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Article

Adaptation of Leaf Water Relations to Climatic and Habitat Water Availability

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Abstract: Successful management of forest systems requires a deeper understanding of the role of ecophysiological traits in enabling adaptation to high temperature and water deficit under current and anticipated changes in climate. A key attribute of leaf water relations is the water potential at zero turgor (π_{tlp}), because it defines the operating water potentials over which plants actively control growth and gas exchange. This study examines the drivers of variation in π_{tlp} with respect to species climate of origin and habitat water availability. We compiled a water relations database for 174 woody species occupying clearly delineated gradients in temperature and precipitation across the Australian continent. A significant proportion of the variability in π_{tlp} (~35%) could be explained by climatic water deficit and its interaction with summertime maximum temperature, demonstrating the strong selective pressure of aridity and high temperature in shaping leaf water relations among Australian species. Habitat water availability (midday leaf water potential), was also a significant predictor of π_{tlp} ($R^2 = 0.43$), highlighting the importance of species ecohydrologic niche under a set of climatic conditions. Shifts in π_{tlp} in response to both climatic and site-based drivers of water availability emphasises its adaptive significance and its suitability as a predictor of plant performance under future climatic change.

Keywords: drought tolerance; leaf water potential; turgor loss; water deficit; climatic distribution; eucalyptus

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1. Introduction

Predicted increases in extremes such as drought events and heat waves, in conjunction with long-term changes in water availability (increasing or decreasing) and temperature regimes (increasing) will potentially drive significant changes in forest productivity. Successful management of existing or new forests to deliver a range of commodities and environmental services under these conditions must include careful consideration of species capacity to absorb future climatic disturbances and adapt to future climate regimes. This requires a deeper understanding of the role of ecophysiological traits in enabling adaptation of species and genotypes to high temperature and water deficit.

Adaptation to water deficit can be defined in relation to mechanisms that control leaf water status and cell turgor [1]. Maintenance of leaf turgor is critical to the continuance of growth and gas exchange in the face of declining water availability [2–4]. The water potential at zero turgor or turgor loss point (π_{tlp}) and the corresponding relative water content helps to define the operating water potentials over which plants actively regulate water status and is often lower in species with greater dehydration tolerance [1,5]. Plants actively accumulate solutes in order to lower their osmotic potential during water deficit, thereby sustaining turgor and prolonging water uptake [6]. Similarly, leaves with highly elastic tissues reduce steep declines in cell turgor because their cells contain more water at full turgor and can sustain larger declines in volume [1]. Pressure-volume relationships are routinely used to estimate these key parameters of leaf physiology [7] and are often interpreted as indicators of species drought tolerance *i.e.*, the ability to maintain physiological function at low water status [8,9].

A large body of work has documented the significance of leaf turgor maintenance traits that enable survival and growth under a range of habitats and climates (see [10] and references therein). The water potential corresponding to zero turgor has been shown to be similar to the point at which stomata close as evidenced by studies involving four tropical [11] and three temperate species [12] and represents an important trait in defining plant hydraulic strategies [13]. Global analyses show that π_{tlp} can vary 3-fold between crop and native arid-land species and lower π_{tlp} appears to be associated with drier environments [10]. These leaf water relations traits have also been shown to correlate with leaf structural attributes in dry [14] and wet habitats [15], indicating either a direct functional link between leaf water management and leaf construction or co-selection for structural and physiological leaf traits. Differences in the ability of species to access and manage water within a particular habitat, *i.e.*, their ecohydrologic niche, also drives a significant amount of variation in species responses to water deficit and associated traits such as π_{tlp}. While meta-analyses by Bartlett *et al.* [10] demonstrated a decline in π_{tlp} with increasing aridity across different biomes, it is unclear how the relative contribution of climatic water availability (across a species climatic envelope) as opposed to local habitat factors and species water management strategies influence patterns in leaf water relations, specifically π_{tlp}. Assessing the significance of both climatic and habitat water availability in driving variation in π_{tlp} may help to clarify role of turgor maintenance in defining species distributions at both the landscape and regional scales.

