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Contributions of Intraspecific Variation to Drought Tolerance in Trees

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Abstract

Purpose of Review The capacity of woody plants to cope with climate change depends on their adjustments to changing environmental conditions by phenotypic plasticity or by genotypic changes (i.e., local adaptation). To determine whether intraspecific trait variation (ITV) translates into resistance or tolerance to drought and eventually how it relates to performance when facing drought, we reviewed the recent literature on the intraspecific variation in woody plant functional traits along aridity gradients.

Recent Findings At the intraspecific level, functional traits vary along aridity gradients, but this variation depends on the considered trait and species. While ITV is ubiquitous and of relevant magnitude, its relationship with tree performance in the case of growth or survival is unclear and very idiosyncratic.

Summary ITV varies along aridity gradients and, for several traits, is of comparable magnitude as interspecific trait variation. However, the relationship between ITV and tree performance is not consistent among species. This makes the use of ITV challenging when quantifying its contribution to drought tolerance.

Keywords Forest dieback · Drought resilience · Root traits · Specific leaf area · Tree growth · Water-availability gradient · Wood density

Introduction

Forests occupy about 30% of the global land surface [1] and provide a diverse and vast number of ecosystem services for human well-being [2, 3]. Currently, climate change, along with interactions with other related global change drivers, is threatening the conservation and management of forests worldwide [4, 5]. Over the past decades, climate change has triggered the occurrence of more frequent and intense droughts and concurrent heat waves (i.e., "hotter droughts", [6]), which have paralleled in time with substantial changes in land use practices and resulted in an increase in disturbance regimes [7]. It is becoming increasingly clear that forest mortality increases in magnitude and intensity in response to hotter droughts [8], and forests at the equatorward limit (dry rear edge) of their distribution range seem to be extremely vulnerable to such aridification trends [9, 10]. In fact, recent studies indicate that background mortality rates of European tree species have increased near their southern distribution limits [11, 12], where important die-off episodes have also been recorded [13]. These findings point to the need to better understand how tree species respond to drought within and across populations as a tool to anticipate climate change impacts on forests [14•, 15, 16•].

It is expected that climate change will alter the distribution of temperate tree species by inducing range contractions at drier climatic edges and at lower elevations of their distribution ranges [14•]. All species have spatially restricted distributions, but the size of their distribution ranges, and thus, the climate threats they face vary considerably [15]. Tree species with high genetic variation, as is generally the case for those widely distributed, are expected to be better

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able to persist in the face of environmental change than species with limited distribution ranges or relict populations [16•]. Adaptation is expected to occur at evolutionary time scales, and peripheral populations will present local adaptations to cope with drought, heat, and cold stress [17–19]. Gene flow between peripheral and core populations will prevent extinction risk, although excessive gene flow from central to peripheral populations will lead to genetic maladaptation, preventing adaptive capacity [20, 21]. The capacity of species to cope with environmental change can also depend on rapid changes due to phenotypic plasticity [22, 23], but plastic responses may depend on adaptive capacity and can also imply trade-offs between functions ultimately impacting fitness [24]. It is thus urgent to understand how tree species respond to changing environmental conditions, as this will in turn determine their capacity to thrive in a drier and warmer world [18, 25]. From a purely ecological perspective, understanding how individuals and populations of species vary in their response to drought is important in order to define tolerance limits due to phenotypic plasticity as well as detect potential genotypic differences between populations and their covariation [26]. From a perspective focused on the provision of ecosystem services, understanding such variations is important to delineate vulnerability scenarios for tree species as well as to assist conservation and management programs, which ultimately could require the translocation of tree populations (i.e., assisted migration) or even the management of novel ecosystems [15, 27, 28].

