

LETTER

Global analysis of plasticity in turgor loss point, a key drought tolerance trait

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Abstract

Many species face increasing drought under climate change. Plasticity has been predicted to strongly influence species' drought responses, but broad patterns in plasticity have not been examined for key drought tolerance traits, including turgor loss or 'wilting' point (π_{tlp}). As soil dries, plants shift π_{tlp} by accumulating solutes (i.e. 'osmotic adjustment'). We conducted the first global analysis of plasticity in $\Delta\pi_{tlp}$ and related traits for 283 wild and crop species in ecosystems worldwide. $\Delta\pi_{tlp}$ was widely prevalent but moderate (-0.44 MPa), accounting for 16% of post-drought π_{tlp} . Thus, pre-drought π_{tlp} was a considerably stronger predictor of post-drought π_{tlp} across species of wild plants. For cultivars of certain crops $\Delta\pi_{tlp}$ accounted for major differences in post-drought π_{tlp} . Climate was correlated with pre- and post-drought π_{tlp} , but not $\Delta\pi_{tlp}$. Thus, despite the wide prevalence of plasticity, π_{tlp} measured in one season can reliably characterise most species' constitutive drought tolerances and distributions relative to water supply.

Keywords

osmotic adjustment, plasticity, turgor loss point, drought tolerance, ecosystem water availability, mixed effects models, ecophysiology.

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INTRODUCTION

Droughts are expected to become more frequent and severe worldwide due to climate change (Sheffield & Wood 2007). Quantifying the physiological traits that correlate with drought survival and ecosystem water supply, such as the leaf water potentials associated with stomatal closure, wilting and hydraulic dysfunction (Brodribb *et al.* 2003; Choat *et al.* 2007; Bartlett *et al.* 2012b) have potential to improve predictions of shifts in species' distributions and community composition, functional diversity and ecosystem services (Higgins *et al.* 2012). However, most models of species responses to climate change have assumed fixed trait values and climate niches (Dormann 2007) even though plants express plasticity in many traits in response to resource availability (Choat *et al.* 2007; Valladares *et al.* 2007; Nicotra *et al.* 2010) that could widen the range of tolerable climatic conditions (Dormann 2007; Nicotra *et al.* 2010). Little is known about the magnitude of plasticity in drought tolerance traits across diverse species and ecosystems. We present the first global analysis of plasticity in a well-recognised drought tolerance trait, the turgor loss point, to elucidate its variation across ecosystems, especially relative to ecosystem water supply.

The turgor loss point (π_{tlp} ; unit: MPa) is the negative water potential at which leaf cells lose turgor and the leaf wilts, closing stomata and ceasing gas exchange and growth (Cheung *et al.* 1975; Brodribb *et al.* 2003; Blackman *et al.* 2010). The π_{tlp} also represents the soil water potential below which the

plant cannot take up sufficient water to recover from wilting. Plants with more negative π_{tlp} values maintain stomatal and hydraulic conductance, photosynthetic gas exchange and growth under drier soil conditions and generally occur in drier ecosystems (Becker *et al.* 1988; Brodribb *et al.* 2003; Lenz *et al.* 2006; Blackman *et al.* 2010; Bartlett *et al.* 2012b). The π_{tlp} is one of the key leaf physiological traits estimated from the relationship between the leaf water potential and leaf water volume, known as the pressure–volume (p–v) curve. The π_{tlp} is mechanistically related to the other pressure–volume parameters: osmotic potential, or the water potential produced by the cell solute concentration at full hydration (π_o ; unit: MPa); elastic modulus of the cell wall, or cell wall stiffness (ϵ ; unit: MPa) and apoplastic fraction, or the proportion of water found outside the cell protoplasts (a_p) (Cheung *et al.* 1975; Bartlett *et al.* 2012b). Because the π_{tlp} represents both the leaf and soil dryness that induce wilting, it is considered to be the 'higher-level' trait that most directly quantifies plant drought tolerance, and plants are expected to vary the other p–v parameters to achieve a sufficiently negative π_{tlp} value for their habitat water availability (Lenz *et al.* 2006; Bartlett *et al.* 2012b). A related pressure–volume parameter, the relative water content at turgor loss point (RWC_{tlp} ; unit: %), or the leaf hydration at wilting, has also been considered an important measure of plant drought tolerance (Sinclair & Ludlow 1985). The relative importance of RWC_{tlp} and π_{tlp} to drought tolerance has long been debated in the literature (Sinclair & Ludlow 1985), and a recent meta-analysis concluded

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that π_{tlp} and not RWC_{tlp} drives species associations with habitat water supply (Bartlett *et al.* 2012b).

That same meta-analysis also showed that differences among species in π_{tlp} are primarily driven by differences in π_o rather than ϵ or a_f . Similarly, shifts in π_{tlp} for *given species* during drought are driven by shifts in π_o caused by changes in the symplastic solute concentration (i.e. 'osmotic adjustment') rather than by shifts in ϵ or a_f , which typically have negligible effects (Bartlett *et al.* 2012b). Plants of many species can decrease their π_{tlp} in response to seasonal or occasional soil droughts by accumulating solutes to decrease π_o in existing leaves, including ions (K^+ , Ca^{2+}), sugars, polyols (glycerol, mannitol), amino acids (proline), amines (glycine betaine) and organic acids (Morgan 1984; Chen & Jiang 2010), or by developing new leaves with greater solute concentrations (Wright *et al.* 1992). Additionally, plants also show shifts in RWC_{tlp} in response to drought-induced changes in both π_o and ϵ (Bartlett *et al.* 2012b). Although plasticity in these traits has itself been considered a key drought tolerance trait for decades in comparisons of coexisting species or crop cultivars (Zhang *et al.* 1999; Blum 2005), there has been no synthesis of the quantitative importance of plasticity in π_{tlp} and RWC_{tlp} across species and ecosystems. We compiled a novel global database to conduct a meta-analysis of seasonal changes in π_{tlp} and RWC_{tlp} , and in particular to address the following questions:

(1) For droughted plants, is the primary determinant of π_{tlp} and RWC_{tlp} the pre-drought values, or the plastic shift during the drought? Significant plasticity in these traits could modify species' drought tolerance over the course of wet and dry seasons, and may influence community-level processes if shuffling of species' rankings in these traits influences trait-mediated interactions among co-occurring species (Valladares *et al.* 2007). However, if pre-drought π_{tlp} and RWC_{tlp} are the main determinants of post-drought π_{tlp} and RWC_{tlp} , then measurements taken at any season could be used to characterise species drought tolerances within or across communities, considerably simplifying sampling and modelling in diverse communities.

(2) How does plasticity in π_{tlp} and RWC_{tlp} ($\Delta\pi_{\text{tlp}}$ and ΔRWC_{tlp}) vary across ecosystems, and is that variation explained by ecosystem differences in water supply? Plants generally exhibit greater plasticity in leaf morphology, and photosynthetic and biomass allocation traits in environments with greater seasonal or interannual variation in water supply (Matesanz *et al.* 2010), as do plants from generally resource-rich communities, associated with their more rapid growth and development (Grime & Mackey 2002). However, plasticity in traits that reflect cellular acclimation instead of new tissue growth, such as solute accumulation, may be largely independent of overall resource availability (Grime & Mackey 2002). If the magnitude of plasticity varies with average habitat water availability or seasonality in water availability, then it should exhibit considerable variation among ecosystems, and correlations of plasticity with climate variables may then improve estimates of phenotypic plasticity for future species distribution models.

(3) Do crop species exhibit greater plasticity in π_{tlp} and RWC_{tlp} than wild species (i.e. species growing in natural

ecosystems)? Improving crop drought tolerance through selective breeding for increased osmotic adjustment has been a long-standing objective of agricultural research (Zhang *et al.* 1999; Chen & Jiang 2010). However, it remains unknown whether selective breeding has made drought-induced plasticity more important in crops than wild species, and more important to differences in drought tolerance across crop cultivars within species than across species.

METHODS

We compiled a novel database from 88 previously published studies of turgor loss point (π_{tlp}), osmotic potential at full hydration (π_o) and total relative water content at turgor loss point (RWC_{tlp}) measured in well-watered soil and during drought. We did not find sufficient data for a comparable analysis of symplastic RWC_{tlp} , which only includes the water lost from inside cells. We compiled studies from the literature by searching for the keywords 'osmotic adjustment', 'turgor loss point' or 'pressure–volume curve' combined with 'seasonal', 'adjustment', 'plasticity', 'drought', 'dry season', 'water stress', 'agriculture' or 'crop' in the Web of Science and AGRICOLA databases and the Google Scholar search engine, and for the sources that cited or were cited by studies that met our criteria for inclusion. We applied six criteria to minimise variation in our π_{tlp} and plasticity data due to ontogenetic and methodological factors that are known to affect these measurements. Thus, we included studies that: (1) sampled mature, fully expanded leaves from (2) sapling or adult plants and not seedlings experiencing (3) seasonal and not interannual changes in water availability in (4) naturally occurring ecosystems for wild species, as we sought to characterise ecosystem differences in plasticity, and experimental drought treatments for crop species. We also only selected studies that (5) rehydrated samples for ≥ 6 h prior to measurement, unless the study tested for and reported no effect of rehydration time on the p–v curve parameters, and measured these variables by (6) generating pressure–volume curves. We allowed an exception to criterion 6 to include new osmometer measurements for 13 species from the Xishuangbanna Tropical Botanical Garden forest plot in Yunnan, China, which we converted to pressure–volume curve values using a published calibration (Bartlett *et al.* 2012a), and we verified that the uncertainty of these π_{tlp} values was within the range of the p–v curve values (see Supplementary Methods). We checked if this calibration could be applied to other published osmometer data, but these measurements are highly sensitive to sampling technique (Brown & Shouse 1992), and the studies that collected osmometer data and met the other criteria either used different techniques or did not provide enough information to determine whether the sampling procedures were similar.

We collected species means for each variable, as all the studies reported species summary statistics and not values for individual plants. This produced a data set of 246 wild and 37 crop species for π_{tlp} plasticity, 207 wild and 33 crop species for π_o adjustment and 90 wild and 30 crop species for RWC_{tlp} plasticity. For the studies that did not define wet and dry seasons but instead measured these variables throughout the year, we used their soil water potential or precipitation data

to identify the wettest and driest sampling times at which leaves would be fully expanded.

Environmental data and categorization of biomes and functional types

Climate data were determined for each wild species in the database. Study site coordinates were used to extract local climate data at a 30 arc-second resolution for mean annual precipitation (MAP) from the WorldClim database, and annual potential evapotranspiration (PET) and aridity index (AI = MAP/PET) from the CGIAR-CSI database, which used the WorldClim data to calculate these variables (Hijmans *et al.* 2005; Trabucco & Zomer 2009) (Table S1, S2; Fig. S1). We used these variables to calculate a simple index of annual water balance (WB = MAP – PET). To determine whether plasticity was related to seasonality, we also calculated water balance for the months in which pre- and post-drought measurements were taken in each study, and calculated seasonal changes as post-drought pre-drought values.