Until recently, the influence of functional traits such as π_{tlp} on species distributional limits has been unclear and species distribution modelling has relied predominately on the known presence and/or absence of species based observations of their occurrence [16]. The inclusion of definitive functional attributes that can link a species climatic niche back to relevant physiological or ecological thresholds offers much promise in better utilising the rapidly improving species databases and high resolution climate data. This may be achieved by gaining a better understanding of how particular traits or clusters of traits control plant performance and survival under stressful (or non-stressful) conditions and how these traits vary within and between species with respect to their observed climatic envelope and their ability to access and regulate water within the landscape. In the context of water deficit and heat stress, such analyses would help clarify the extent to which a trait plays an adaptive role in defining species distribution and vegetation function. This information will assist in characterising species sensitivity within existing and new environments, making it possible to quantify the likely impact associated with exposure from future climates.

Australia is a predominately water-limited environment and its vegetation has been shaped by water availability [17,18]. The long history of water relations research in Australia provides a unique data resource and opportunity to test the adaptive significance of leaf water relations traits across well delineated aridity and temperature gradients. This study tests the hypothesis that π_{tlp} is a key adaptation to water stress and lower values of π_{tlp} enable survival in drier and warmer environments. Specifically, we addressed the following questions: (1) Which climatic indices, derived from a species observed climatic niche (including the middle and tail regions of this distribution), are more closely associated with variation in π_{tlp} among Australian species? (2) What is the significance of species habitat water availability or ecohydrologic niche and associated leaf water relations traits in modulating adaptation to drier and warmer climates?

2. Experimental Section

2.1. Leaf Water Relations Database

A traits database was compiled using published literature from Australian studies ($n = 45$) or studies involving Australian species conducted elsewhere ($n = 2$). A literature search, using Web of Science and Google Scholar, as well as locally available library databases (CSIRO Library) was conducted to find studies that had measured key plant water relations traits, in particular, studies that had conducted pressure-volume analyses and collected leaf water potential on Australian species. All studies included in the meta-analysis used the bench-drying technique to derive leaf water relations parameters [7]. Thus, all entries included, at a minimum, osmotic potential at zero turgor (π_{tlp}) as well as osmotic potential at full turgor (π_0) and bulk tissue elasticity (ε). The database also included details on species name (updated where necessary), experiment type and treatment, vegetation type, tree size/age, site location and study timing.

The extent to which plants were subjected to water deficit, whether it was imposed experimentally or was experienced as part of a seasonal pattern, was classified into three levels: Well-watered—no evidence of water deficit relative to seasonal patterns; moderate—Usually the initial or intermediate level of water stress imposed inducing partial stomatal closure or coinciding with a marked dry season; severe—Water deficit invoking full stomatal closure and/or significant drought damage or mortality. An assessment of the levels of water deficit experienced during a study allowed us to compare species at relatively similar levels of water stress and investigate the significance of osmotic and elastic adjustment among different studies. Where studies involved intra-specific comparisons of populations and/or provenances, a species mean for all corresponding leaf water relations data across different populations/provenances was used in the analysis.

2.2. Species Climatic Envelope Analysis

The approach in this study was to use observed values of π_{tlp} obtained at a particular site as being representative of the species more broadly and relate these data to different portions of the species climate niche across its observed range. The climatic conditions of observed species distributions were assessed using the Atlas of Living Australia (ALA). The ALA is one of the most sophisticated national biodiversity databases offering access to high quality data on individual observations of species occurrence and high resolution climate surfaces [19]. The ALA now includes more than 40 million records of plant and animal species distributions and more than 300 layers of information on environmental, social and economic factors across Australia [19]. The species occurrence records include natural and introduced locations collected from a range of sources that are either specimens (records managed as part of a scientific collection) or observations (records of the sighting by an individual or member of an organisation). These data are supplemented by a range of other data such as images, molecular DNA data, identification keys or relevant literature describing the species. Species occurrences (using only validated records) were downloaded from the ALA using the "mapping and analysis" portal.