In the last two decades, plant functional traits have been heralded as a useful proxy to explain variation in plant form and functioning [29] and to predict plant responses to disturbances and climate change [30, 31]. Functional traits are measurable plant anatomical, morphological, and physiological attributes that are assumed to be directly linked with individual performance [29, 32] and that show variation along climatic gradients [33]. At the beginning, much emphasis was put on determining how traits varied between species and across environmental gradients to understand essential trade-offs in plant functioning and related strategies [19, 34–37]. Studies accounting for species replacement and changes in mean trait values along environmental gradients suggested the existence of essential trade-offs between functional traits in response to changes in limiting factors [33, 38, 39]. For example, when resources are limited due to stressful conditions, plants will tend to show trait values that maximize stress tolerance and resource conservation at the expense of reducing size or growth [19]. For instance, at a global scale, species inhabiting sites where water and light are not limiting tend to have low wood density (WD), high specific leaf area (SLA), and high growth rates, which make them better competitors, i.e., they follow a resource-acquisitive strategy [40]. Species from areas where water is a limiting resource invest more in traits conferring drought tolerance (high WD, low SLA, low growth rates), which make them better competitors in water-limited environments, i.e., they follow a more resource-conservative strategy [40, 41]. The spectrum of resource acquisitive-conservative trade-offs in life strategies is also related to the fast–slow leaf economics spectrum [36]. The fast–slow leaf economics spectrum has mainly been found to occur at the interspecific level, and few studies have found it to occur at the intraspecific level [42].

This preferential focus on species replacement along environmental gradients has resulted in a generalized lack of knowledge on how traits vary and covary along environmental gradients at the intraspecific level, reducing the ability to assess tree adaptive capacity in response to stress [15]. Both adaptation and phenotypic variation can induce changes in trait values between and within populations [43]. The variation in trait values between individuals and populations can be as extreme as that between species, so inducing similar changes in ecosystem functioning as species replacement could do [43]. Over the past decades, several studies have acknowledged that intraspecific trait variation (ITV) plays a fundamental role in determining species sorting along environmental gradients [44–48] and that it can influence species responses to environmental stress [49], particularly increased aridity [50•] and drought stress [51••]. Responses to drought tend to imply the coordination of different traits either due to rapid environmental changes (phenotypic plasticity) or in response to local conditions (phenotypic integration), both potentially implying trade-offs between functions and changes in fitness [24, 52, 53]. Thus, the ability to detect linkages between ITV and tree performance depends upon multiple factors, including the selection of functional traits [32], the length of the gradient considered [50•], and the effect of confounding factors. Hard traits (i.e., those directly linked to physiological processes [54]) are expected to outperform soft traits (morphological traits) in predicting tree performance [55], but this will depend on the capacity to control confounding factors and measure associated errors [32].

Assuming that the negative impacts on forests of longer and more frequent, severe, and hotter droughts are projected to increase [6, 8], understanding how tree species respond to drought within and across populations is relevant and important for the conservation and management of forests [14•, 15, 16•]. Thus, the more knowledge we gain about the intraspecific variation of species, the closer we will be to making knowledge-based decisions [18, 56••]. In this study, we first reviewed empirical studies published in the last 10 years or so regarding how tree traits vary along aridity gradients and how this variation translates into variations in performance in response to drought. Particularly, we focused on field studies that measured trait-performance relationships along aridity gradients to evaluate the extent to which

ITV translates into growth or mortality differences. Here, we apply an ample definition of aridity gradient, referring to those studies that compare differences in precipitation or water balance. We synthesized general trends in ITV-performance associations across aridity gradients to determine which are the most important traits driving tree responses to drought. We hypothesized that both growth and trait variations at the intraspecific level along aridity gradients are ubiquitous but that their relationship is species and gradient-specific. That is, the selection of the trait, the strength of the aridity gradient, and other confounding factors such as forest structure and composition will affect the capacity to determine if there exists a variation in growth at the expense of the variation in certain traits and to quantify how ITV contributes to drought tolerance.

Literature Search and Analysis

We performed a literature survey in August 2022 in the Web of Science databases for all types of documents that were related to ITV and water scarcity in trees or forests. We searched for all types of documents containing the words "forest*" OR "tree*" AND "intraspecific" AND "trait*" AND "drought" OR "aridity" OR "precipitation" in the title, abstract, or key words. We evaluated a total of 322 articles.

Given that we are interested in studies evaluating the variation of ITV in trees along aridity gradients and how it relates to tree performance (e.g., growth or mortality) in response to drought, we performed a refined selection by reading the abstracts of the studies and selecting only those that fully satisfied our criteria. First, we searched for studies that accounted for the variation of functional traits within species across gradients of 1) precipitation, 2) drought intensity, and 3) aridity (i.e., the ratio between precipitation and potential evapotranspiration). A total of 151 articles in which intraspecific trait variation was either studied or reviewed were selected. This first list of studies included, among others, 68 field studies, 66 provenance trials, and 6 reviews.

