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Review

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# How woody plants adjust above- and below-ground traits in response to sustained drought

Author for correspondence:
*Lucy Rowland*
*Email:* rowland@exeter.ac.uk

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**Lucy Rowland**[1], **Jose-Alberto Ramírez-Valiente**[2], **Iain P. Hartley**[1] and **Maurizio Mencuccini**[2,3]

[1]Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter, EX4 4RJ, UK; [2]CREAF, Campus de Bellaterra (UAB), Cerdanyola del Vallés, Barcelona 08193, Spain; [3]ICREA, Barcelona 08010, Spain

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## Summary

Future increases in drought severity and frequency are predicted to have substantial impacts on plant function and survival. However, there is considerable uncertainty concerning what drought adjustment is and whether plants can adjust to sustained drought. This review focuses on woody plants and synthesises the evidence for drought adjustment in a selection of key above-ground and below-ground plant traits. We assess whether evaluating the drought adjustment of single traits, or selections of traits that operate on the same plant functional axis (e.g. photosynthetic traits) is sufficient, or whether a multi-trait approach, integrating across multiple axes, is required. We conclude that studies on drought adjustments in woody plants might overestimate the capacity for adjustment to drier environments if spatial studies along gradients are used, without complementary experimental approaches. We provide evidence that drought adjustment is common in above-ground and below-ground traits; however, whether this is adaptive and sufficient to respond to future droughts remains uncertain for most species. To address this uncertainty, we must move towards studying trait integration within and across multiple axes of plant function (e.g. above-ground and below-ground) to gain a holistic view of drought adjustments at the whole-plant scale and how these influence plant survival.

## I. Defining and measuring plant adjustment to drought

There is a growing body of literature within the field of plant ecology concerning the capacity of plants to adjust their traits in response to drought. This, in part, may be related to the recent sustained and extreme drought events that have occurred globally, for example in 2010 and 2015 across Amazonia, in 2017 across the Mediterranean and in 2018/9 across Europe. For this review, we define sustained drought as a period where a plant experiences abnormally low soil moisture availability driven by either low rainfall or excessive atmospheric water demand over periods of months to years.

How drought adjustment is defined varies substantially. From an evolutionary perspective, it can include adaptation (Gould & Lewontin, 1979), defined as phenotypic changes at a population level caused by heritable changes in the genome across generations. In addition, adjustment can include changes in phenotype in response to environmental cues, without a change in the genetic sequence (Box 1). Adjustments to drought that do not involve

**Box 1** Glossary

**Adaptation** – Phenotypic changes at a population level which increase fitness and are caused by heritable changes in the genome across generations (Gould & Lewontin, 1979).
**Phenotypic plasticity** – An expression of different phenotypes in response to environmental conditions, which occur without a change to the genome sequence. These may be both reversible and nonreversible (developmental) changes (Beaman *et al*., 2016).
**Adaptive plasticity** – Plastic changes to phenotype which increases fitness or survival (Nicotra & Davidson, 2010).
**Nonadaptive plasticity** – Plastic changes to phenotype with no impact on fitness, that is a neutral change (Ghalambor *et al*., 2007).
**Maladaptive plasticity** – Plastic changes to phenotype which reduces fitness (Ghalambor *et al*., 2007).
**Acclimation** – Reversible changes in a functional trait in response to changes to a single environmental variable (usually under controlled laboratory conditions; Wilson & Franklin, 2002).
**Acclimatisation** – Reversible changes in a functional trait in response to changes to one or more environmental variables (usually under field conditions; Wilson & Franklin, 2002).
**Developmental plasticity** – Plastic changes to phenotype which occurs at the early stages of development of an organism in response to its environment (Beaman *et al*., 2016). These changes can be reversible changes in functional traits, but are more often associated with irreversible structural changes, which influence the mature form of the organism.
**Passive plasticity** – Plastic changes to phenotype driven by growth-limiting resource shortages (Brooker *et al*., 2022). These are automated responses of the organism which solely reflect the constraint of biochemical and biophysical laws (Havird *et al*., 2020).
**Active plasticity** – Plastic changes to phenotype manifested through a physiological response mechanism activated by the plant as it adjusts to a change in the environment (Brooker *et al*., 2022).

changes in genetic sequence can be termed plasticity (Box 1). Separating out genetic and plastic drivers of adjustment is, however, not simple. Plasticity to drought could shield a plant from selective pressures, limiting adaptive evolution (Ghalambor *et al.*, 2007). Moreover, epigenetic modifications can make distinguishing plastic and heritable genetic changes more complex, because they can also be transmitted from parents to offspring, but do not involve changes to the DNA sequence. Rather, most commonly for plants, they reflect changes in DNA methylation, which alters gene expression (Erdmann & Picard, 2020). The boundaries and links between genetic and plastic processes of plant adjustment to drought warrant substantially more consideration. Consequently, to avoid confusion, in this review, we investigate types of adjustment that exclude changes in the genome sequence and focus on plastic adjustments that can occur within the lifetimes of long-lived woody plants, except where sparse evidence forces us to include model organisms. We start by defining what we mean by the key terms we use throughout this text to describe drought adjustment and focus on understanding the assumptions associated with what each term is used to describe. This standardisation is vital to being able to make meaningful comparisons across studies and, ultimately, to determine robustly how likely plants are to use short-term, nonevolutionary changes to their phenotype to limit the impact of sustained drought stress.

Plasticity can generate both reversible and irreversible responses within plants. Reversible responses are generally associated with changes in plant functional traits in response to either a change in single environmental variable (Acclimation, Box 1) or multiple environmental variables changing together (Acclimatisation, Box 1). Acclimation can generally only be robustly detected under highly controlled laboratory conditions, whereas acclimatisation can be measured in field conditions (Box 1). By contrast, developmental plasticity can involve both reversible adjustments (acclimation or acclimatisation), but is more often associated with irreversible changes to plant structure (Box 1). In terms of drought, these irreversible adjustments may involve plants being exposed to drought during the early stages of development and altering the way they grow in ways that persist to impact the form and function of the mature organism, for example water-limited growth generating a shorter statured plant. Quite often, there is the erroneous assumption that all forms of plasticity, be it reversible or irreversible, are adaptive; however, they can have a range of positive and negative impacts on the plants (Ghalambor *et al.*, 2007).

Plasticity has been described as 'adaptive' when it increases fitness, 'nonadaptive', when there is no impact on fitness, or 'maladaptive' when there is a negative impact on fitness (Box 1). These three types of plasticity can arise from active processes, involving a response mechanism activated by the plant, or passive processes, involving responses from the plant related to resource shortages (Box 1). Separating out active and passive processes in response to drought is notoriously difficult (Brooker *et al.*, 2022). For many physiological traits, it is essential to remove resource limitations to identify patterns in plasticity (e.g. controlling for water content allows identifying 'active' osmoregulation, i.e. actual changes in number of moles of solute, as opposed to solute concentration, a passive change). Nevertheless, in general, plant functions can be both actively and passively regulated in response to different types or intensities of resource use change. Experimentally separating out active and passive responses is more complex at the scale of whole plants, than for the individual traits (Forsman, 2015; Brooker *et al.*, 2022), but may be important as active, rather than passive processes, are more likely to allow for mitigation of sustained drought effects.

The occurrence of nonadaptive plasticity in plants may be more common than adaptive plasticity, because prolonged or intense stress is likely to push a plant away from optimal functioning (van Kleunen & Fischer, 2005; Caruso *et al.*, 2006; Ghalambor *et al.*, 2007). Yet, studies explicitly identifying nonadaptive and maladaptive plasticity in response to drought are less common (Caruso *et al.*, 2006; Ramírez-Valiente *et al.*, 2021). However, elevated mortality or decreased growth in response to drought (Allen *et al.*, 2010; Hubau *et al.*, 2020) would suggest adaptive plasticity is likely to be at best incomplete (Ghalambor *et al.*, 2007). Evidence of drought legacies (Muller & Bahn, 2022), however, is likely to be at least partly the result of maladaptive or nonadaptive plasticity, for example xylem cavitation fatigue leading to enhanced mortality (Anderegg *et al.*, 2013). Additionally, many studies of plasticity only consider changes in traits (Cui *et al.*, 2020; Stotz *et al.*, 2021), yet to prove whether plasticity is adaptive it is vital to assess the impact on long-term fitness (van Kleunen & Fischer, 2005; Valladares *et al*., 2006).