The climate layers used in the analysis were based on a gridded dataset (~ 1 km × 1 km) extracted from the environmental layer portal on the ALA. These climate layers were derived using version 3 of the national, 9 second DEM, re-sampled to 0.01 degrees, with the ESOCLIM module of ANUCLIM version 6.0 (beta) with the Australian Climate Surfaces version 2.1 [20]. The derived climate variables are 12-monthly mean values for minimum temperature, maximum temperature, precipitation, solar radiation, evaporation, wind and others. Three statistics were derived from the 12 monthly layers—Annual minimum, annual maximum and annual mean. The key climate variables used in the analysis were mean annual precipitation (MAP), mean annual aridity index (mean annual evaporation divided by mean annual precipitation), mean annual precipitation deficit (MAPD; mean annual precipitation minus mean annual evaporation), mean annual temperature (MAT) and maximum temperature of hottest month (MTHM). These climate variables were chosen based on their relevance to the characterisation of water deficit and high temperature stress for a given species distribution.

From the extracted climate data we computed indices based on the middle (median) and the driest and warmest tails of the observed species climatic envelope to provide an indication of the climate at the middle region and the margins of the species climatic niche (see Figure 1 for an example). A 0.02 percentile value was used to represent the dry tails of the MAP, aridity index and MAPD data and a 0.98 percentile value was used to represent the warm tails of the MAT and MTHM data. These percentile values were used to represent relatively "extreme" edges of the species climatic niche based on previous work that identifies these values as important thresholds for plant survival under drought across Australian vegetation types [21]. The presence of outliers in the species occurrence data was identified as either any value less than 0.05 percentile and less than one and a half times the inter-quantile range (IQR) or greater than 0.95 percentile and greater than one and a half times the IQR.

Unless otherwise stated, reference to the five climatic variables derived from the species distribution refer to their median value.

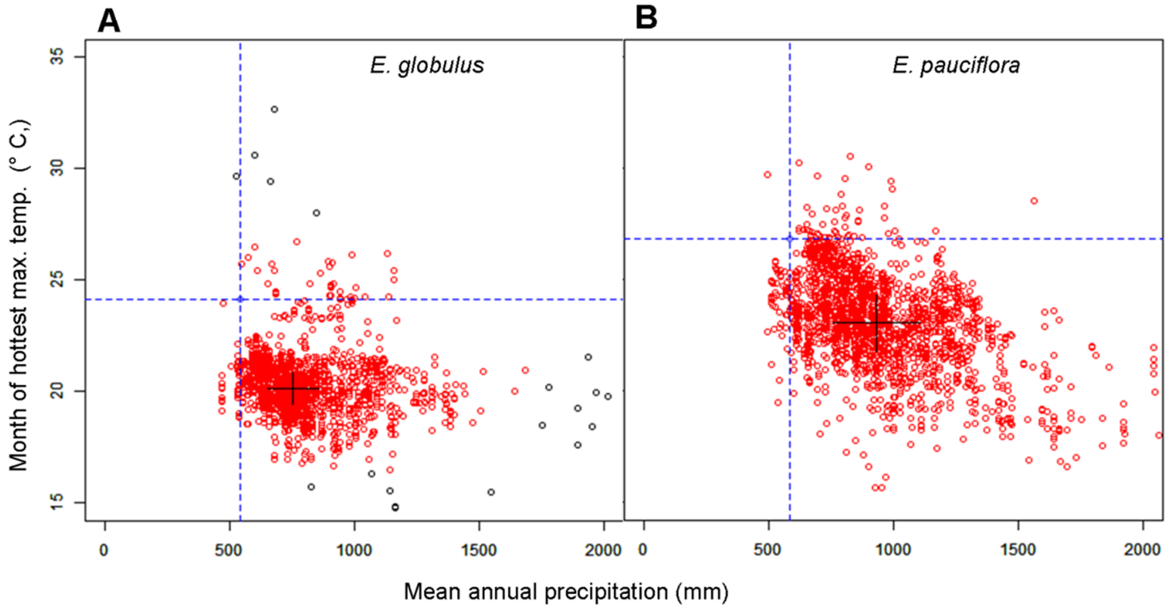

Figure 1. Scatter plot of mean annual precipitation (MAP) *versus* maximum temperature of hottest month (MTHM) for all recorded species locations for (**A**) *Eucalyptus globulus* and (**B**) *E. pauciflora*. The solid vertical and horizontal lines denote the interquartile range and the dashed blue lines denote the 0.02 and 0.98 percentile for MAP and MTHM respectively. Black symbols denote outliers, that weren't included in calculations of climatic indices, whereas red symbols were included in the analysis.