We classified species into biome categories based on the Global Plant Trait Network (GLOPNET) definitions, including temperate conifer ($n = 15$ species for $\Delta\pi_{\text{tlp}}$) and broadleaf forests ($n = 37$), tropical dry forest ($n = 83$), Mediterranean/dry temperate ($n = 55$), semidesert ($n = 27$), grassland ($n = 4$), alpine/subalpine ($n = 6$) and coastal/wetland ($n = 17$) (Wright *et al.* 2004) (Table S2). Functional types within each biome were further categorised as herbaceous, deciduous and evergreen for biomes with at least five species per category.

Statistical analyses

We calculated the plasticities of π_{tlp} ($\Delta\pi_{\text{tlp}}$), π_{o} ($\Delta\pi_{\text{o}}$) and RWC_{tlp} (ΔRWC_{tlp}) as post-drought minus pre-drought species means for each variable. Thus, a negative plasticity in $\Delta\pi_{\text{tlp}}$ and $\Delta\pi_{\text{o}}$ and a positive plasticity in ΔRWC_{tlp} signify an improvement in drought tolerance.

We first analysed variation across species without accounting for variation within species for all 246 wild and 37 crop species; this is the principal analysis presented here, because it represents the widest possible range of species and ecosystem diversity. We also performed a traditional meta-analysis, which analyses effect sizes weighted by precision, and can achieve greater statistical power, but within-species variation (i.e. standard errors for species values) was only reported for 85 wild and 18 crop species in our compiled data set. We compared the findings of analyses of the full data set not weighted by precision (i.e. within-species variation) with analyses weighting by precision for the subset of species for which this was available and also with findings for all the species in the full data set after assigning to species lacking precision measures the lowest precision reported in the subset of species with sufficient information (Supporting Information). Findings using all these analyses were in accordance in almost every case, including all those specifically addressing the study hypotheses (see Results and Supporting Information Results for full details).

We followed recent ecological meta-analyses in increasing rigour by using multi-level mixed effects models to account

for the non-independence of species nested within the same study (Qian *et al.* 2010; Nakagawa & Santos 2012). Because most studies in our compiled data set contained multiple species, and each species was only represented in one study, we tested for significant mean plasticity across species with the model:

$$Y_{kj} = \mu + \alpha_j + \varepsilon_{kj} \quad (1)$$

where Y_{kj} is the plasticity for the k th species in the j th study, α_j is the effect of study j , μ is the mean plasticity across species after accounting for study-level variation and ε_{kj} is the residual error. We determined 95% confidence intervals for μ from 1000 nonparametric bootstraps, because $\Delta\pi_{\text{tlp}}$ was non-normal even with log or square-root transformations. The bootstraps sampled the study sites with replacement and the species within the selected sites without replacement (Ren *et al.* 2010). We analysed the wild and crop species separately. Models were fit with the *lme4* package in R (version 3.1.0).

We used two methods to assess the relative importance of plasticity and pre-drought π_{tlp} and RWC_{tlp} to post-drought values. We focused in these analyses on π_{tlp} and not π_{o} , as π_{tlp} is the 'higher-level' drought tolerance trait that plants shift using osmotic adjustment (Bartlett *et al.* 2012b). First, we calculated the contribution of plasticity to post-drought values of π_{tlp} and RWC_{tlp} for each species as:

$$\pi_{\text{tlp}} \text{ plasticity contribution} = \frac{\Delta\pi_{\text{tlp}}}{\text{post-drought } \pi_{\text{tlp}}} \times 100 \quad (2)$$

$$RWC_{\text{tlp}} \text{ plasticity contribution} = \frac{\Delta RWC_{\text{tlp}}}{\text{post-drought } RWC_{\text{tlp}}} \times 100 \quad (3)$$

We calculated the mean and 95% confidence intervals for plasticity contribution across species as described above. If the mean plasticity contribution across species was $< 50\%$, the magnitude of the pre-drought value was a more important determinant of the post-drought value than plasticity. To test for differences in plasticity contribution between wild and crop species, we fitted the following model with species type as a fixed effect and study as a random effect:

$$Y_{kj} = \mu + \alpha_j + \beta X_{kj} + \varepsilon_{kj} \quad (4)$$

Symbols follow eqn 1, with β as the regression coefficients for the species types. We tested for significant differences with 1000 iterations of a permutation test, as plasticity contribution was also non-normal, even with standard transformations.

Second, we compared the correlations of post-drought values with (1) pre-drought values and (2) with plasticity values using the model structure in eqn 4, accounting for study as a random effect and analysing pre-drought or plasticity values as a fixed effect. We tested for significance with 1000 iterations of a permutation test and compared correlation strengths by determining 95% confidence intervals for the marginal r^2 for each correlation (Nakagawa *et al.* 2013), which represents the variance explained by the fixed effects. Correlations (1) and (2) are not statistically independent, as one variable will be nearly equal to the residuals of the regression between the post-drought values and the other variable if the slope is close to 1, as in these correlations. However, this

does not predispose either pre-drought or plasticity values to be more strongly correlated with post-drought values than the other, so this test was able to determine which variable was most predictive of post-drought values.