Measuring fitness is not simple in wild plant populations and is dependent on the metric used to define it (Brooker *et al*., 2022). The ultimate metric for fitness is reproductive success, but this can only be assessed at population level and requires assessment over long timescales in long-lived plant species, or those with irregular seed production. At a multi-decadal tropical forest drought experiment, in the years directly following the implementation of the drought, there was a considerable decline in flower and fruit production, but more than a decade later, this greatly increased to levels above those in nondroughted control forest (Rowland *et al*., 2018). Experimental droughts on decadal timescales to detect such changes are extremely rare (Meir *et al*., 2018; Kroel-Dulay *et al*., 2022; Limousin *et al*., 2022); therefore, survival metrics, like growth and mortality, are often more appropriate metrics of drought-related fitness on shorter timescales and at the scale of individual plants. Using these metrics requires caution, however, as a growth-mortality trade-off in response to drought is likely to exist (Russo *et al*., 2021). For example, an increase in wood density in response to drought may reduce growth, but increase survival, making it more challenging to link changes in wood density to fitness. However, monitoring growth and mortality is vital to understanding the processes occurring during drought, even if they cannot be directly linked to fitness. How woody plants use water and carbon for growth during a drought will directly alter the whole-plant carbon and water budgets for both individual tree and its surrounding competitors. If both growth and survival were monitored alongside trait changes over sufficiently long periods of time before, during and after drought, they could provide a powerful database to assess how changes in traits influence whole-tree survival.

It is important to consider how experimental set-ups influence the hypotheses which can be tested regarding drought. Traits within a single species often vary across moisture or aridity gradients (Fig. 1; Anderegg & HilleRisLambers, 2016; Rosas *et al*., 2019; Lopez *et al*., 2021). Although the intraspecific phenotypic variability across gradients could be indicative of a plant's potential for individual-level plasticity, the observed trait differences could also be genetically determined. Such genetic changes across populations have been shown to promote drought survival within model species (Kalladan *et al*., 2017). However, attributing variation in functional traits to genetic differences within wild populations is rare, even if genetic differences within species across aridity gradients are common (Honorio Coronado *et al*., 2014). Techniques are being developed that could link more cost-effectively genetic and functional changes to identify the genetic component of drought stress adaptation (Klápště *et al*., 2020). Yet, without separating out plastic and genetic causes of trait variation, attributing intraspecific variation across a gradient to adaptive plasticity is likely to lead to overestimating the capacity of plants to respond to drought on the timescales associated with climate change.

Experimentally testing for plasticity in controlled environments or through common garden experiments by exposing individuals from the same local population, that are assumed to be genetically similar, to different growth and/or episodic drought conditions removes the impact of genetic differences among populations. These studies can be used to build reaction norms or response functions to environmental changes (Box 2; Collyer & Adams, 2007), as well as to evaluate how plasticity differs between populations from different environmental origins (Fig. 1). Furthermore, controlled experiments can evaluate the impact of varying drought intensity, duration and stress memory, through implementing multiple cycles of drought and recovery, and so assess the effects of acclimation during subsequent droughts (Fig. 1). This is important as plants can adjust to drought through increasing resistance to the drought event, or through increasing capacity to recover from the drought event (Ingrisch & Bahn, 2018). However, the duration of the drought and recovery are likely to alter both of these drought adjustments (Zweifel *et al*., 2020).

Unlike studies of natural gradients, experimental studies are normally only possible on seedlings of woody species, or herbaceous species. Seedlings can have different drought response relative to large trees (e.g. Cavender-Bares & Bazzaz, 2000), due to greater potential for developmental plasticity. The combined developmental and environmental plasticity can mean drought-related plasticity can have greater consequence for survival and fitness of seedlings, relative to mature trees. This is particularly important if drought-induced mortality of large trees releases additional light and soil water resource for seedlings to compete for in dry conditions (Bartholomew *et al*., 2020; Giles *et al*., 2022). These responses can only be measured in natural conditions, and plants in controlled conditions will give very different responses (Poorter *et al*., 2016). This makes extrapolation from experiments complex and likely to give biased assessments of plasticity, if viewed in isolation. Consequently, there is currently no perfect way to test for drought plasticity within wild populations of long-lived plants. Ideally, we should seek to use multiple experimental approaches (Fig. 1) in order to more robustly identify common patterns of drought adjustment across contrasting approaches.

## II. Summarising plasticity in key traits in response to drought

Within this section, we summarise the changes which have been observed in key individual plant traits in response to sustained drought stress, evaluating the variability with which both above- and belowground components of a plant can respond to drought.

### 1. Drought and aboveground traits

Several mechanisms are involved in plant adjustments to reduced water availability. In this section, we summarise how aboveground traits may respond to sustained drought stress, while also considering the impact potential changes in aboveground morphology may have on these traits and more generally on a plant's capacity to resist drought stress.

**Plant hydraulic traits** Plant hydraulic traits are vital controls on drought-related resistance and tolerance; however, relatively few

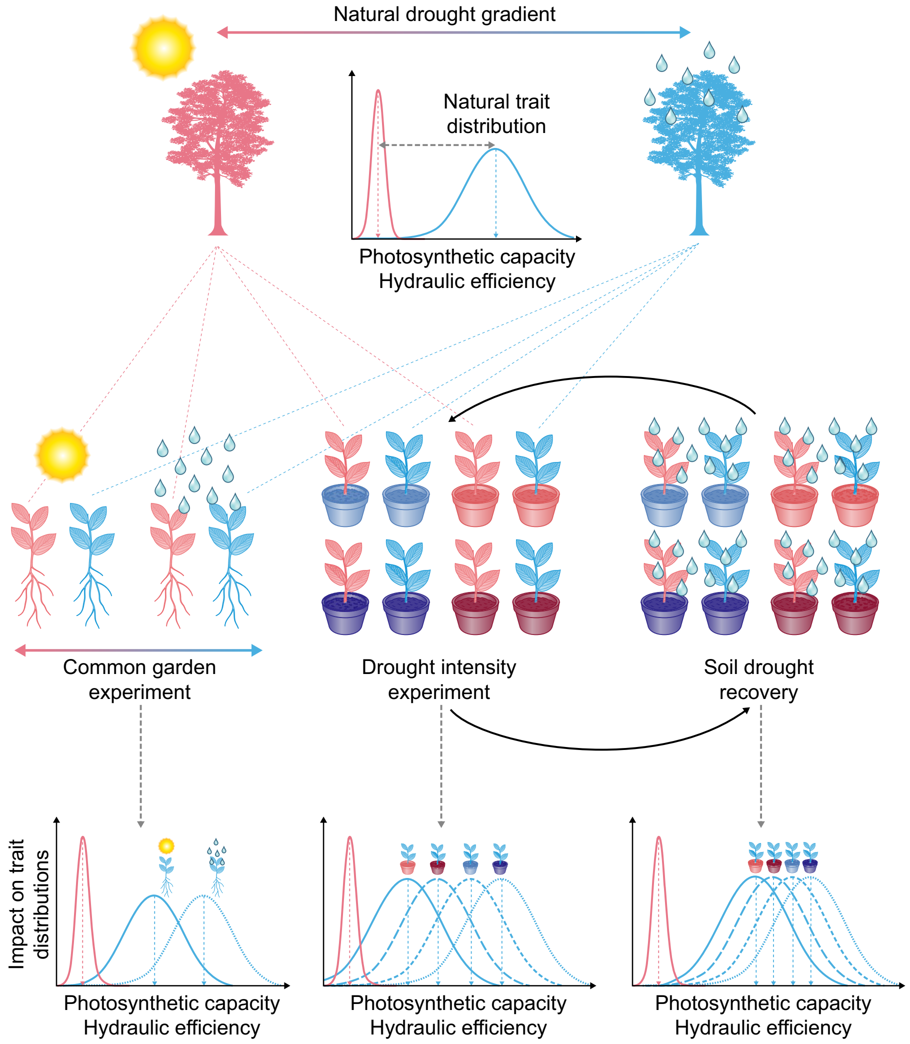

**Fig. 1** Conceptual figure showing the different experimental set-ups, which are commonly used to evaluate how plants adapt to drought. The experimental set-ups include natural drought gradients, common garden experiments and drought intensity experiments in laboratories, including soil drought recovery. Trees and seedlings in red indicate those which have come from a dry end of a natural gradient and which have no capacity for plasticity in either photosynthetic capacity or hydraulic efficiency. Blue trees and seedlings indicate those which have come from a wet end of a natural drought gradient and have equally high potential for plasticity in both photosynthetic capacity and hydraulic efficiency in response to both drought and irrigation. Similarly, the coloured lines indicate how the coloured seedlings are linked to the mother trees. The colours of the pots indicate the differing intensities of water addition (blue) or water removal (red). Grey dashed arrows indicate the theoretical results from each experiment in the form of a probability density function (PDF) for each tree type within each experimental type. These PDFs show how trait distributions may be altered by the experimental set-up, assuming drier conditions foster shifts in mean and more limited variance (Sections I, III), the colours of the lines in the PDFs correspond to the colours of the trees and seedlings. Repeated application of the same treatment can be employed to assess whether acclimation impacts on subsequent plant responses and fitness levels. Note the red lines in the PDFs never move as the species from this environment has no capacity for plasticity.