2.3. Statistical Analysis

Single and multiple regression analyses were done on non-transformed data at $p < 0.05$ significance level. Model comparisons of two-way relationships between climate indices *versus* π_{tlp} were undertaken using the model selection function in MuMIn package [22]. The Alkalike information criterion (AIC) was used to select candidate models. Correlation tests were performed between trait data using Pearson's moment correlation tests. All statistical analyses were performed in R (v2.15.0, R Foundation for Statistical Computing).

3. Results

The Australian water relations traits database included 174 species and 74 genera for which there were data for π_{tlp}, π_0 and/or ε. About half of these studies also measured predawn leaf water potential (Ψ_{pd}) and/or midday leaf water potential (Ψ_{md}). The vast majority of studies were conducted on plants that were either sampled during periods of high water availability or under well-watered conditions (in the case of experimental studies). Values of π_{tlp} obtained under non-stressed conditions have shown to be good predictors of any subsequent changes in π_{tlp} in response to water deficit [23].

According to Whitakers global biome classification [24], the majority of species in the database belong to the savanna, grassland, Mediterranean and desert biomes (Figure S1). The bulk of the species within the database were derived from climates with MAP < 1000 mm and MAT > 10 °C, reflecting the relatively dry and warm climates experienced across much of the Australian landscape. The number of records obtained from the ALA for describing the climatic niche of the 174 species in the traits database ranged from 4 to 30,560 (mean = 2376).

3.1. The Relationship between Turgor Loss and Climate

Of the five climatic indices examined, the median value of MAP and the MAPD were the best single predictors of π_{tlp} (Table 1, $R^2 = 0.29$–0.30). π_{tlp} was positively correlated with MAPD and MAP and showed a consistent decline across all four bins in response to decreasing MAPD ($y = 0.006x - 2.23$, Figure 2). Overall, π_{tlp} varied from −1.16 to −4.72 MPa and showed largest statistical dispersion (based on interquartile range and standard deviation) at values of MAPD between −150 and −50 mm (−1.43 to −4.72 MPa). Mean annual precipitation deficit was also a strong predictor of the π_{tlp} for the eucalypt species within the database (Figure 2; $R^2 = 0.32$, $n = 47$). In contrast to MAPD and MAP, there were negative correlations between mean annual temperature and π_{tlp}, and while the relationship was statistically significant, this relationship was weak (Table 1, $R^2 = 0.06$). However, maximum temperature of the hottest month (MTHM) performed reasonably well (Table 1, $R^2 = 0.21$). We also tested how well the values of these climate variables at the warm and dry edges of the species' climatic distributions could predict π_{tlp}. The results show that values that represent either warm or dry tails of the distribution (0.98 and 0.02 percentiles respectively) consistently explained slightly less of the variation in π_{tlp} but were still significant (Table 1; $R^2 = 0.06$–0.27). The climate variables evaluated here were only weakly positively correlated with π_0 (e.g., MAP, $R^2 = 0.17$, $p < 0.05$) and there were no relationships between any of the climate indices analysed and bulk tissue elasticity (data not shown).

Table 1. Results from regression analysis between osmotic potential at zero turgor *versus* five different climate indices (aridity index, mean annual precipitation, precipitation deficit, mean annual temperature and mean maximum temperature of hottest month) extracted from observed species occurrences ($n = 174$). The 0.50 and 0.98/0.02 percentile values from the species climatic distribution.

Percentile of Distribution	Variable	Parameter Estimate	SE	p Value	Adjusted R^2
0.50	Aridity index	0.33	0.05	<0.001	0.16
	Mean annual precipitation	0.001	0.0001	<0.001	0.29
	Precipitation deficit	0.006	0.0007	<0.001	0.30
	Mean annual temperature	−0.05	0.01	<0.001	0.06
	Max. temperature of hottest month	−0.07	0.01	<0.001	0.21
0.02	Aridity index	0.78	0.11	<0.001	0.21
	Mean annual precipitation	0.001	0.0001	<0.001	0.25
	Precipitation deficit	0.005	0.0006	<0.001	0.27
0.98	Mean annual temperature	−0.04	0.01	<0.001	0.05
	Max. temperature of hottest month	−0.06	0.01	<0.001	0.20