To determine the variation in $\Delta\pi_o$ and $\Delta\pi_{tlp}$ across ecosystems, we tested for mean biome differences in $\Delta\pi_o$ and $\Delta\pi_{tlp}$ for all nine biome and functional type categories with ≥ 5 species (Table S2). We modelled biome as a fixed effect and study as a random effect nested within biomes, following eqn 4. There was insufficient replication to analyse RWC_{tlp} . We also used this model structure to test trait correlations with annual, pre-drought month, post-drought month, and seasonal differences in water balance, and annual aridity index for pre- and post-drought and plasticity in π_{tlp} and RWC_{tlp} . We tested significance with 1000 iterations of a permutation test.

We did not investigate phylogenetic patterning among species in our analyses for two technical reasons. Most importantly, published studies were not designed to resolve phylogenetic patterns, so data are not yet available for many closely related species within lineages that have diversified across moisture gradients, which would provide the strongest insight into the evolutionary trajectory of these traits. Second, the data for $\Delta\pi_{tlp}$ and plasticity contribution were significantly non-normal (Fig. 1), and there do not yet exist nonparametric tests that can account for phylogeny, to our knowledge (Supporting Information). The importance of phylogenetic relatedness to variation in drought tolerance plasticity remains to be resolved, in particular in studies that would sample within genera or families that have radiated across moisture gradients.

RESULTS

Plasticity in drought tolerance in response to seasonal changes in water availability was pervasive among wild and crop plants. Wild species exhibited significant osmotic adjustment

and plasticity in π_{tlp} (Fig. 1a, b), with a mean [95% confidence intervals] of -0.29 MPa [-0.25 to -0.36 MPa] for $\Delta\pi_o$ and -0.44 MPa [-0.37 to -0.53 MPa] for $\Delta\pi_{tlp}$. (Note that by ‘mean’, here and henceforward, we refer to the intercept in the mixed model, i.e. the mean adjustment across species when accounting for the non-independence of species within the same study). Species varied widely in plasticity, with the Australian wetland species *Casuarina obesa*, Australian dry temperate species *Grevillea patentiloba* and North American semidesert species *Prosopis glandulosa* achieving extremely high π_{tlp} plasticities of at least -2 MPa. For a minority of species, the mean $\Delta\pi_o$ and $\Delta\pi_{tlp}$ were ≥ 0 , indicating that plants did not undergo osmotic adjustment or π_{tlp} plasticity to improve drought tolerance in the dry season; this was the case in 31 species for π_o (15% of the 207 species in our data set) and for π_{tlp} (13% of 246 species total).

The RWC_{tlp} also showed significant plasticity across species, with a mean adjustment of -0.74% [95% CI = -3.63 to -0.72%], suggesting that acclimating to water stress causes wild plants to experience small but significant declines in their ability to maintain cell hydration at wilting point.

Pre-drought π_{tlp} is a stronger predictor of post-drought π_{tlp} than plasticity

Despite the prevalence of and considerable variation in π_o and π_{tlp} plasticity across species (Fig. 1a, b), pre-drought π_{tlp} is the main determinant of π_{tlp} during drought. Across wild species, the plasticity contribution accounted for 16.0% of the magnitude of post-drought π_{tlp} [95% CI = 14.0 to 18.9%]. Indeed, the plasticity contribution accounted for the majority (contribution $> 50\%$) of post-drought π_{tlp} for only 2% of species, or 4 of 246 species (Fig. 1c).

Across species, pre-drought π_{tlp} was a stronger determinant of π_{tlp} during drought than $\Delta\pi_{tlp}$. Thus, across species, the post-drought π_{tlp} was more strongly correlated with pre-drought π_{tlp} (marginal r^2 [95% CI] = 0.51 [0.29 to 0.64],

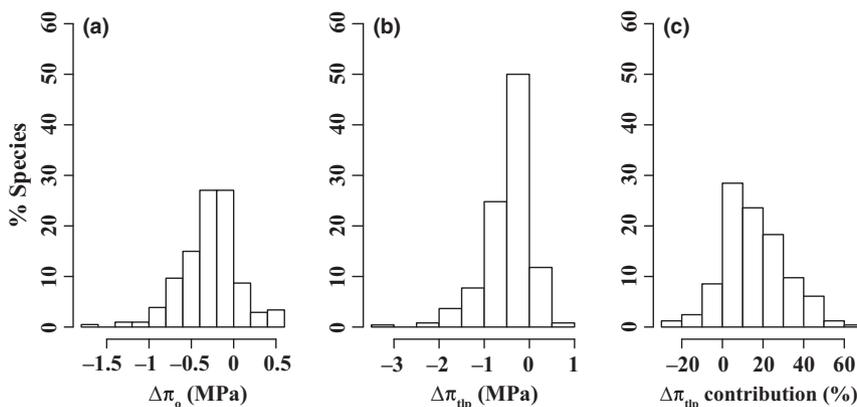


Figure 1 Histograms summarising data in a global database for wild species for the plasticities between the wet and dry season of (a) osmotic potential ($\Delta\pi_o$) ($n = 207$ species) and (b) turgor loss point ($\Delta\pi_{tlp}$) ($n = 246$) and (c) the percentage of post-drought π_{tlp} attributable to $\Delta\pi_{tlp}$, i.e. the ‘plasticity contribution’ ($n = 246$). Most species improved their drought tolerance, with mean $\Delta\pi_o = -0.29$ MPa and mean $\Delta\pi_{tlp} = -0.44$ MPa. (‘Mean’ here refers to the intercept in the mixed model in eqn 1, i.e. the mean adjustment across species when accounting for the non-independence of species within the same study). Thirty-one species did not make π_{tlp} or π_o more negative ($\Delta\pi_{tlp}$ or $\Delta\pi_o \geq 0$ MPa) in response to drought, representing 12.6% and 15% of species respectively. On average, $\Delta\pi_{tlp}$ accounted for 16.0% of post-drought π_{tlp} , suggesting that pre-drought π_{tlp} was the more important determinant of post-drought π_{tlp} .