studies have examined plasticity in plant hydraulic traits. In response to drought stress, many species construct a xylem more resistant to embolism (Beikircher & Mayr, 2009; Awad *et al.*, 2010; Corcuera *et al.*, 2011; Lamy *et al.*, 2011). More negative values of $P_{50}$ (the water potential at 50% loss of xylem hydraulic conductivity) allow plants to maintain photosynthesis under lower soil water potentials and have been associated with increased survival, potentially representing adaptive plasticity. However, changes in $P_{50}$ in response to drought are lower than 1 MPa across almost all studies (Corcuera *et al.*, 2011; Lamy *et al.*, 2011; Wortemann *et al.*, 2011; Aranda *et al.*, 2015; Bittencourt *et al.*, 2020). Changes in $P_{50}$ of this magnitude are not sufficient to compensate for the decrease in minimum leaf water potentials experienced during sustained drought, ultimately decreasing hydraulic-safety margins (Fichot *et al.*, 2010). By contrast, increases in xylem vulnerability to embolism have been found under dry conditions for some species (Martinez-Vilalta *et al.*, 2009; Barnard *et al.*, 2011; Bucci *et al.*, 2012). This may represent maladaptation or be driven by higher water storage and acquisition capacities of populations growing under dry conditions, supported by reductions in wood density and greater hydraulic conductivity (Bucci *et al.*, 2012). These studies provide a good case study of the difficulties to define active vs passive plasticity. Native hydraulic conductivity decreases for stress levels

### **Box 2** Plasticity and trait coordination

We use exemplary values to illustrate the potential relationships existing between reaction norms, plasticity of coordination and coordination of plasticity between two traits. Here, we employ values of predawn water potential, $\Psi_{pd}$, rooting depth and water potential at turgor loss point $\Psi_{tlp}$.

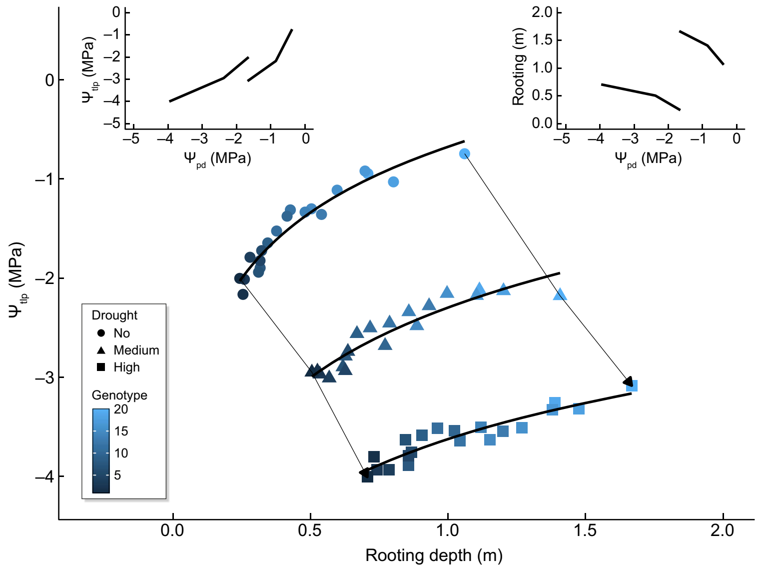

**Fig. B1** Reaction norms of $\Psi_{tlp}$ and rooting depth as a function of $\Psi_{pd}$ (left and right inset, respectively) and plasticity of coordination between rooting depth and $\Psi_{tlp}$ (main panel) are simulated here for 20 different genotypes (cf., shade of blue) under three different levels of drought stress (No, Medium, High) in a common garden experiment. Hence, both $\Psi_{tlp}$ and rooting depth differ for each genotype and drought treatment. For the two genotypes with extreme values, the two reaction norms of $\Psi_{tlp}$ and rooting depth are plotted in the inset and their respective values (circle, triangle and square for the three drought levels) are connected with black arrows in the main panel. The three thick black curves in the main panel give the cross-genotype coordination of the two traits at each drought level.

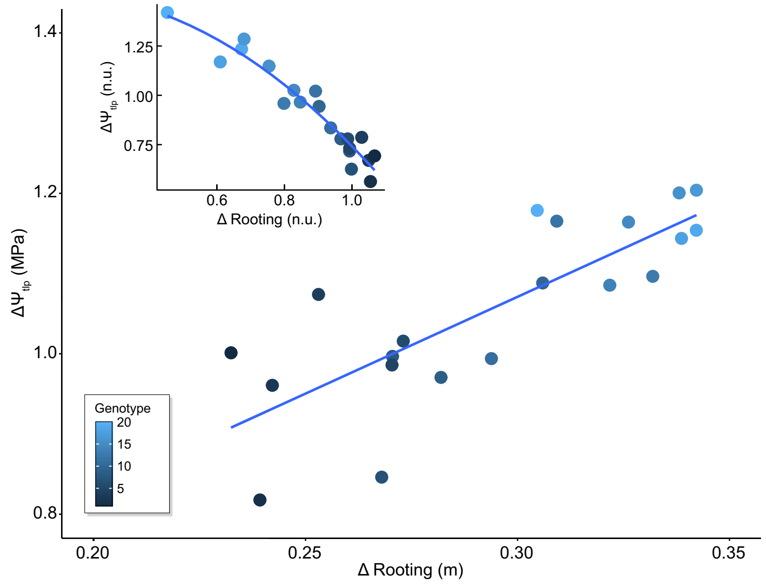

**Fig. B2** Using the same data used in Fig. B1 of this Box, this figure plasticity estimates (abbreviated with the symbol Δ) can be constructed using either the standard deviations of $\Psi_{tlp}$ and rooting depth for each genotype across the three levels of water availability (main panel) or the log ratios of the values of high Drought/no drought (inset). The apparent inversion in the relationship when log ratios are employed is caused by the fact that standard deviations measure the absolute range of the responses, whereas log ratios provide metrics of proportional responses in the traits. Hence, attention is required in the interpretation of plasticity metrics; n.u., unitless quantity.

greater than the xylem air-entry point, a form of passive plasticity. Upon a rainfall event, assuming no xylem refilling or regrowth, the vulnerability curve shifts towards a more negative $P_{50}$, following the embolisation of vulnerable conduits (Sperry *et al.*, 2017). This apparent acclimatisation to drought suggests that xylem vulnerability curves should be determined only in current-year wood before seasonal drought events. This approach determines a potential vulnerability curve under optimal conditions, but leaves open the question of what level of vulnerability should be expected for older xylem under natural conditions. However, it should be considered that $P_{50}$ may not be the most relevant parameter to determining embolism resistance (Meinzer *et al.*, 2009). Considering this and the evidence above, it seems adaptive plasticity in $P_{50}$ is unlikely to significantly mitigate against future droughts.

Much greater plasticity has been observed in both sapwood-area and leaf area-specific branch conductivities ($K_s$ and $K_l$, the second variable being less frequently determined than the first), albeit with lower, similar and greater values being reported when comparing dry vs mesic environments (Maherali *et al.*, 2004; Cornwell *et al.*, 2007; Martinez-Vilalta *et al.*, 2009; Corcuera *et al.*, 2011). Greater $K_s$ may be beneficial under short dry periods by avoiding negative xylem water potentials and preventing xylem embolism (Martinez-Vilalta *et al.*, 2009; Peguero-Pina *et al.*, 2011). Similarly, under conditions where light is not limiting, increasing $K_s$ in response to limited water availability may allow trees to compete more effectively for water (Giles *et al.*, 2022). By contrast, a reduction in $K_s$ in response to drought is usually related to a reduction in vessel size, which might result in a xylem less vulnerable to embolism. Given the variability which exists across these data, there appears to be insufficient evidence on whether and how adaptive plasticity in hydraulic efficiency can help minimise future drought impacts. The fact that plasticity in $K_s/K_l$ is substantially greater than the plasticity observed in $P_{50}$ suggests a strict safety–efficiency trade-off is unlikely. Instead, changes in $K_s$ may reflect plant structural changes (see 'Plant structure' in Section II), such as changes in Huber values HV, the sapwood cross-sectional divided by the distal leaf area, given that these two properties covary negatively across species (Mencuccini *et al.*, 2019), even when phylogeny is accounted for (Sanchez-Martinez *et al.*, 2020).