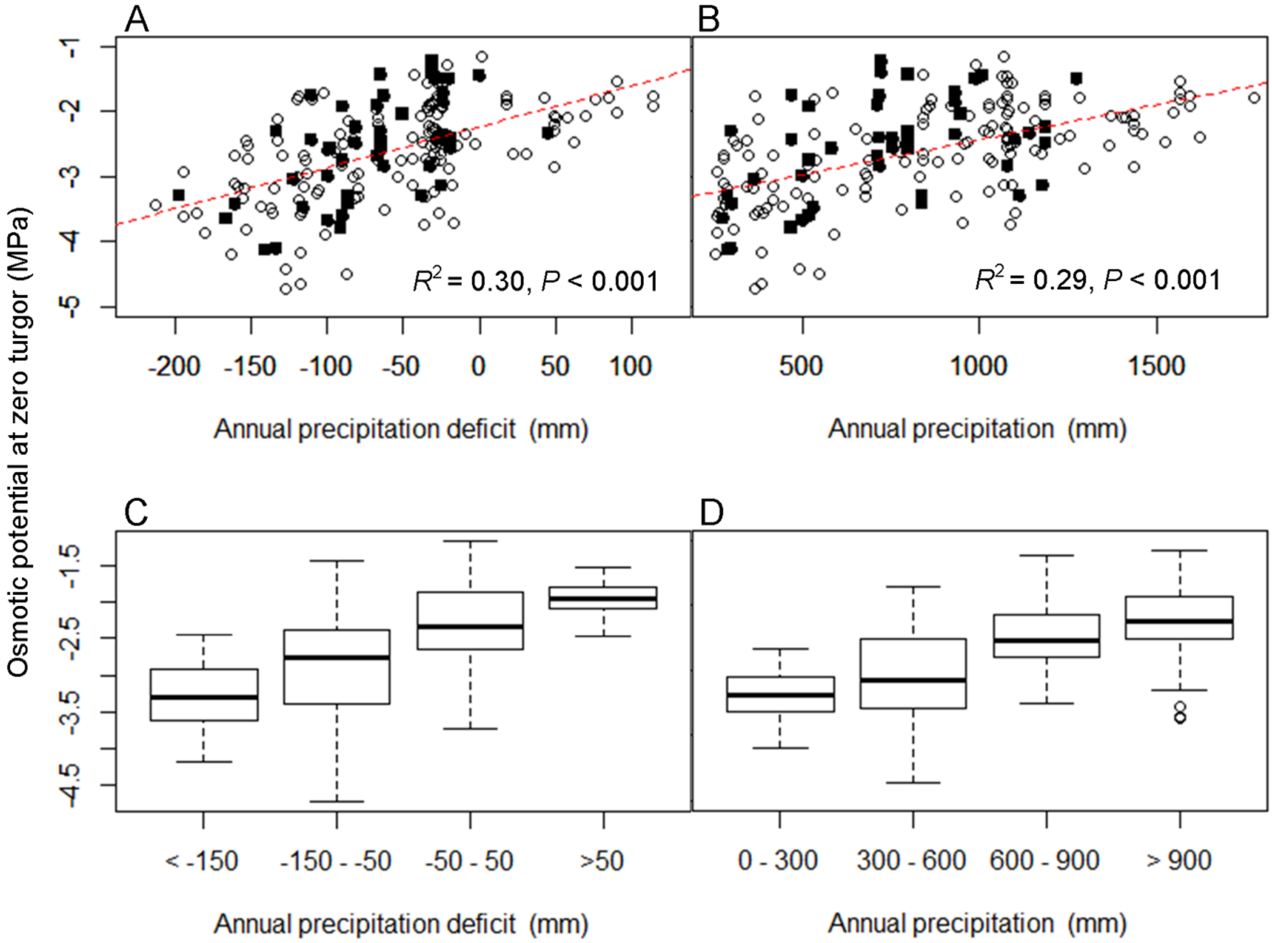

Figure 2. Relationship between species climatic water availability and osmotic potential at zero turgor for all species in the database (n = 174). Scatter plot of (**A**) mean annual precipitation deficit (R^2 = 0.30, $p < 0.001$) and (**B**) mean annual precipitation *versus* osmotic potential at zero turgor (R^2 = 0.29, $p < 0.001$) and box (spanning the 25th to 75th percentiles and bold line at the median) and whiskers (spanning the 5th to 95th percentiles) of binned data for (**C**) mean annual precipitation deficit and (**D**) mean annual precipitation. (**A**) and (**B**) are fitted with linear regression (red dashed line) see Table 1 for details. The solid square symbols in (**A**) and (**B**) represent values for *Eucalyptus* spp. (n = 47).