$p < 0.0001$, $n = 246$ species) than with $\Delta\pi_{\text{tip}}$ (marginal $r^2 = 0.19$ [0.10 to 0.27], $p < 0.0001$) (Fig. 2a, b).

The plasticity contribution of RWC_{tip} accounted for -2.7% of post-drought RWC_{tip} [-4.8 to -0.9], as plants tended to slightly decrease their RWC_{tip} in response to water stress. Across species, post-drought RWC_{tip} was more strongly correlated with pre-drought RWC_{tip} (marginal r^2 [95% CI] = 0.42 [0.14 to 0.67], $p < 0.0001$, $n = 90$ species) than with plasticity (marginal $r^2 = 0.13$ [0.04 to 0.45], $p < 0.0001$) (Fig. S2).

The π_{tip} but not plasticity is strongly associated with site-level environmental conditions

Given that overall the pre-drought π_{tip} was a stronger predictor of post-drought π_{tip} across wild species than $\Delta\pi_{\text{tip}}$, we tested whether the relative importance of $\Delta\pi_{\text{tip}}$ might still vary across ecosystems. For example, plasticity might be larger and more influential in biomes prone to seasonal drought. While previous work has demonstrated that π_{tip} varies strongly

across biomes (Bartlett *et al.* 2012b), we did not find significant differences among biome and functional type categories for $\Delta\pi_{\text{tip}}$ and $\Delta\pi_{\text{tip}}$ (Fig. 3) (both $p > 0.4$), when analysing data for 240 species (all species in biome categories with ≥ 5 species) without accounting for within-species variability (i.e. without weighting by precision). For the smaller subset of 85 species for which within-species variability was available, weighting effect sizes by precision resulted in significant differences among biomes, but not according to biome water availability (Supplementary Results).

Stronger correlations of π_{tip} than of plasticity with climatic water supply

Site-level means for pre- and post-drought π_{tip} were positively correlated with site-level means for annual water balance (precipitation – potential evapotranspiration) (both $p < 0.001$, $n = 231$ species) and water balance during the dry season (both $p < 0.04$) and negatively correlated with annual aridity