**Plant turgor** Plasticity in the regulation of cell volume and/or turgor via osmotic and elastic changes has been studied extensively for leaves (much less so for roots) with regard to the impacts of the accumulation of solutes inside cells (osmotic adjustment), especially in crop physiology and yield (Hsiao *et al.*, 1976), contrasting the limited study of other hydraulic traits. A review of pre- vs postdrought values (Bartlett *et al.*, 2014) found a moderate degree of plasticity in turgor loss point ($\Psi_{tlp} < 0.5$ MPa on average, i.e. 16% change relative to the mean $\Psi_{tlp}$) and even lower plasticity in osmotic potential at full turgor ($< 0.3$ MPa on average). No significant differences were found across biomes, albeit with a tendency towards higher plasticity in dry biomes. Because a large range of compatible solutes exist (inorganic ions such as potassium, sugars, amino acids such as proline or glycine betaine, and sugar alcohols), exploration of their role in osmotic adjustment is benefiting from current advances in metabolomics. Solute accumulation in leaves has often been shown to occur also at the daily time scale (e.g. Sancho-Knapik *et al.*, 2016), via soluble nonstructural carbohydrates. Osmotic adjustment during daytime can be equivalent in magnitude to the seasonal effects reported above (i.e. $< 1$ MPa changes in osmotic potential). Although little is known on the mechanisms regulating this process, it is likely that if sustained for long periods, consistent daily osmoregulation may have long-term consequences for allocation to sinks (including turgor regulation in roots) and levels of carbohydrate storage during/following droughts. Overall, plasticities in $\Psi_{tlp}$ and in resistance to embolism appear to be of similar and relatively small magnitude, suggesting that significant limitations and/or costs exist in their expression. Whether plasticities in these two traits are coordinated remains unclear, as one would expect given the strict coordination between water status, stomatal behaviour and vulnerability to embolism.

**Photosynthetic traits** In contrast to most hydraulic traits, many more studies on plasticity in photosynthetic traits exist. However, adaptive plasticity is rare in these studies, as prolonged drought generally has a negative impact on photosynthesis, either through stomatal conductance limitations or nonstomatal limitation, such as reduced mesophyll conductance or maximum photosynthetic capacities (Flexas *et al.*, 2004; Martin-Stpaul *et al.*, 2013; Zhou *et al.*, 2016; Gourlez de la Motte *et al.*, 2020; Rowland *et al.*, 2020). There are examples of plastic responses which enable plants to maintain or increase photosynthetic output under drought conditions, for example, plants that have evolved facultative CAM, the ability to reversibly change from $C_3$ to CAM photosynthesis during drought stress (Winter & Holtum, 2014). This enables a plant to switch to undertake $CO_2$ uptake and fixation during the night prolonging net carbon gain at a lower water cost. However, the majority of CAM plants are succulents, and within woody plants, particularly large ones, CAM is rare, possibly because fixation of carbon in the day is highly restricted by total storage capacity for night-time fixation products (Keeley & Rundel, 2003). Given this, the fact that the switch from $C_3$ to CAM is mostly a very long evolutionary process (Keeley & Rundel, 2003) and that only a handful of plants to date have been observed to plastically switch from $C_3$ to CAM during water stress (Winter & Holtum, 2014), it is perhaps more appropriate to focus on the potential adaptive gains that reduced photosynthesis offers a plant during sustained drought.

Downregulating photosynthesis may be a form of drought adjustment to protect the hydraulic system (Martorell *et al.*, 2014), or limit the metabolic costs of maintaining the photosynthetic machinery needed to generate high photosynthetic outputs when environmental conditions are unfavourable (Rowland *et al.*, 2020). These adjustments could serve to increase long-term survival and growth. However, changes in leaf biochemistry can also happen in response to changes in leaf structure, which may be an equally or more important driver of drought adaptations in plants (see 'Plant structure' in Section II).

**Plant structure** Structural changes, such as changes in HV, may be the most likely mode for achieving plasticity aboveground, especially considering the potential for developmental plasticity (Tyree & Ewers, 1991) and the high within-species variation (including phenotypic plasticity) observed in HV and other allocation traits, relative to hydraulic or leaf economic spectrum traits (Anderegg *et al.*, 2022). It has been widely observed that a plant's hydraulic system can become more vulnerable to drought as trees grow taller (Bennett *et al.*, 2015; Rowland *et al.*, 2015; Bittencourt *et al.*, 2020). Shorter individuals and individuals which are multi-stemmed, rather than single-stemmed, have also been shown to be less sensitive to drought, maintaining greater growth during sustained drought events (Alfaro-Sánchez *et al.*, 2020). As changes in height are likely to be a mechanism responsible for altering the hydraulic system of a plant (Fajardo *et al.*, 2019; Soriano *et al.*, 2020; Anfodillo & Olson, 2021; Bittencourt *et al.*, 2022), changes in architecture in response to sustained drought are potentially the most viable way a plant can adapt its hydraulic system. These changes in height are most likely a passive response to a drier climate reducing the turgor for growth; however, they are likely to lead to drought adaptive changes in the plant hydraulic system. Within wild plant populations, there is limited evidence to link developmental plasticity in architecture and growth to the mechanisms that underpin such changes in the plant hydraulic system, particularly at the cellular level (Fajardo *et al.*, 2019). For mature trees, this may be because any changes in the function of newly grown wood are likely to be masked by the function of existing old wood. Given this, it may be that a tree could more efficiently change through throwing away old tissues, particularly those with larger, more vulnerable vessels, or indeed more drastic changes such as branch shedding (Anfodillo & Olson, 2021).

Developmental changes in leaves also occur during prolonged drought to limit water losses. Leaves grown in drought conditions can have reduced stomatal density and size (Xu & Zhou, 2008). Leaf mass per area (LMA) can also increases in response to drought, enabling a tree to create leaves which are more resistant to wilting (Poorter *et al.*, 2009; Anderegg *et al.*, 2021). Such changes in LMA will have subsequent impacts on leaf biochemical relationships, potentially changing water, light and nutrient-use efficiency. Similarly, changes in LMA are directly tied to changes in whole-plant leaf area and HV, making it potentially difficult to isolate leaf-level plasticity from whole-plant structural changes. Joint experimental and modelling studies have suggested that leaf shedding or reduced leaf growth is the most effective strategy to protect trees from subsequent drought events (Nadal-Sala *et al.*, 2021; Sabot *et al.*, 2022). This is supported by evidence from local and global environmental gradients, where plants in drier environments tend to have greater HV to minimise water losses (Mencuccini *et al.*, 2019; Anderegg *et al.*, 2021). Thus, when the potential for structural changes in wood and leaves are considered together, it is possible that developmental changes to canopy architecture (HV), height and branching architecture (e.g. branch shedding) could be more relevant to facilitating long-term drought adjustment than acclimatisation of functional traits; however, considerably more data are necessary to robustly establish this.

## 2. Drought and belowground traits

The response of belowground traits to drought depends on soil properties that control water availability in space and time. Long-lived plants growing in soils with substantial water storage at depth, or access to groundwater, may increase belowground allocation and rooting depth to maintain water access (Hacke *et al.*, 2000; Pivovaroff *et al.*, 2021). On the contrary, where there is limited soil water storage, or short-lived plants cannot invest in accessing deep reserves, highly efficient water uptake and transport may be essential to take advantage of infrequent rainfall events (Alder *et al.*, 1996). Such strategies may result in small root xylem hydraulic-safety margins and high rates of root mortality, with implications again for resource allocation belowground (Chenlemuge *et al.*, 2015). When considering root adjustments during drought, it should also be emphasised that water transport from the root surface to the xylem may represent a greater proportion of root hydraulic resistance than transport through the xylem itself (Bartlett *et al.*, 2022). Therefore, adjustments to enhance symplastic and apoplastic water movements may be extremely important (Vadez, 2014).

In this section, we summarise how belowground traits may respond to drought, but emphasise that detecting trait plasticity is even more challenging below ground. Because the belowground strategies that plants employ have direct implications for temporal patterns of water uptake, monitoring predawn and midday leaf water potentials may help identify how above- and belowground strategies combine to control responses to drought.