While MAP and MAPD were the best single predictors of π_{tlp}, using an interaction term between MAPD and MHMT (at 0.98 percentile) improved the fit to the data (Figure 3; R^2 = 0.35, $p < 0.001$). Species climate envelopes that included extremely high summer temperatures (MHMT > 35 °C) tended to have more negative π_{tlp} than those species with cooler summer maximum temperatures (Figure 3).

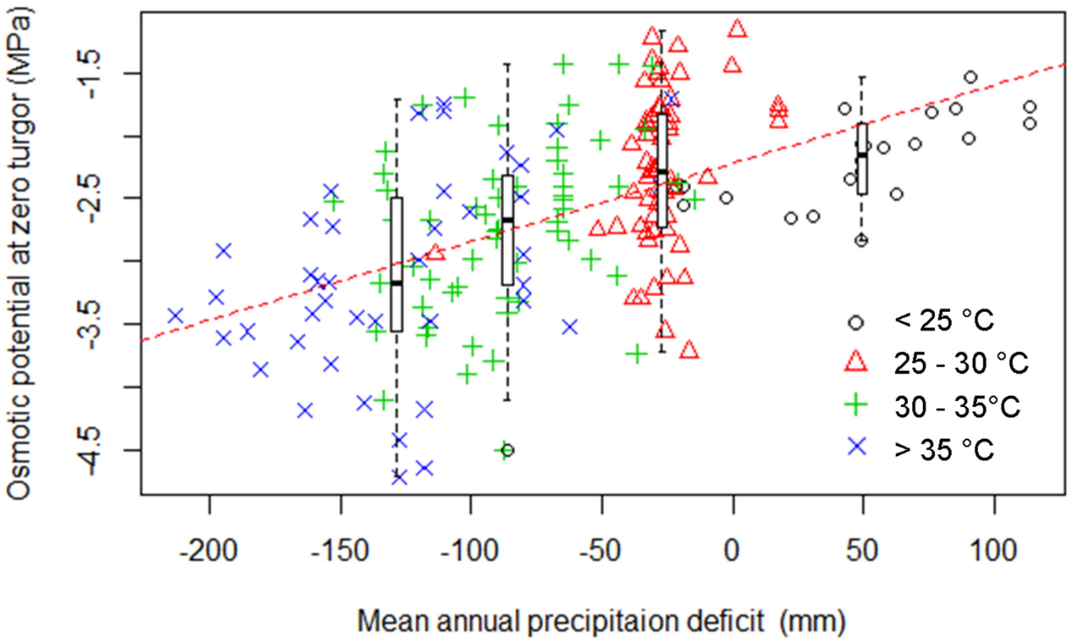

Figure 3. Relationship between mean annual precipitation deficit *versus* the osmotic potential at zero turgor ($R^2 = 0.30$, $p < 0.001$). Data are binned by maximum temperature in hottest month (0.98 percentile) and box and whisker plots are drawn based on this binned data. Data are fitted with linear regression (red dashed line), see Table 1 for details.

3.2. Relationship between Turgor Loss and other Leaf Traits

We observed a positive relationship between π_{tlp} and Ψ_{md} (Figure 4, R^2 =0.43, $P < 0.001$) and for Ψ_{pd} (Figure 4, $R^2 = 0.42$, $p < 0.001$). For some of the species in the database the π_{tlp} was less than Ψ_{md} indicating periods of zero turgor during the study period (Figure 4). A similar relationship was observed between Ψ_{md} and the relative water content at zero turgor (Figure 5). We observed a strong positive relationship between π_0 and π_{tlp} (Pearson's $r = 0.90$, Figure 5). There was a negative relationship between π_0 and ε (Pearson's $r = 0.44$, Figure 5). There were fewer species data for many of the additional traits included in the database including; specific leaf area and wood density and these showed weak correlations to the plant water relations traits (Figure 5).