A further refined search was done to select those field studies that accounted for the relationship between ITV and growth or mortality. We considered studies that reviewed intraspecific responses of tree species along climatic gradients or those that used altitudinal or latitudinal gradients as surrogates of changes in water availability, temperature, or aridity. Finally, we retained a list of 12 studies that dealt with the relationships between intraspecific trait variation and any measures of performance (e.g., growth or mortality) along aridity gradients under natural conditions. For those studies, we extracted the relationship between individual traits and performance to quantify the extent to which ITV affects performance. It should be noted that tree growth was quantified in several ways depending on the study, ranging from stem size increments to whole tree growth responses to drought. Thus, how traits affect performance depends on such estimations. We also tentatively estimated whether the aridity gradient studied covers the aridity the species experience along their distribution ranges. This was done based on the extent of the study area and also considering what was written in the articles. We then determined whether the gradients studied were large (i.e., covering the distribution of the species) or regional (i.e., only including some particular sites).

Results

We found 12 case studies in which the relationship between trait variation and performance (either growth or mortality) was implicitly tested along aridity gradients (Table 1). Collectively, these studies covered 14 tree species (6 conifers and 8 broadleaf species) and 35 functional measures (including functional traits, measures of functional richness, and ordination axes), accounting for 320 traits per species or site combination. Most studies were performed in Europe (9), and *Pinus sylvestris* was the most studied species among them. The environmental (aridity) gradients studied also varied between studies, with some of them encompassing variations along wide altitudinal and latitudinal gradients [57, 58], while others focused on differences between trees of different vigor classes within the same forest [59]. Despite the wide variation in the traits studied, leaf traits, wood density, and plant height were common in several studies (Fig. 1; Table 2). Given that the studies were done under field conditions, most of them accounted for the variation in climate conditions, soil parameters, and forest structure and composition between sites. According to these studies, significant relationships between traits and performance were trait and species dependent (see below for a detailed description of the results). It is important to note here that measures of performance vary between studies (Table 1), and they go from the growth of the stem, from which traits are measured [45], to measures of basal area increment derived from national forest inventories [60•]. In some cases, performance was explicitly measured as a growth response to drought [51••, 61] or drought-induced mortality [59, 62••].

A first subset of studies comprises the evaluation of ITV and its relationship with growth at the stem level [45, 57, 58]. Strong relationships between ITV in hydraulic traits and growth have been found along wide environmental gradients in *P. sylvestris* [45, 57]. These studies covered most of the distribution range of the species in Europe and included rear-edge populations. The authors found negative impacts of leaf-specific conductivity and tracheid density [45] and positive impacts of HV (defined as the ratio between leaf area and sapwood area) and tracheid diameter on stem growth. Besides, Sterck et al. [57] found a negative relationship between WD

Table 1 List of studies testing for the existence of relationships between intraspecific trait variation and performance (either growth, growth response to drought, or mortality) along aridity gradients