**Allocation and rooting depth** Across spatial gradients, the proportion of carbon allocated belowground tends to be greater where soil water availability is lower, with the vertical or horizontal extent of rooting systems increasing (Hacke *et al.*, 2000; Addington *et al.*, 2006; Xu & Li, 2008). Where there is water storage at depth, deeper-rooted species can maintain greater access to water during droughts, as indicated by less negative predawn leaf water potentials (Nardini *et al.*, 2016). Furthermore, during a drought, or drought recovery (Hikino *et al.*, 2022), the proportion of carbon allocated belowground also tends to increase (Zhang *et al.*, 2019; Brunn *et al.*, 2022) together with rooting depth in some cases; in a long-term drought experiment in Queensland, rainforest trees increased average rooting depth (Pivovaroff *et al.*, 2021). Overall, greater root dry matter per unit leaf area (Potkay *et al.*, 2021) may help maintain water supply, but greater belowground allocation may also limit the potential for aboveground traits to respond to drought (Zhou *et al.*, 2020; Agee *et al.*, 2021; Pagay *et al.*, 2022), while increases in rooting depth could be maladaptive under nondrought conditions if nutrient uptake is reduced (Berkelhammer *et al.*, 2022).

**Root hydraulic and morphological traits** Where plants cannot access soil water reserves, changes in root hydraulic traits are key to maintaining water uptake (Vadez, 2014). Hydraulic resistance is thought to be greater below than aboveground, especially under drought conditions (Hacke *et al.*, 2000; Xu & Li, 2008; Bartlett *et al.*, 2022). Within species, across gradients of water variability, root hydraulic traits can vary substantially serving to reduce spatial variability in water uptake (Hacke *et al*., 2000). High hydraulic conductivity through wide xylem vessels may be crucial in allowing plants to move water greater distances through more extensive root systems (Domec *et al*., 2010), or to compete to take up water rapidly following infrequent rainfall events (Alder *et al*., 1996; Chenlemuge *et al*., 2015). The need to maintain high maximal conductivities may explain why xylem tends to be more vulnerable to embolism in roots than in aboveground tissues (Alder *et al*., 1996; Hacke *et al*., 2000), although differences between stem and root vulnerabilities are not always substantial (Peters *et al*., 2021). This vulnerability also suggests that the ability of plants to rapidly recover damaged xylem vessels may be a key drought recovery adjustment (Alder *et al*., 1996; Schenk *et al*., 2021). In addition, because water transport from the root surface to the xylem often contributes more to hydraulic resistance in the root system than transport through the xylem itself (Bartlett *et al*., 2022), increases in symplastic (e.g. through aquaporins) and/or apoplastic water movement within roots may be crucial in promoting greater rates of water uptake (Vadez, 2014). However, there is much less understanding of these processes in wild plants than in crops.

In terms of root morphology, very fine roots or root hairs can increase the contact between plants and soils, allowing plants to explore finer soil pores that may be the last sources of water in drying soils, so reducing the effect of drought on leaf water potentials (Marin *et al*., 2021). Furthermore, the roots produced during droughts themselves tend to relatively fine (Zhang *et al*., 2019), maximising the volume of soil explored as resources for constructing roots decline. In addition, finer roots may help reduce hydraulic resistance (Bartlett *et al*., 2016) by shortening distances between root surfaces and xylem vessels via a thinner cortex (Zhang *et al*., 2019). Ultimately, interactions between root morphological and hydraulic traits are likely key in maintaining water uptake during drought.

**Extended phenotype: symbioses, exudation and plant–soil interactions** Symbioses with fungi and bacteria may reduce drought impacts in multiple ways. Extensive ectomycorrhizal networks may promote water uptake distal to the root surface (Usman *et al*., 2021; Wang *et al*., 2021), while colonisation by arbuscular mycorrhizal fungi, dark septate endophytic fungi and plant growth-promoting bacteria can induce physiological, biochemical and morphological changes in roots that promote drought tolerance. Such responses include increases in root hydraulic conductivity (Quiroga *et al*., 2017) and enhanced osmolyte and anti-oxidant enzyme production (Kivlin *et al*., 2013; Ngumbi & Kloepper, 2016; He *et al*., 2019; Li *et al*., 2019). Given that the nature of these symbioses can change during droughts (Grams *et al*., 2021), they may be a critical and overlooked component of the overall plant drought response.

Changes in interactions with free-living soil microbes may be equally significant. Plants release exudates that can promote the growth of beneficial soil microbes (Williams & de Vries, 2020). Under drought, exudation rates can increase with exudates also changing chemically (Gargallo-Garriga *et al*., 2018) and can induce: microbial production of antioxidants and associated enzymes and so reduce root damage; and/or changes in soil physical or chemical properties that increase soil water access (Bitterlich *et al*., 2018; Gargallo-Garriga *et al*., 2018; Williams & de Vries, 2020). Reflecting this, plants inoculated with microbial communities from soils that had previously experienced droughts performed better under subsequent droughts (Li *et al*., 2022). Finally, changes in relationships between plants and soil microbes may also be crucial in maintaining or re-establishing nutrient cycling during drought and drought recovery (Lehto & Zwiazek, 2011).

## III. Plasticity and trait integration

Individual traits covary in trait spectra, where the term spectrum implies the coordination of traits along one axis to optimise a well-defined set of physiological functions under prevailing environmental conditions (nutrient stoichiometry, leaf, wood or root economics spectra, wood anatomical/hydraulic properties). Therefore, plasticity can exist not only in individual traits, but also in the manner in which traits covary within each axis of the spectrum (shifts in trait syndromes, upwards or downwards along common regression lines, intercept and/or slope shifts), creating synergistic or compensatory effects (Nielsen & Papaj, 2022). *Plasticity in trait coordination* (first part of Box 2) has seldom been studied in the context of multivariate plasticity of drought-related trait spectra. To illustrate these concepts, we use a bivariate framework where we consider the example of the potential coordination between $\Psi_{\text{tlp}}$ (water potential at the turgor loss point) and plant rooting depth. Reaction norms are commonly built by quantifying how phenotypic traits vary as a function of external environmental variables, for example precipitation or temperature. We employ here instead $\Psi_{\text{pd}}$, which indicates the level of soil water stress as perceived by the plant, to describe the potential reaction norms of rooting depth and $\Psi_{\text{tlp}}$ (insets of Fig. B1 in Box 2). These reaction norms may represent acclimation via developmental plasticity and osmoregulation, respectively. We now consider the potential coordination between $\Psi_{\text{tlp}}$ and rooting depth across several genotypes under three levels of drought stress (main panel of Fig. B1 in Box 2). This coordination is relevant, because it relates to the degree of water status regulation (e.g. hydroscape area, Meinzer *et al*., 2016). These positive relationships can be thought of as representing a continuum from drought avoidance (deep rooting) to drought tolerance (more negative $\Psi_{\text{tlp}}$). The shifts from one line to the other, as well as the changes in the position of the points along the curves, represent estimates of the cross-genotype plasticity in the $\Psi_{\text{tlp}}$-rooting depth coordination. In this example, with declining water availability, the coordination between $\Psi_{\text{tlp}}$ and rooting depth follows a flatter curve.

Using the same data, the range of variability in the reaction norm for each genotype across treatments is a measure of plasticity of the two traits. Plotting the plasticity in $\Psi_{\text{tlp}}$ as a function of plasticity in rooting depth is a measure of the *coordination of the plasticity* of the two traits (second part of Box 2). In this case, the relationship in the main panel suggests that genotypes with a deep rooting system have greater absolute plasticity in $\Psi_{\text{tlp}}$ (i.e. they are more buffered against variability in water availability) compared with genotypes with more superficial roots, but the opposite trend is also possible

(Fig. B2). As an example, Charrier *et al.* (2018) examined the relationships between predawn and midday water potentials and showed that this iso-anisohydricity axis shifted for two grapevine varieties depending on whether the plants were grown in the field or in the glasshouse. They were able to trace these shifts to the constituent traits controlling stomatal and xylem responses to soil and atmospheric drought.

*Coordination of trait plasticity* may explain the variability encountered in the $K_s$–$P_{50}$ relationships reported in the literature, whereby in certain species, exposure to drought results in smaller $K_s$ and more negative $P_{50}$, while in other cases, higher $K_s$ and less negative $P_{50}$ values are observed (avoiding more negative water potentials). Coordination of plastic responses across traits regulating different plant functions has been found. For example, Cavender-Bares (2019) reported a negative association between osmotic adjustment and leaf abscission in response to drought, such that decreased $\Psi_{tlp}$ did not reduce transpiring leaf area and vice versa. This is consistent with a trade-off between drought avoidance and drought tolerance strategies. These analyses are useful in situations where knowledge of trait coordination allows identification of a continuum in the behaviour of different species and populations with regard to fundamental control points (e.g. hydraulic-safety margins, degree of turgor or osmotic regulation).