For 57 species in the database, there were data for changes in π_0 between well-watered conditions and either seasonal water deficit under natural conditions (for saplings and adults, $n = 42$) or water deficit imposed through an experimental treatment (for seedlings, $n = 23$) (Supplementary Figures S2 and S3). Several studies involved comparisons among different clones or provenances for species ability to adjust π_0 in response to water deficit. The majority of species showed osmotic adjustment within 1.0 MPa, while some species adjusted π_0 by up to 1.7 MPa (Figure 6) and π_0 (under well-watered conditions) was a good predictor of the extent to which species adjusted π_{tlp} during periods of water deficit. The largest adjustments (negative) in π_0 was observed in species from drier environments (MAP < 600 mm), however these species also showed greatest variation in osmotic adjustment ($R^2 = 0.06$, not significant, Figure 6) and this relationship (change in π_0 *versus* MAP) was particularly weak for the data that included seedlings only (data not shown).

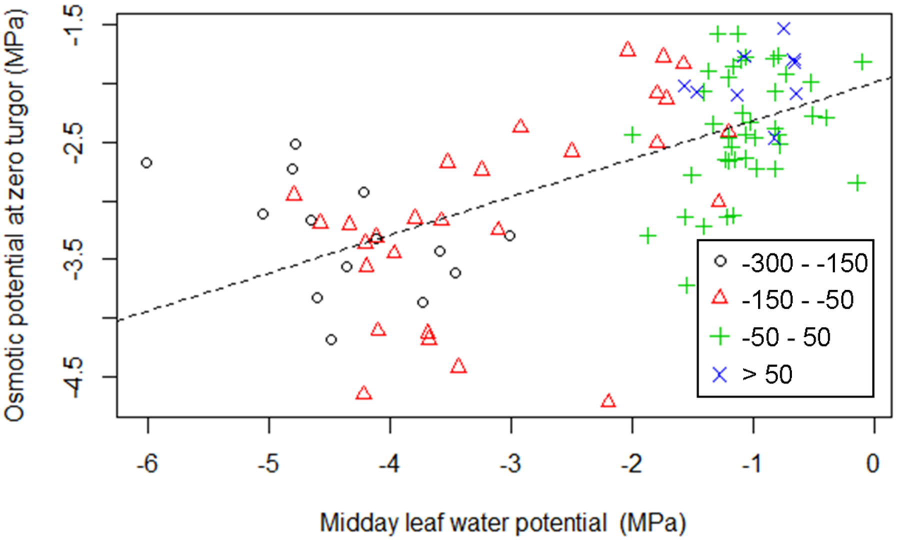

Figure 4. Relationship between the midday water potential and osmotic potential at full turgor (n = 92). The data are grouped by four different levels of mean annual precipitation deficit (mm). The data are fitted with linear regression (red dashed line; r^2 = 0.43, $p < 0.001$).