Study	Tree species	Functional traits	Measure of performance	Type of gradient
45	*Pinus sylvestris*	WD, tracheid diameter and density, specific hydraulic conductivity, pressure causing 50% embolism, branch leaf-to-sapwood area ratio, leaf-specific hydraulic conductivity, leaf ^{13}C, nitrogen content in needles, SLA	Stem radial growth	Large aridity gradient
57	*Pinus sylvestris*	HV, Dh, WD, leaf-specific conductivity, specific conductivity, cell-wall thickness, water potential at 50% xylem conductivity loss	Stem radial growth	Large aridity gradient
64	*Pinus sylvestris*	WD, maximum tree height, leaf nitrogen content, SLA, HV	Radial growth	Regional aridity gradient
66	*Pinus sylvestris* var. *mongolica*	Needle and twig elemental stoichiometry (concentrations of C, N, P, K, Ca, and Mg)	Radial growth	Regional aridity gradient
58	*Embothrium coccineum, Nothofagus antarctica Nothofagus pumilio*	WD	Radial growth	Regional precipitation and elevation gradient
61	*Abies alba, Pinus sylvestris, Pinus nigra, Pinus halepensis, Quercus humilis, Quercus ilex*	SLA, WD	Resilience to drought	Regional (core vs. rear-edge populations)
51	*Quercus pubescens*, *Fagus sylvatica*	Tree height, WD, SLA, leaf ^{13}C, leaf N concentration, leaf water potential at turgor loss point, HV, hydraulic conductivity, resistance to xylem embolism	Resilience to drought	Regional aridity gradient
65	*Pinus uncinata*	WD, leaf area, SLA, leaf dry matter content	Radial growth	Regional (core vs. rear-edge populations)
63*	*Quercus ilex*	leaf area, leaf thickness, LMA, leaf density, leaf dry matter content, leaf concentrations of P, K, Ca, Mg, Na, Fe, Mn, Cu, and Zn	Relative growth rate	Regional aridity gradient
60	*Fagus sylvatica*, *Quercus humilis*, *Quercus ilex*, *Pinus sylvestris*, *Pinus nigra*, *Pinus halepensis*	Leaf mass per area, leaf nitrogen concentration, leaf ^{13}C, leaf water potential at turgor loss, WD, HV, leaf-specific hydraulic conductivity, sapwood-specific hydraulic conductivity, resistance to xylem embolism	Basal increment and growth efficiency	Regional aridity gradient
59	*Abies alba*	^{18}O, WUEi, tree height, SLA, WD, leaf concentrations of N, Ca, Cu, K, Mn, Ni, P, Si, and Sr	Resilience to drought and drought-induced mortality	Regional (core vs. rear-edge populations)
62	*Populus tremuloides*, *Pinus ponderosa*	SLA, HV, partial pressures of atmospheric and leaf intercellular CO_2, percent loss of conductance, leaf water potential at the turgor loss point, native leaf area-specific conductivity, maximum sapwood area-specific conductivity, native sapwood area-specific conductivity	Drought-induced mortality	Regional aridity gradient

Dh hydraulic diameter, *HV* Huber value, *LMA* leaf mass per area, *PLC* percent loss of hydraulic conductivity, *SLA* specific leaf area, *WD* wood density, *WUEi* intrinsic water-use efficiency.

*The authors found relationship between ITV and productivity but not between ITV and relative growth rate.

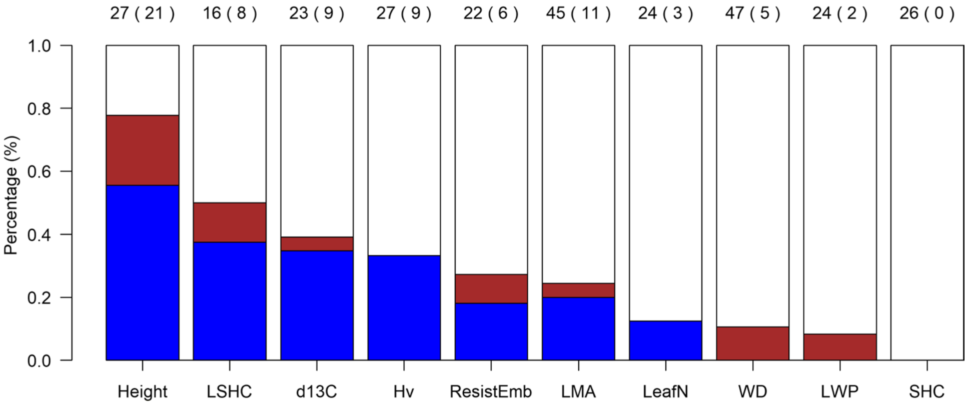

Fig. 1 A summary of the relationships between ITV and performance. For the 10 most commonly measured traits, the number of positive (blue), negative (brown), and non-significant (white) responses found with performance is shown. The numbers above the columns indicate the number of comparisons (and studies) in which the trait was measured and studied. Trait abbreviations are the following: height, tree height; LSHC, leaf-specific hydraulic conductivity; d13C, leaf isotopic carbon composition; Hv, sapwood to leaf area ratio (Huber value); ResisEmb, resistance to embolism; LMA. leaf mass per area (inverse of SLA); leaf N, leaf nitrogen content; WD, wood density; LWP, leaf water potential; SHC, specific hydraulic conductivity