There is increasing interest in understanding how drought alters patterns of trait coordination; however, the literature remains sparse (Damián *et al.*, 2020). Collyer & Adams (2007) developed a method to quantify phenotypic plasticity in a multivariate framework that can be used to test for differences among groups (e.g. species and populations) and provide inferences of their adaptive value. This method estimates two properties of the phenotypic change vector between two contrasting environments: the magnitude (vector length) and the direction of the phenotypic plasticity (vector angle). Fig. 2 shows an example of this analysis in a bivariate framework, using the two traits represented in Fig. 1 (photosynthetic capacity and hydraulic efficiency) measured in a common garden under two contrasting environments, dry and wet. Magnitude defines the overall phenotypic change across environments, while direction represents changes in trait covariation and defines the traits involved. Magnitude and direction can be estimated for distinct genetic or phylogenetic groups to test for associations with their climatic niche, which would provide inferences on the adaptive value of multi-trait plasticity.

Beyond the coordination of trait means and variances within individual spectra, plasticity in whole-plant behaviour may be controlled by the manner in which spectra become more or less integrated under environmental pressures (Schlichting, 1989; Marks, 2007; Fontana *et al.*, 2021). As a result of this multidimensional plasticity, sets of (functional, structural and phenological) traits that form an integrated unit in one environment may be only loosely integrated in a different environment, independent of trait coordination within individual functional spectra (Rowland *et al.*, 2021). In other words, plasticity can blur the distinction between independent axes of trait coordination via increased or decreased integration of multiple spectra (Pigliucci & Kolodynska, 2002; Nielsen & Papaj, 2022), for example, the relationships between flowering time, water-use efficiency and leaf economics spectrum traits (Vasseur *et al.*, 2014). Similarly, concurrent plasticity in plant structure and functional traits can also facilitate integration across different spectra (Nolting, 2020; Ramírez-Valiente *et al.*, 2020; Nolting *et al.*, 2021; Sole-Medina *et al.*, 2022).

The analyses of plasticity of coordination, coordination of plasticity and multi-trait plasticity illustrated in previous paragraphs following bivariate frameworks can also be conducted for multiple traits from multiple spectra to provide information on integrated responses at the whole-plant level. Fig. 3 shows one example of how a multivariate analysis could be done for a dataset of physiological, morphological, allometric and growth traits measured in 11 oak species growing in a common garden experiment under two contrasting water availabilities. Fig. 3(a) shows plasticity of integration under two contrasting environments for traits related to three functional axes. In the well-watered conditions, strong correlations were observed within the three functional axes, photochemistry and area-based gas exchange, leaf morphology and the leaf economic spectrum, and allometric and growth traits, indicating trait coordination. Some correlations among traits from different functional axes were observed, for instance, between leaf area, mass-based gas exchange and allometric traits, which is indicative of trait integration. When plants were grown under dry conditions, correlations between traits both within spectra and between spectra changed, indicating plasticity in both trait coordination and trait integration. For example, species with higher photochemical efficiency (as measured by $F_v'/F_m'$) had significantly larger absolute growth rate under dry conditions, but not under mesic conditions. Early studies proposed tighter trait coordination in drier environments, presumably as result of an integrated phenotypic response under more stressful conditions (Schlichting, 1989; Gianoli, 2004; Gianoli & Palacio-Lapez, 2009). Results from some empirical studies are consistent with this hypothesis (Sole-Medina *et al.*, 2022). However, results shown in Fig. 3(a) are in line with findings from other studies that suggest this is not the general rule (e.g. Mallitt *et al.*, 2010; Matesanz *et al.*, 2010, 2021; Ramírez-Valiente *et al.*, 2020). The third panel in Fig. 3(a) shows that correlations between plasticities largely occurred within spectra (i.e. plasticity of trait coordination) and that only leaf morphologic and allometric traits showed correlations between plasticities from different spectra (i.e. plasticity of trait integration).

Fig. 3(b) shows the results from the multivariate analyses following Collyer & Adams (2007) for the same dataset. The magnitude of plasticity (the length of the vector in the multivariate space) was associated with the species' precipitation niche (Fig. 3c), supporting the idea that differences among species resulted from evolution under contrasting climates. The direction of plasticity (the angle of the vector) ranged between 40° and 80° for most species, with the angles mainly aligned with variations in physiological traits, such that decreased gas exchange and photochemistry under drought were the main drivers of the multivariate plastic response across environments. Note that for *Quercus coccifera*, the direction of plasticity was completely different compared with any other species, suggesting that different processes were at play.

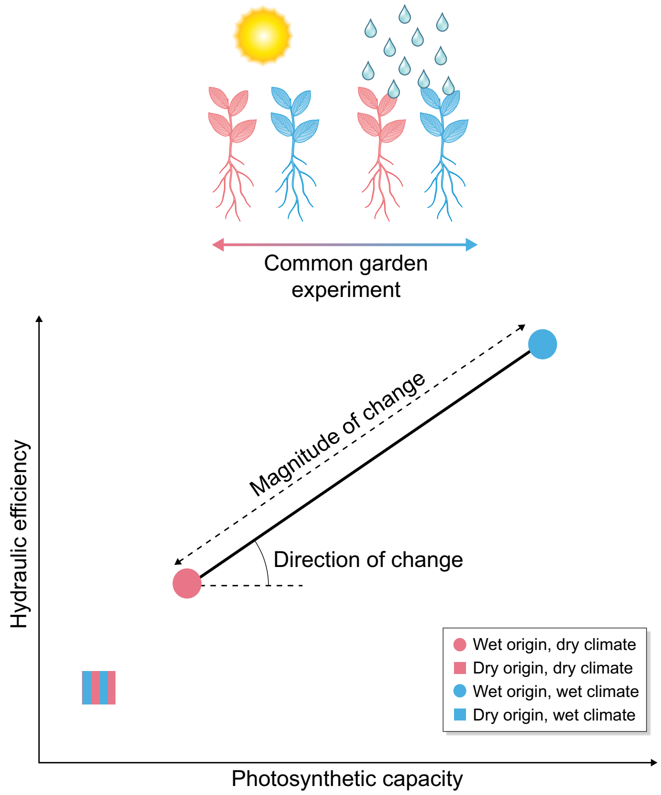

**Fig. 2** Theoretical diagram of a multivariate reaction norm based on theory from Collyer & Adams (2007). Using the example of potential results from the common garden experiment from Fig. 1, we demonstrate how the magnitude and the direction of drought plasticity in photosynthetic capacity and hydraulic efficiency could vary as individuals of a species from the wet end of a climate gradient are shifted to the dry end (from blue to red circle), and individuals of a species from the dry end of a climate gradient are shifted to the wet end (from red to blue square). Colours indicate the climate the individuals are being grown within, either wetter (blue) or drier (red). The magnitude of the plasticity response in each trait is determined by the length of the vector line between individuals derived from the same original populations, but exposed to different climates (overall phenotypic change across environments). The direction of the plasticity change is calculated from the angle of the slope between individuals derived from the same original populations, but exposed to different climates (the change in trait covariation). In this hypothetical example, individuals originally derived from the drier end of the environmental gradient (squares) have no potential for plasticity so the squares overlap (striped red and blue square). The individual from the wet climate origin decreases both its photosynthetic capacity and hydraulic efficiency as it moves into the drier climate (see also Fig. 1).

Finally, it is important to bear in mind that multivariate estimates of magnitude and direction of plasticity might be affected by the number of traits and functional axes used for their calculation. Two principal component analyses are presented for a subset of physiological (Fig. 4a) or morphological (allometric, growth and leaf morphology traits, Fig. 4b) traits. Both the magnitude and the direction as well as the associations with the species' climatic niche varied across PCAs. In Fig. 4(a), the patterns are very similar to Fig. 3(a), with species responses ordered by decreasing gas exchange in response to drought. By contrast, in Fig. 4(b), the magnitude and especially the direction of plasticity changed. Since the direction of multivariate plasticity indicates the traits involved in the phenotypic change across environments, it might be expected to not follow the same patterns across PCAs with different sets of traits. However, changes in magnitude of multivariate plasticity across sets of traits show the need to be cautious when interpreting multivariate properties of phenotypic plasticity, particularly if a reduced number of traits and spectra are measured. In summary, these analyses represent different approaches to explore multivariate responses to environmental changes and demonstrate the need to move towards a more integrated functional perspective to study how species adjust to a drier environment.

