolerance. Comparison between data from different studies must be done with care. Factors such as the environmental conditions, the plant material sampled for conductivity measurements and the age of the plant may change the shape of the vulnerability curve. In any case, Fig. 6 illustrates two main strategies in woody species resistance to embolism. On the one hand, those species such as *Q. coccifera* or *Cedrus atlantica* Manetti. that do not usually experience, under field conditions, a xylem water potential lower than the corresponding one to embolism threshold. On the other hand, those species that operate with relatively high loss of conductivity throughout the growing season

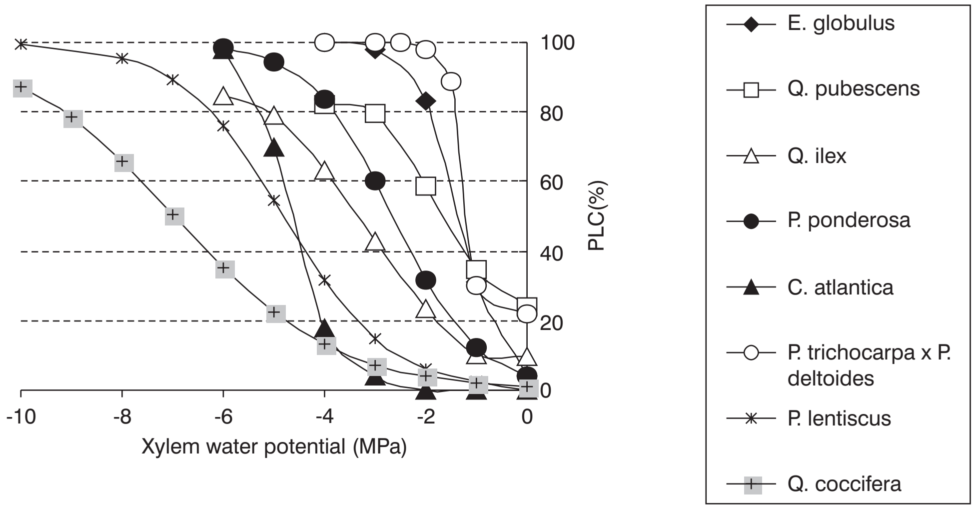

Figure 6. Vulnerability curves for six tree species. Sources of data: *E. globulus:* Pammenter and Vander Willigen (1998), *Quercus pubescens* & *Quercus ilex:* Tognetti *et al.* 1998, *Cedrus atlantica:* Cochard, 1992. *Pistacia lentiscus* & *Quercus coccifera:* Vilagrosa *et al.* 2003.

(Zwieniecki and Holbrook 1998). This is the case of *E. globulus,* that looses 50% of conductivity at a xylem water potential of –1.3 MPa (Vander Willigen and Pammenter 1998). Riparian species like *Populus* sp. or *Salix* sp. (Wikberg and Ögren 2004) are among the most vulnerables.

Hydraulic traits and growth

In a study with five tropical species grown in a common environment, Tyree *et al.* (1998) concluded that high plant hydraulic conductance is a necessary condition for high productivity in forest trees. Thus, if low hydraulic conductance is manifested at early stages of growth and all low-conductance genotypes are slow growing, then early selection of hybrids with high hydraulic conductance can be used in breeding programmes (Tyree 2003). Measurement of hydraulic conductance may be useful even when breeding looks for increasing growth in drought-prone environments, because high hydraulic conductance is not necessarily linked to high vulnerability to embolism (Froux *et al.* 2002). Despite early results showing a trade-off between hydraulic conductance and vulnerability to embolism, that was attributed to higher vulnerability of the wider conduits, it is now widely accepted that vulnerability to embolism induced by water deficit is related to the maximum pit pore size, which may be or not related to conduit size.

Conclusions

Results from several studies carried out in *E. globulus* show that the species must be considered as a dehydration avoider, because higher survival and yield are achieved through lower water use efficiency and embolism tolerance. This does not mean that the species cannot show some dehydration-tolerant traits, such as osmotic adjustment (Pita and Pardos 2001, Guarnaschelli *et al.* 2003). Working at the edge of catastrophic xylem failure enhances *E. globulus* to reach the highest yield among forest species in south-western Spain, but it is certainly risky. Knowing the species strategy may help to increase both survival and growth through genotypic selection. First results on *E. globulus* show the relevance of hydraulic traits such as maximum permeability, maximum leaf conductivity and vulnerability to cavitation and its relationship to stomatal conductance. These results must be related to data from field trials, before arriving to any concluding remark on the use of physiological traits in *E. globulus* breeding for improved yield in drought-prone environments.

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