Table 2 A list of traits that can help to understand how individuals and populations within species vary in response to changes in aridity and drought stress

Trait	Abbreviations	Explanation	References
Tree height	H	A measure of competitive ability and light acquisition potentially reflecting the capacity to explore soil resources as well	51
Specific leaf area / leaf mass per area	SLA / LMA	Greater LMA (lower SLA) is expected in individuals form dry sites and will reflect changes in leaf thickness and density as well	62
Leaf nutrient content (N)	Leaf N	A measure of nutrient concentration in leaves	51
Huber value (ratio of stem sapwood area to leaf area)	HV	Represents the balance of hydraulic supply (sapwood area) relative to hydraulic demand (leaf area)	45
Wood density or specific gravity	WD	A measure of stem robustness and is expected that individuals with denser xylem tissues have narrow conduits less susceptible to embolism	58
Vessel density and hydraulic diameter	VD and Dh	A measure of the xylem conductive area. Vessels with small lumen area and lower vessel density are expected in response to aridity, but also to cold stress, across individuals and populations	72
Xylem and water isotope composition $\left(\delta^{13}C, \delta^{18}O, \delta^{2}H\right)$	$\delta^{13}C, \delta^{18}O, \delta^{2}H$	They allow to quantify intrinsic water-use efficiency (WUEi), regulation of stomatal conductance but also to infer the depth of soil water uptake	59
Xylem vulnerability to embolism (percent loss of hydraulic conductivity)	PLC	Resistance of xylem to cavitation	60
Leaf- and xylem-specific hydraulic conductivity		It is a measure of xylem transport efficiency and sufficiency	60

and growth. Fajardo et al. [58] studied the variation in WD and its covariation with xylem traits and growth along aridity and temperature gradients for three species with ample niche breadth in southern South America. They found that WD was related to xylem traits in a species-specific way, but no relationship between WD and growth was found in any of the three species studied. This was confirmed in another study in the same area at the community level, where although WD and leaf size did predict tree growth at the interspecific level, non-significant relationships were found at the intraspecific level (Fajardo et al. under review).

Another set of studies evaluated the variation in ITV and its relationship to growth (and mortality [59, 62••], along regional aridity gradients while considering whole tree growth. In this case, performance estimates were repeated measures of diameter increments [60•, 63], radial growth [64, 65], or radial growth responses to drought [59, 61]. Non-significant relationships between performance and WD were found in most studies (Fig. 1), except for negative relationships in the cases of growth resistance and recovery after drought in *F. sylvatica* [50•], growth in *P. uncinata* [64], and mortality in *Abies alba* [59]. Higher leaf mass per area (LMA, the inverse of SLA) enhanced growth efficiency (basal area increment per unit of total leaf area) in three pine species (*P. sylvestris*, *P. nigra*, and *Pinus halepensis* Mill.) and three Fagaceae species (*F. sylvatica*, *Quercus humilis* Mill., and *Q. ilex*) along a precipitation gradient in NE Spain [60•], but higher LMA resulted in higher cumulative growth reductions after drought in *F. sylvatica* in the same region [51••]. Along this line, *A. alba* trees with high SLA presented higher cumulative growth reductions in response to successive drought than trees with low SLA in the western Pyrenees [61], while *P. sylvestris* and *A. alba* trees with low SLA grew more when moisture was available, i.e., in wet years [61]. In other studies, no significant relationships between LMA and SLA with growth were found, but a greater mortality of *Populus tremuloides* Michx. after drought was found in trees with leaves showing higher SLA values [62••].

Positive associations between HV and growth have been found at the whole tree level in *P. sylvestris* [64] and also with growth efficiency in temperate tree species [60•], while no significant impacts have been found on growth resilience to drought [51••]. Tree height has been found to positively affect growth [60•, 62••, 64] and responses to drought in some species [51••], while reducing growth resilience after drought in *A. alba* [59].