## IV. Future directions

Based upon the analyses undertaken in the three sections above, here we outline four key areas for future research to advance our knowledge of how plants can adjust to drought.

### 1. Going beyond studies of spatial trait variation to understand drought impacts

As a community, we must recognise the limits of using spatial differences in traits as a way to understand plant plasticity. Spatial variation in traits may provide some insight into the potential of species to adjust their phenotypes in response to drought; however, it confounds genetic changes and plastic processes. Variations in

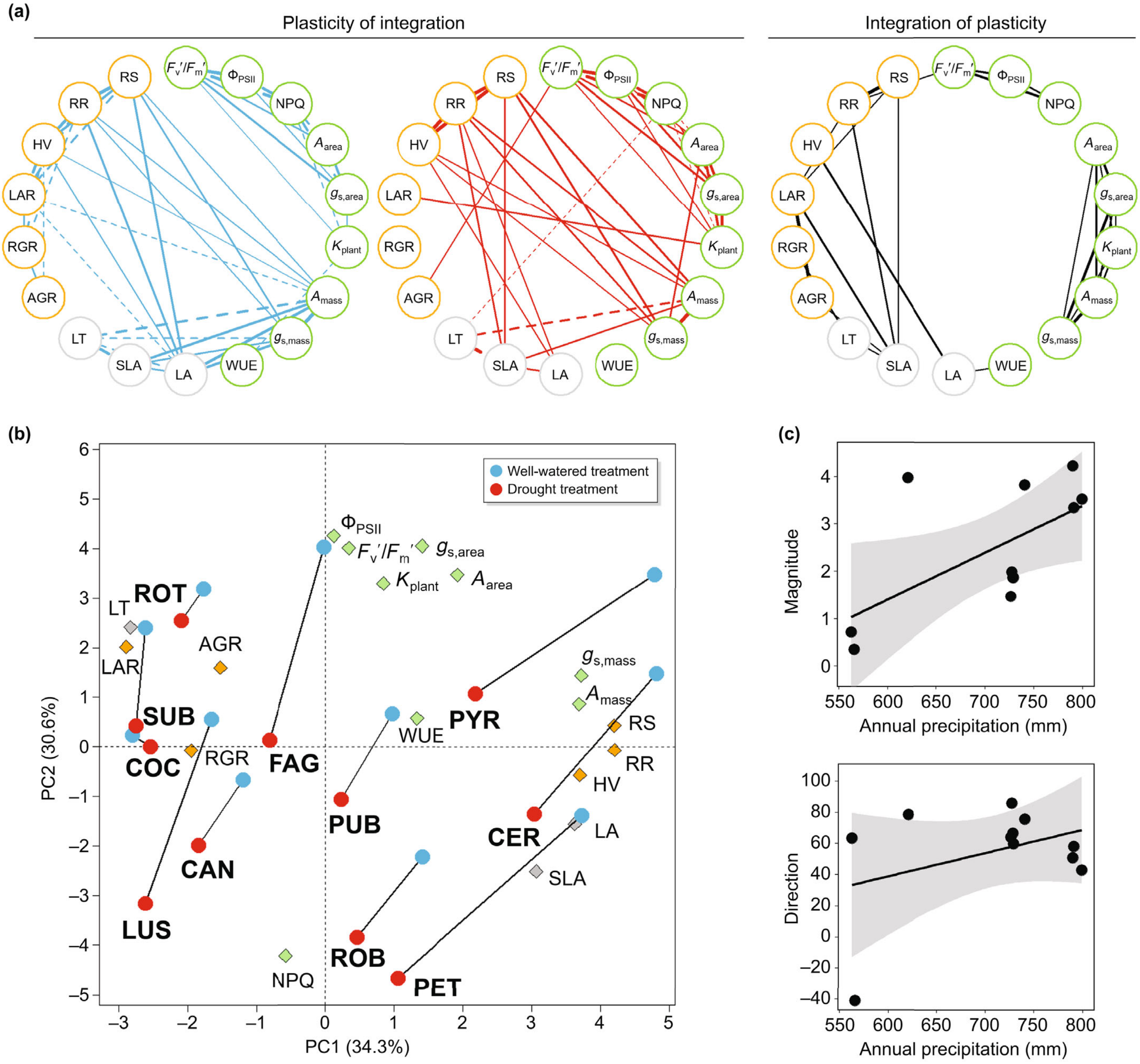

**Fig. 3** Multivariate analyses of phenotypic plasticity conducted for a dataset of 11 oak species grown under contrasting water availability treatments in a common garden experiment. (a) Plasticity of integration (blue and red networks) and integration of plasticity (black network) analyses. Network diagrams depict pairwise species correlations between traits in the well-watered (blue network) and drought (red network) treatments and between plasticity of traits across treatments (black network). Positive and negative relationships are depicted by continuous or dashed lines, respectively. Only significant correlations ($P < 0.05$) are shown. Coloured circles represent physiological (green), morphological (grey) and growth and allometric traits (orange). (b) Multivariate phenotypic plasticity for each species for the first two axes of a principal component analysis of species trait means measured in well-watered and drought conditions. Diamonds indicate trait loadings, with colours representing physiological (green), morphological (grey) and growth and allometric traits (orange). Circles indicate species scores under well-watered (blue) and drought treatments (red) with connecting lines representing vectors of phenotypic change for each species. (c) Associations between the average climatic niche (annual precipitation) of species and the magnitude (upper) and direction (lower) of multivariate phenotypic plasticity. Black dots represent species magnitudes and directions obtained from vectors of phenotypic change in (a). Grey-shaded areas represent 95% confidence intervals. The traits are the following: maximum quantum yield of PSII in light ($F_v'/F_m'$), effective quantum yield of PSII ($\Phi_{PSII}$), nonphotochemical quenching (NPQ), area-based photosynthesis rate ($A_{area}$), area-based stomatal conductance ($g_{s,area}$), whole-plant leaf-specific hydraulic conductance ($K_{plant}$), mass-based photosynthetic rate ($A_{mass}$), mass-based stomatal conductance ($g_{s,mass}$), water-use efficiency (WUE), leaf lamina area (LA), specific leaf area (SLA), absolute growth rate (AGR), relative growth rate (RGR), leaf area ratio (LAR), Huber value (HV), root biomass ratio (RR), root-to-shoot ratio (RS). CAN, *Quercus canariensis*; CER, *Quercus cerris*; COC, *Quercus coccifera*; FAG, *Quercus faginea*; LUS, *Quercus lusitanica*; PET, *Quercus petraea*; PUB, *Quercus pubescens*; PYR, *Quercus pyreanica*; ROB, *Quercus robur*; ROT, *Quercus rotundifolia*; SUB, *Quercus suber*. Data extracted from Ramírez-Valiente *et al*. (2020).