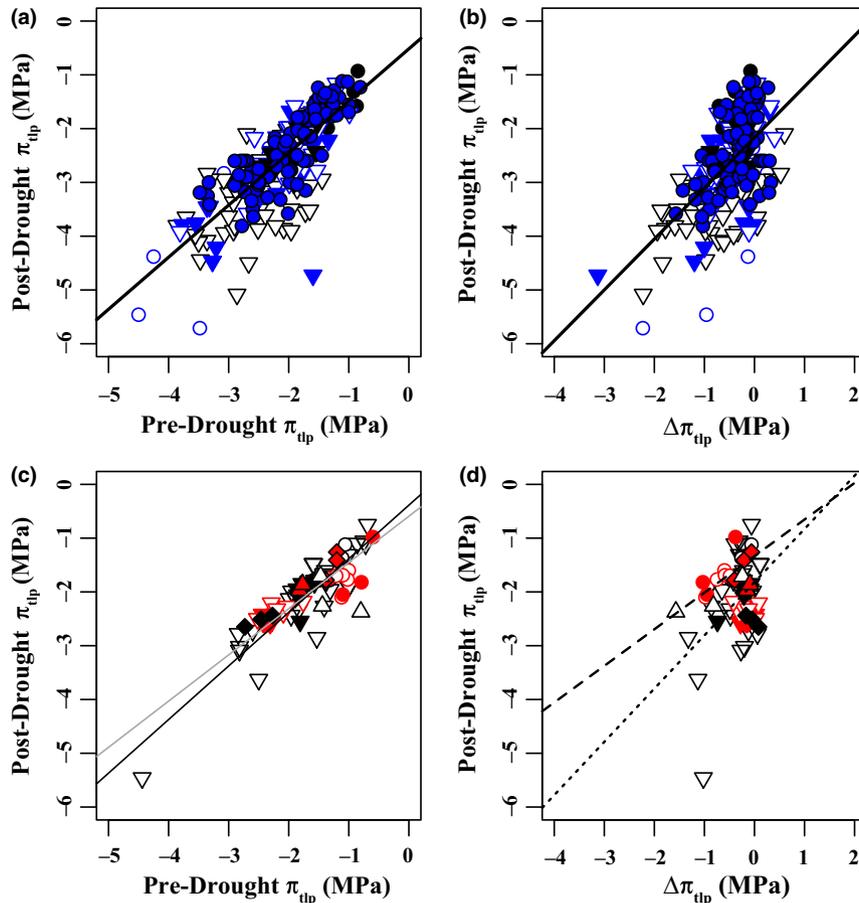


Figure 2 Across 246 wild species (panels a, b) and 37 crops (c, d), post-drought turgor loss point (π_{tip}) was more strongly correlated with pre-drought π_{tip} (a; $r^2 = 0.51$, $p < 0.0001$; c; $r^2 = 0.84$, $p < 0.0001$) than with π_{tip} plasticity ($\Delta\pi_{\text{tip}}$) (b; $r^2 = 0.19$, $p < 0.0001$; d; $r^2 = 0.16$, $p = 0.01$). Post-drought π_{tip} was correlated with $\Delta\pi_{\text{tip}}$ but not pre-drought π_{tip} across cultivars of *Coffea arabica* (dashed line) and *Zea mays* (dotted line) (d), and neither variable across cultivars of *Zoysia japonica* and *Zoysia matrella*. Biome symbols (a, b): alpine/subalpine (∇), grassland (\bullet), temperate conifer (\blacktriangledown), semidesert (\blacktriangledown), Mediterranean/dry temperate (∇), coastal (\circ), temperate broadleaf (∇) and dry tropical (\bullet). Crop species symbols (c, d): *Helianthus annuus* (\circ), *Saccharum* (sugarcane) (\bullet), *Zea mays* (\circ), *Phaseolus vulgaris* (\bullet), *Zoysia japonica* (\blacktriangledown), *Zoysia matrella* (∇), *Festuca arundinacea* (\blacklozenge), *Coffea arabica* (\blacktriangledown), *Capsicum chinense* (\blacklozenge), *Olea europaea* (\triangle) and *Ceratonia siliqua* (\blacktriangle). ∇ = all species with < 3 cultivars. Dark line = regression for species means, grey line = regression across cultivars.

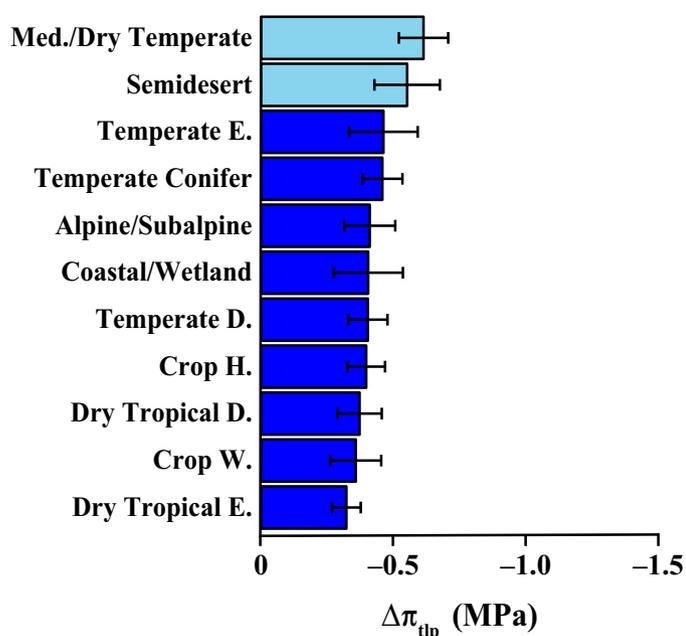


Figure 3 Biome means for wild species for seasonal plasticity in turgor loss point ($\Delta\pi_{\text{tlp}}$) ($n = 240$ species), for biomes with at least five species. Functional types within each biome are categorised as herbaceous (H.), woody (W.), deciduous (D.) and evergreen (E.) for biomes with at least five species per category. Tropical conifer and grassland biomes are excluded due to small sample sizes, and experimental drought results in 37 crop species are graphed for comparison. Light blue bars indicate dry biomes (mean aridity index ≤ 0.65 ; Trabucco & Zomer 2009), and dark blue bars are wet biomes (aridity index > 0.65). There were no significant differences in $\Delta\pi_{\text{tlp}}$ among biomes (permutation test, $p = 0.9$).

index (both $p < 0.01$). All these correlations were consistent with more drought-tolerant species occurring in drier sites (Table 1). Pre- and post-drought π_{tlp} were not correlated with any other climate variables (all $p > 0.2$).

Table 1 The proportion of variance of drought tolerance traits explained by climate. To account for variation among studies, we present marginal r^2 values, or the proportion of variance explained by fixed effects (Nakagawa *et al.* 2013), for mixed effects models predicting drought tolerance traits with climate as a fixed effect and study as a random effect. Traits are pre- and post-drought turgor loss point (π_{tlp}), and the plasticities of π_{tlp} and π_o . Climate variables are annual, wet season and dry season water balance [WB = mean precipitation (MP) – mean potential evapotranspiration (PET)], seasonality (ΔWB = dry season – wet season WB) and annual aridity index (AI = MP/PET)

	Pre-drought π_{tlp}	Post-drought π_{tlp}	π_{tlp} plasticity	π_o plasticity
Water balance (WB)				
Annual	0.12	0.14	0.02	0
Wet	0	0.02	0.01	0
Dry	0.04	0.06	0.02	0
ΔWB	0	0.01	0	0
Aridity index (AI)				
Annual	0.07	0.07	0	0

Bold values are significant (permutation test; $p < 0.05$). 0 values indicate an $r^2 < 0.01$. Sites with lower annual water balance, water balance in the dry season, and AI contained species that were more drought tolerant in both seasons. Plasticity was not correlated with climate.

In contrast, there were no significant correlations between $\Delta\pi_{\text{tlp}}$ and $\Delta\pi_o$ values and any climate variables (all $p > 0.08$). There were also no significant correlations between climate and pre- and post-drought RWC_{tlp} or ΔRWC_{tlp} (all $p > 0.4$). Thus, π_{tlp} and not RWC_{tlp} or plasticity is a potential determinant of species distributions relative to water supply.