Leaf- and sapwood-specific hydraulic conductivity have been found to be only weakly related (positive effect) to growth efficiency [60•], while resistance to xylem embolism increased the growth resistance and resilience of *F. sylvatica* and *Q. pubescens* and reduced their recovery time after drought [51••]. Along with this, negative leaf water potential at the turgor loss point was associated with greater growth losses after drought. Leaf C isotopic composition and water use efficiency have been found to affect the growth [60•] and growth recovery after drought [51••] of several temperate tree species, but with limited and inconsistent impacts on mortality [59]. Leaf N content increased *P. sylvestris* radial growth [64] and the recovery after drought of *Q. pubescens* and *F. sylvatica* [51••], and *A. alba* trees with higher foliar concentrations of several micronutrients (P, K, and Cu) performed better in response to drought [59]. Linkages between leaf nutrient concentrations and growth were less clear in other studies [63, 66].

Discussion

During the past decades, functional traits have emerged as powerful tools to explain variation in plant responses to climate change at the intraspecific level. Latitudinal and altitudinal gradients are often used to study how ITV varies in space because this allows understanding the potential of species to acclimate or adapt to increasing temperatures or drought stress [23, 33, 57, 58, 60•, 62••, 68, 69••, 70•] and can help refine model forecasts [15, 71]. However, it is also important to link trait variations along environmental gradients with measures of tree performance [45, 51••, 60•]. Unfortunately, in most field studies, the covariation between trait and performance is assumed rather than tested. To our knowledge, this is the first review summarizing the studies testing for the relationship between ITV and tree performance in response to drought under natural circumstances. Our results indicate that relationships between ITV and measures of performance (either growth or mortality) vary depending on the trait considered, the gradient, and the species. Overall, the relationships between growth responses to drought and single traits at the intraspecific level are scarce and species-specific. Along this line, mortality in response to drought is weakly related to ITV [62••]. It is in general hard to find a strong relationship because traits vary at the intraspecific level and along environmental gradients in complex ways [67, 72], and linkages between individual functional traits and tree growth are difficult to address without considering trait covariations [51••, 60•,73]. This suggests that the relationship between trait variation and performance in response to drought is not universal.

First, it is important to assume that gradients can be complex (e.g., non-linear relationships) and depend on the covariation of different environmental variables [50•, 66], which might partially explain why responses are species-specific [70•]. Thus, to draw robust conclusions, it is important to account for potential effects across the different ends of the gradient [23], confounding factors [71, 74], and trait coordination varying along the gradient. For instance, Anderegg et al. [50•] argued that coordination between traits belonging to different tissues only emerges when there are strong differences in aridity between sites and gradients that are not confounded with variations in other stress factors such as coldness. Thus, how different functional traits covary between them and how the environment modulates this covariation emerges as an important question that has received little attention [73]. Most studies included in this review account for the potential influence of stand characteristics and tree intrinsic features on performance. However, aridity gradients varied considerably, and they rarely included whole species distribution ranges. In fact, the studies with the widest gradients have often considered performance at the branch level, suggesting that studies accounting for the relationship between ITV and performance at the tree level and along wide gradients are rare [72]. Moreover, there is a lack of knowledge on which traits are linked to drought response at the species' rear edge [72]. However, this type of information is important for improving our understanding on how species will respond to drought in a warmer and drier future.

Collectively, the reviewed studies indicate the importance of considering wide gradients and, if possible, including rear-edge, climatically marginal tree populations. However, small-scale variations in environmental conditions can be of great value. Endemic species with a narrow range of genetic variability or relict populations are likely the most threatened by environmental changes [16•]. Given that geographic distance affects genetic diversity [75], these populations tend to present intraspecific differences from those populations located in the core of the distribution range [65, 76]. Distinguishing between phenotypic plasticity (including acclimation) and local adaptation (i.e., genetic differences) requires the use of provenance trials or common garden experiments [73]; however, combining genetics and measures of ITV may help to understand if variations in ITV between populations correlate with different gene expressions [48, 77]. Ideally, these measures should be accompanied with estimations of growth responses to drought performed over the same individuals as a tool to better understand linkages between ITV and performance at the whole tree level [73].