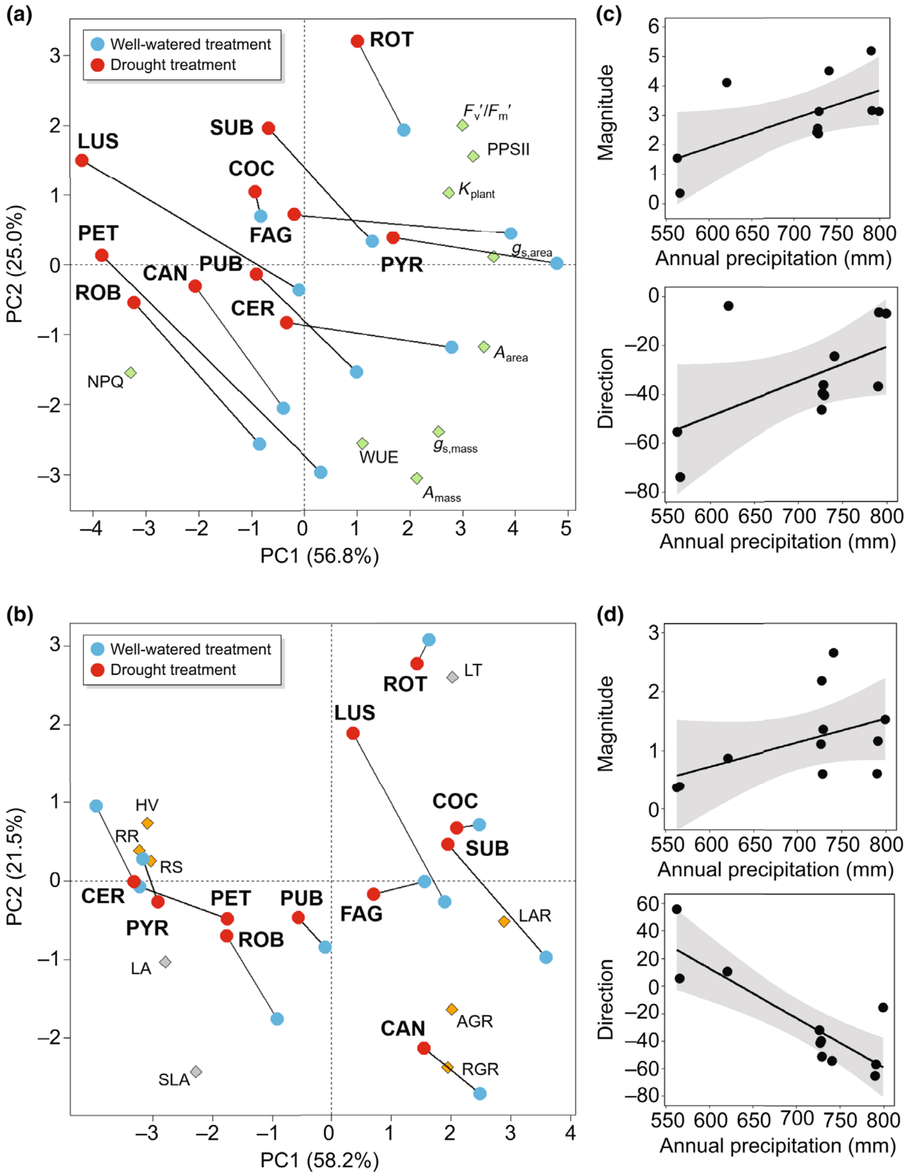

**Fig. 4** Multivariate analyses of phenotypic plasticity for a dataset of 11 oak species grown under contrasting water availability treatments in a common garden experiment as in Fig. 2 for different subsets of traits. In panels on the left, trait loadings (diamonds) and species scores (circles) from a principal component analysis were obtained from (a) only physiological traits (green) and (b) only morphology (grey) and growth traits (orange). Colours for species scores represent well-watered (blue) and drought (red) treatments, respectively. The panels on the right depict associations between the average climatic niche (annual precipitation) of species and the magnitude and direction of multivariate phenotypic plasticity obtained from the different subsets of traits, (c) only physiological traits and (d) only morphology and growth traits. Black dots represent species magnitudes and directions obtained from vectors of phenotypic change. Grey-shaded areas represent 95% confidence intervals. The traits are the following: maximum quantum yield of PSII in light ($F_v'/F_m'$), effective quantum yield of PSII ($\Phi_{PSII}$), nonphotochemical quenching (NPQ), area-based photosynthesis rate ($A_{area}$), area-based stomatal conductance ($g_{s,area}$), whole-plant leaf-specific hydraulic conductance ($K_{plant}$), mass-based photosynthetic rate ($A_{mass}$), mass-based stomatal conductance ($g_{s,mass}$), water-use efficiency (WUE), leaf lamina area (LA), specific leaf area (SLA), absolute growth rate (AGR), relative growth rate (RGR), leaf area ratio (LAR), Huber value (HV), root biomass ratio (RR), root-to-shoot ratio (RS). CAN, *Quercus canariensis*; CER, *Quercus cerris*; COC, *Quercus coccifera*; FAG, *Quercus faginea*; LUS, *Quercus lusitanica*; PET, *Quercus petraea*; PUB, *Quercus pubescens*; PYR, *Quercus pyreanica*; ROB, *Quercus robur*; ROT, *Quercus rotundifolia*; SUB, *Quercus suber*.

traits across drought gradients will likely overestimate the potential for plasticity to respond to rapid climate change. This is particularly pertinent when we think of the ongoing development of optimality models, which predict changes in traits from environmental variables (Harrison *et al.*, 2021). For these models to account for plasticity, we must go beyond using spatial databases such as TRY (Kattge *et al.*, 2011) and start using datasets that exclude potential genetic effects (i.e. trait plasticity meta-analyses, cf., Cui *et al.*, 2020; Stotz *et al.*, 2021). These meta-analyses are in their infancy and substantially greater experimental studies are needed to build on the number of species and biomes included in these studies. These studies should preferably be designed not only to include several elements of the experiments laid out in Fig. 1, but also to test varying extremities of drought to understand how plasticity varies with drought intensity.

### 2. Linking changes in traits to changes in metrics of whole-plant success

We must be cautious not to overestimate the role plasticity will play in mitigating the impacts of increasing drought frequency and severity on plants. While we will not have covered all existing studies, our review suggests plasticity in individual traits (e.g. $\Psi_{\mathrm{tlp}}$, $P_{50}$) is variable and might not be sufficient to fully compensate for the impacts of drought caused by global change forcing in a number of species. In fact, there remains a severe lack of knowledge on the adaptive role of plasticity across environments. In some circumstances, plastic changes may be the result of passive responses and have limited impact on plant survival or growth. Alternatively, active changes in phenotype may have a positive impact on plant survival or growth in one set of conditions, but not necessarily under another set of environmental conditions (i.e. differing impacts under drought and nondrought conditions). To disentangle these various possibilities, it is essential to have continuous measures of fitness proxies that are measurable at the scale of individual plants, like growth and survival to accompany our measures of trait plasticity, which is currently rare within the literature.

### 3. Addressing key knowledge gaps in belowground responses to drought

To identify how whole-plant responses are controlled and whether there are fundamental trade-offs in trait plasticity above vs belowground, it is critical that key belowground knowledge gaps are addressed. Determining the extent to which species can change belowground traits in response to drought, and whether they adopt contrasting drought response strategies depending on soil conditions, requires studies across gradients in soil water availability. For example, where deep soil water stores exist, do species respond to drought by increasing rooting depths (e.g. Williams & Ehleringer, 2000), but where soil water storage is limited do the same species shift above- and belowground traits towards conserving water and/or competing for water after rare rain events? While quantifying changes in belowground traits remains challenging, identifying plasticity in water-uptake vs water-use strategies may be facilitated by measuring changes in aboveground traits in combination with the monitoring of predawn water potentials during drought events in locations with differing soil water resources.

In addition, there remain major knowledge gaps regarding how plant–microbe–soil interactions control drought outcomes and vulnerabilities to future droughts. In many cases, a comprehensive examination of plasticity will need to go beyond the classical definition of the individual plant (Rosado *et al.*, 2018), widening the traditional concept of an extended phenotype. Emerging evidence suggests changes in the relationships between plants and root and rhizosphere microbes may be a critical component of drought, and changes in these relationships may occur rapidly and have long-lasting impacts. Addressing this poorly understood area may require collaboration across multiple research fields, including plant physiologists, ecohydrologists and molecular biologists, ecosystem ecologists, microbiologists, biogeochemists and soil physicists.

### 4. Understanding plasticity within and across trait spectra

Current research must move into studying plasticity within and across trait spectra. Plants are integrated units, and with the purpose of adaptive plasticity being to avoid reductions in fitness under forcing, it is logical that this can be achieved by means of changes in individual traits or through the synergies and/or compensations occurring when combinations of traits act together, both within and across trait spectra (Box 2; Section III). Ideally, we move towards measuring the reaction norms of trait spectra to drought, understanding the relationships between plasticity and trait integration and their impacts on plant growth and survival. These should include measures of coordinated changes in both morphological (height, allometry, architecture and allocation) and physiological traits. Even if the potential for drought-related plasticity of individual traits seems limited, it is possible that many small changes across multiple traits can lead to a significant change in whole-plant function (Marks, 2007) and this is a key area for future research. Network analysis has gained momentum and has begun to produce correlative evidence of how properties of trait networks (centrality, connectivity and clustering) vary across environments within species. Although it is too early to extract general conclusions from these studies (Messier *et al.*, 2017; Michelaki *et al.*, 2019), these types of analyses are very promising for studying how networks of traits change in response to drought.

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## Competing interests

None declared.

## ORCID

Iain P. Hartley https://orcid.org/0000-0002-9183-6617
Maurizio Mencuccini https://orcid.org/0000-0003-0840-1477
Jose-Alberto Ramírez-Valiente https://orcid.org/0000-0002-5951-2938
Lucy Rowland https://orcid.org/0000-0002-0774-3216

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