Plasticity in π_{tlp} is strong for crop cultivars and an important determinant of cultivar differences in drought tolerance

Crop species subjected to experimental drought showed similar responses as wild species undergoing seasonal drought (Fig. 2 and Fig. S2). Thus, droughted crop plants exhibited a significant shift towards more negative π_{tlp} values (mean [95% CI] = -0.38 MPa [-0.10 to -0.42], $n = 37$ species), and also lower RWC_{tlp} values (-2.2% [-0.3 to -3.2], $n = 30$ species). The mean plasticity contribution to post-drought π_{tlp} and RWC_{tlp} across crop species (crops = 18.3% for π_{tlp} and -2.8% for RWC_{tlp}) did not differ statistically from that of the wild species (both $p > 0.06$).

Furthermore, across crop species, as for wild plant species, the post-drought π_{tlp} was more strongly correlated with pre-drought π_{tlp} (marginal r^2 [95% CI] = 0.84 [0.69 to 0.92], $p < 0.0001$, $n = 37$ species) than with $\Delta\pi_{\text{tlp}}$ (0.16 [0.01 to 0.43], $p = 0.01$) (Fig. 2c, d). However, post-drought π_{tlp} was significantly correlated with $\Delta\pi_{\text{tlp}}$ and not pre-drought π_{tlp} within two of the species with sufficient cultivar replication for analysis ($n \geq 5$), *Coffea arabica* ($r^2 = 0.97$, $p = 0.001$ for $\Delta\pi_{\text{tlp}}$; $r^2 = 0.004$, $p = 0.92$ for pre-drought π_{tlp} , $n = 5$) and *Zea mays* ($r^2 = 0.53$, $p = 0.06$ for $\Delta\pi_{\text{tlp}}$; $r^2 = 0.01$, $p = 0.84$ for pre-drought π_{tlp} , $n = 6$) (Fig. 2d), but post-drought π_{tlp} was not correlated with either $\Delta\pi_{\text{tlp}}$ or pre-drought π_{tlp} across cultivars of *Zoysia japonica* ($\Delta\pi_{\text{tlp}}$: $r^2 = 0.16$, $p = 0.18$; pre-drought π_{tlp} : $r^2 = 0.04$, $p = 0.60$, $n = 8$) or *Zoysia matrella* ($\Delta\pi_{\text{tlp}}$: $r^2 = 0.37$, $p = 0.12$; pre-drought π_{tlp} : $r^2 = 0.10$, $p = 0.54$, $n = 6$).

Across crop species subjected to experimental drought, post-drought RWC_{tlp} was significantly correlated with pre-drought RWC_{tlp} (marginal r^2 [95% CI] = 0.80 [0.49 to 0.86], $p < 0.0001$, $n = 30$ species), but not ΔRWC_{tlp} (0.003 [0.0001 to 0.12], $p = 0.75$). However, these relationships were variable across cultivars of given crop species; post-drought RWC_{tlp} not correlated with either pre-drought RWC_{tlp} or ΔRWC_{tlp} across cultivars of *Zea mays* ($r^2 = 0.09$, 0.13, $p > 0.25$; respectively) or *Zoysia matrella* ($r^2 = 0.009$, 0.005; $p > 0.5$), whereas post-drought RWC_{tlp} was significantly correlated with pre-drought RWC_{tlp} but not ΔRWC_{tlp} across *Zoysia japonica* cultivars ($r^2 = 0.52$, 0.06, $p = 0.03$, 0.6) (Fig. S2).

Thus, while on average $\Delta\pi_{\text{tlp}}$ makes a low contribution to overall drought π_{tlp} for both wild and crop species, among different cultivars of given crop species subjected to experimental drought, $\Delta\pi_{\text{tlp}}$ can be a major determinant of relative drought tolerance. Plasticity in RWC_{tlp} did not contribute to stronger drought tolerance in wild or crop plants.

DISCUSSION

Our results showed a great prevalence across species of plasticity in π_{tlp} between the wet and the dry season ($\Delta\pi_{\text{tlp}}$), with 87% of the wild species in our data set exhibiting a $\Delta\pi_{\text{tlp}} < 0$ MPa,

and a mean shift of -0.44 MPa from pre- to post-drought π_{tlp} across wild species, (Fig. 1). However, the $\Delta\pi_{\text{tlp}}$ accounted for a relatively small proportion (16%) of post-drought π_{tlp} , and was a weaker predictor of post-drought π_{tlp} than were pre-drought values (Figs 1 and 2). Wild plants exhibited a small but significant decline in RWC_{tlp} , with a mean shift of -0.74% , which highlights the fact that plants can maintain nearly constant RWC_{tlp} values even as π_{tlp} declines, especially via elastic adjustment (Bartlett *et al.* 2012b).