With the idea that drought will be one of the main limiting factors for forests in the future [8], it is important to consider traits that determine how trees cope with drought stress [62••, 68] (Table 2). Plant height is an important trait, which in turn is correlated with other traits such as WD or SLA [64]. Relying solely on tree height, larger trees have longer hydraulic path lengths, and because of this, they have wider hydraulic conduits, which can make them more vulnerable to hydraulic failure when water is scarce [78, 79]. However, larger size is often correlated with a greater capacity to obtain water from different sources (provided that there is water), which might mitigate drought-induced stress [59, 80, 81], as well as with adjustments in conduit size and density, potentially implying that what holds at the interspecific level (i.e., greater vulnerability of taller trees) shifts at the intraspecific level [79]. There is a hydric continuum from the roots to the leaves, and drought impairs the transport of water, which may cause xylem embolism in some species [60•]. Hydraulic conductivity is thus a process that depends on the coordination of different traits that vary independently along aridity gradients [70•, 81].

Leaf area, thickness, and density, and related morphological traits such as SLA, have also been suggested as important traits determining the alignment of species to aridity [36], and so SLA has been widely studied at the intraspecific level [58, 61, 62••,63, 82, 83]. Higher SLA will reduce growth efficiency [60•], lead to higher drought-induced growth reductions [61], and enhance mortality [62••]. Sapwood to leaf area ratio, that is, HV [84], is also a prominent trait as it informs on variations in hydraulic efficiency [57]. Overall, higher HV enhances growth and growth efficiency, but its role in growth resilience to drought and mortality is unclear, and studies along wide aridity gradients are required in this respect. The leaf water potential at the turgor loss point relates to stomatal closure and is expected to decrease in response to aridity (i.e., more negative values in arid sites [85]). Along this line, the intrinsic water-use efficiency (iWUE), which is defined as the ratio between photosynthesis and stomatal conductance rates, is related to drought tolerance [60•]. These traits have been found to vary along regional aridity gradients in temperate tree species [67], but their relationship with growth [60•] and growth resilience remains unclear [51••].

At the interspecific level, trees with denser wood grow more slowly, have longer lifespans, and are less prone to drought-induced mortality [37, 86, 87]. Low growth rates have been associated with higher resistance to xylem embolism [88, 89]. Therefore, WD is a good proxy for drought tolerance when comparing species [90], while the relationships between WD, growth, and drought tolerance at the intraspecific level are unclear [58, 61]. In fact, the role played by WD at the intraspecific level is not evident, with some studies reporting lower WD in dry sites [91], a lack of differences between populations [71], or higher WD as aridity increases (e.g., [50•, 58, 68]. Thus, results are species- and site-specific, as different species will respond differently depending on the type of gradient and most likely the plant species strategy (i.e., the combination of traits). Clough et al. [92] used a large database of intraspecific variation in WD combined with species inventories to show that for five gymnosperms, WD decreased with the increase in aridity, whereas in the case of angiosperms, an increase or neutral pattern was found depending on the species considered. However, in a review based on provenance trials, Nabais et al. [93] found that in 8 out of the 25 tree species considered, there was a tendency toward higher WD in populations from drought-prone sites. Provided that provenance trials act as a common garden experiment, the result of Nabais et al. [93] points out that for some species, trait differences are the result of local adaptation. These results suggest that WD is not a universal trait that can be used to detect changes along aridity gradients in an unequivocal way (i.e., higher density in drier sites). That is, WD can covary with other factors, allowing species to tolerate aridity. For example, a greater allocation of biomass to the roots in response to dryness can be associated with lower stem WD [93].

There are other traits that have received less attention so far. Root traits are rarely considered in field studies [94–97], and several studies pointed out their importance in understanding ITV along climatic gradients [23, 51••, 59]. Trees have the capacity to modify their roots in response to drought with growth and anatomical changes, as well as by changing symbioses and relations with free-living soil organisms, but these have been less studied than aboveground reactions [73, 95]. Interestingly, rooting depth capacity can be estimated by using ^{18}O and ^{2}H measurements in soil and xylem water samples [80, 98]. Recent advances also make it possible to measure rooting depth in the field by using techniques such as ground penetrating radar [99]. These belowground estimations of water uptake can be combined with aboveground measures of leaf water potential and growth to study responses to drought at the whole tree level [73]. Besides, belowground responses to drought may depend not only on specific tree features such as age or size but also on species interactions and site conditions, a myriad of factors that operate simultaneously [100]. It is thus advisable to evaluate how measures of growth resilience to drought relate to rooting depth capacity both at the intra- and interspecific level to widen the understanding of how trait variation affects drought tolerance capacity.