Our analysis showcased the strong variation in π_{tlp} plasticity and the π_{tlp} plasticity contribution to post-drought π_{tlp} across species globally, as well as within sites and biomes (Fig. 2a, b). Co-occurring species may exhibit differences in $\Delta\pi_{\text{tlp}}$ because of landscape-level heterogeneity in water availability, differences in drought tolerance among functional types, and/or differences in species' abilities to generate and accumulate solutes. Local topographical heterogeneity can produce differences in soil water availability and air temperature greater than mean annual differences among sites and biomes, and species that occur in drier microhabitats within a given site generally exhibit more negative turgor loss points than co-occurring specialists on wetter microhabitats (Becker *et al.* 1988; Austin & Van Niel 2011). Species with greater rooting depths also have access to greater water supply during the dry season and maintain higher leaf water potentials and photosynthetic rates (Wright *et al.* 1992; Cao 2000), although species with deeper roots have been found to have more (e.g. Wright *et al.* 1992) and less negative (e.g. Davis & Mooney 1986) turgor loss points in different ecosystems. Species in the same site may therefore experience highly different water stresses during drought (Becker *et al.* 1988). Plant functional type is another known contributor to species differences in π_{tlp} . On average, woody species are generally more drought tolerant than herbaceous species, and evergreens tend to be more tolerant than deciduous species (Calkin & Pearcy 1984). Our database did not contain enough replication of functional types within sites to test for an effect of functional type on differences in $\Delta\pi_{\text{tlp}}$ among co-occurring species.

Species may also differ in their ability to generate or tolerate an increased symplastic solute concentration. Indeed, species vary strongly in the solutes upregulated during osmotic adjustment, which can include sugars, amino acids (proline), ions (K^+ , Ca^{2+}), amines (glycine betaine), organic acids and polyols (glycerol, mannitol) (Morgan 1984; Zhang *et al.* 1999; Chen & Jiang 2010). Proline can also indirectly contribute to drought tolerance by removing reactive oxygen species to protect cell membranes, enzymes, proteins and other cellular components from chemical damage (Chen & Jiang 2010). The metabolic cost may vary significantly among different solute types, resulting in species differences in their capacity to osmotically adjust. The species for which osmotic adjustment is more costly due to metabolic constraints may instead depend more strongly on plasticity in other anatomical and physiological traits to survive drought, such as root morphology, water use efficiency or xylem cavitation vulnerability (Choat *et al.* 2007; Nicotra *et al.* 2010). Data are lacking on the degree to which species' solute preferences, metabolic pathways and costs of osmotic adjustment might be phylogenetically conserved. Furthermore, for a given osmotic adjustment

($\Delta\pi_o$), the effect on $\Delta\pi_{\text{tlp}}$ can vary, according to other pressure–volume parameters; a lower elastic modulus allows a given $\Delta\pi_o$ to drive a larger $\Delta\pi_{\text{tlp}}$ (Bartlett *et al.* 2012b). Understanding species-level variation in plasticity and its underlying biochemistry will improve with characterization of ecological and phylogenetic patterns in osmolyte preference, their metabolic costs, and the underlying functional genetics (Zhang *et al.* 1999).

Improving crop resilience to drought through increased osmotic adjustment has been a long-standing goal in crop development, to ensure food and land-use sustainability under climate change (Blum 2005; Nicotra *et al.* 2010). However, our analysis has shown that the contribution of plasticity to post-drought π_{tlp} in crop species was not significantly greater than that of wild species. Importantly, for cultivars within species, plasticity but not pre-drought π_{tlp} was significantly correlated with post-drought π_{tlp} . However, the differences between the findings for crop cultivars vs. wild species may also be due to their experiencing experimental rather than seasonal drought. The experimental droughts may have been imposed more rapidly than the seasonal droughts, and in some cases the droughts were applied to plants without previous exposure to drought, known as drought hardening or conditioning (Hsiao *et al.* 1976). Plants experience their largest osmotic adjustment during their first drought exposure, and maintain a more negative π_{tlp} for longer periods of time during wet conditions when exposed to more cycles of drought stress, reducing their subsequent plasticity (Hsiao *et al.* 1976). Most of the crop species, including the *Coffea arabica*, *Zea mays* and *Zoyzia* cultivars, were well-watered prior to the drought experiments, which may exaggerate the contribution of plasticity to drought tolerance compared to wild species, which were likely to have undergone numerous cycles of seasonal drought. In sum, these findings point to a potentially greater contribution of plasticity to drought tolerance differences across crop cultivars than across wild species, and highlight the general benefits of $\Delta\pi_{\text{tlp}}$ as a trait for crop improvement.

For wild plants, the close correlation of pre- and post-drought π_{tlp} values, and the correlations with climate variables of pre- and post-drought π_{tlp} but not $\Delta\pi_{\text{tlp}}$ (Table 1), showed that π_{tlp} measurements from either season can be used to reliably assess species' relative drought tolerances and relate physiological traits to ecology. This result, together with readily available high-resolution climate data and rapid methods for assessing π_{tlp} and π_o (Bartlett *et al.* 2012a), can facilitate the incorporation of drought tolerance data into species distribution modelling, and improve the prediction of species composition, functional diversity and overall ecosystem function for diverse communities. Such a simplified approach treats species as having similarly negligible values for plasticity in π_{tlp} , which will provide a useful baseline that will be accurate, on average. However, we found that plasticity can be considerable for a minority of species, which can potentially shape their range of tolerable climatic conditions and ability to adapt to future conditions. Therefore, while point measurements of π_{tlp} provide a reasonable simplification for characterising drought tolerance for many species or communities, determining the underlying mechanistic constraints on π_{tlp} plasticity and its variation across species will further improve

the accuracy of predictions of species responses to climate change.

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AUTHORSHIP

MB and LS designed and conducted the analyses in this paper. MB, YZ, NK, SS, and RA compiled and collected the data, and all authors contributed to writing.

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