The temporal dimension of trait variation is also a factor that deserves further attention. Estimating phenotypic plasticity in mature forest stands can be achieved by measuring temporal variation in functional traits, where temporal variation in climate conditions generates different environmental conditions, and genotype is controlled by measuring the same individual trees over time [43, 101]. For example, Kerr et al. [62••] studied the variation in drought-related traits of *P. tremuloides* and *P. ponderosa* along an aridity gradient and found that temporal variation was in general higher than spatial variation. To date, few studies have compared intraspecific differences in traits such as leaf size [102] and leaf lifespan [103] across environmental gradients or how previous growth patterns affected intraspecific variations [104]. Xylem trait variation can depend on the climate of origin, with populations from dry sites presenting higher resistance to drought due to the presence of a higher number of vasicentric tracheids [105]. However, Fajardo et al. [106] found that tree height, not climate, is the factor driving vessel diameter across contrasting climates in two Patagonian tree species. Besides, traits such as xylem vessel density and lumen area can vary considerably from 1 year to another, so this temporal variation also needs to be accounted for [69••, 74]. Refining measures of xylem anatomy and leaf variations over time may help to understand relationships between growth and functional traits at the intraspecific level.

It is important to note that we did not consider provenance trials in our study, as we were interested in how mature trees behave under natural conditions and whether the potential effects of local adaptations and plastic responses are apparent even when species interactions and microenvironmental conditions affect performance. Provenance trials represent special situations that are mainly performed considering the seedling or sapling stages since seedling establishment and development are bottlenecks of forest regeneration [107, 108]. To what extent do tree populations show adaptive differences to aridity? How does their phenotypic expression vary between populations? These are questions that can be approached using provenance trials [56••]. Besides, if maintained over several years, they allow for testing how trait variations translate into growth responses to drought [109]. In a scenario in which temperatures are expected to increase and droughts will become more severe, identifying those tree populations that better tolerate drought appears to be an attractive natural solution to mitigate deforestation [16•]. Achieving these objectives requires studies under controlled conditions that allow us to understand adaptive variations and phenotypic plasticity, as well as how ITV relates to tree performance under natural conditions, which is the focus of this review.

Conclusions

Here we provide an overview of how functional traits vary at the intraspecific level, considering field studies, and how this variation relates to measures of plant performance. The results show that while we have a good degree about information for some tree species (mostly European tree species), our knowledge of others is quite limited. Species with a wide distribution and important ecological value, such as *P. sylvestris* or several oaks, have been the focus of many studies. As usual, hundreds of tree species from the tropics remain understudied, and therefore, our conclusions will always be partial. It would be essential to have ITV studies come from tropical dry forests, as these represent communities adapted to drought.

Evidence coming from field studies indicates that ITV exists, is non-negligible, and responds to changes in water availability. However, such responses are contingent on the species, traits, and gradients considered. In the case of temperate species, gradients of water availability overlap with gradients of coldness, which complicates finding clear trait-climate relationships. In more arid regions, when gradients are wide enough and not confounded by different factors, it is possible to find clear coordination for some traits but not for others. This suggests including as wide gradients as possible and considering rear-edge populations [72].

How ITV translates into differences in performance (i.e., growth and survival) should be the goal of understanding how species will respond to climate change. This implies trying to understand how traits and their relationship to drought vary along gradients while also focusing on the set of traits that make some individuals or tree populations more resistant to drought stress. Thus, it is important to scrutinize different traits so that we can identify the sets of traits able to predict within species variations in response to drought [61]. Besides, it is important to assume that both ITV (phenotypic plasticity) and performance vary in time and that their variation may differ between populations (phenotypic integration). Monitoring how the relationships between ITV and tree performance change as a function of climate change across species distribution ranges is fundamental to advancing our understanding of how tree species will thrive in a warmer and drier future [73].

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Declarations

Competing Interest The authors declare no competing interests.

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- •• Of major importance

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