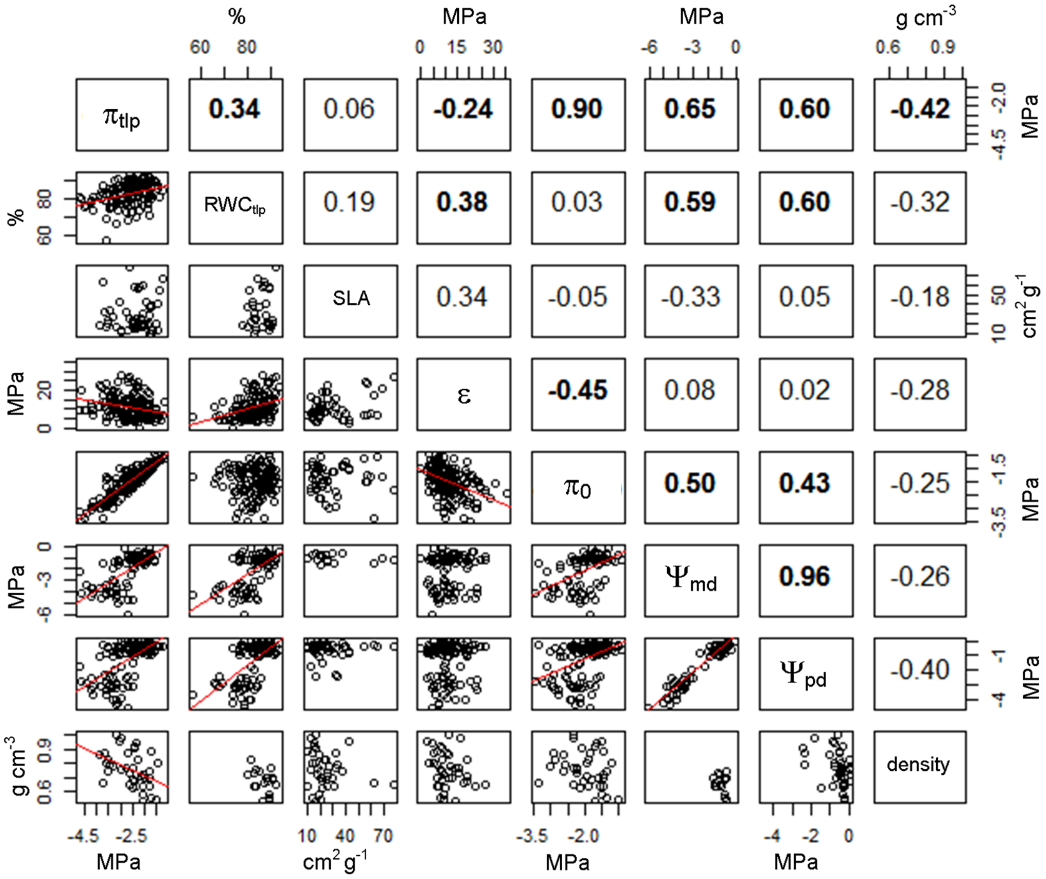

Figure 5. Correlation matrix of all plant traits included in the database. Scatter plots in lower, left quadrant are fitted with a linear function for significant correlations ($p < 0.01$). Values in the upper right quadrant are Pearson's correlation coefficients with bold text denoting significant correlation ($p < 0.01$).

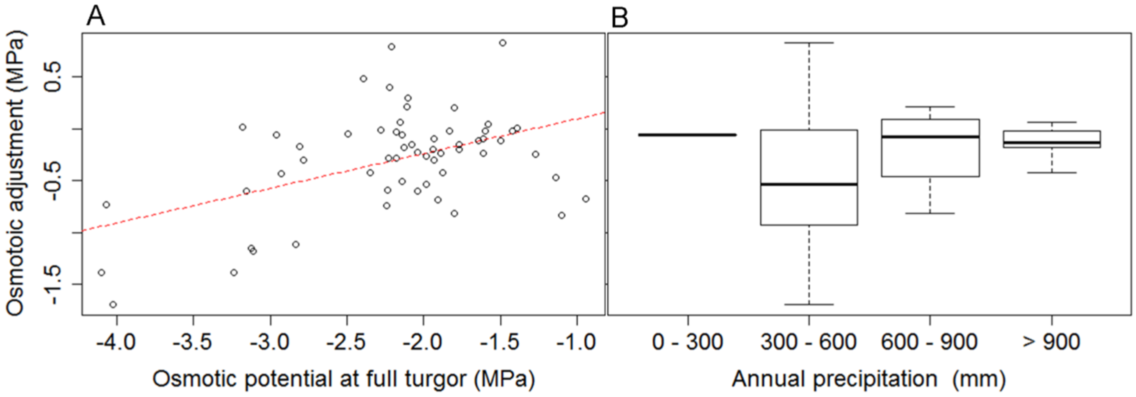

Figure 6. Relationship between osmotic adjustment and (**A**) osmotic potential at full turgor (under high water availability) and (**B**) mean annual precipitation. Data in (**A**) are fitted with linear regression (red dashed line; $r^2 = 0.22$, $p < 0.001$).

4. Discussion

We compiled a database of species leaf water relations that spanned almost 50 years of plant water relations research in Australia and covered a considerable range of vegetation and plant functional types across the Australian continent. In this study, key climatic indices were extracted from different middle and tail regions of species climatic envelopes in order to assess the role of aridity and high temperature as selection pressures on leaf water relations among a large group of species ($n = 174$). By also evaluating the influence of habitat water availability across these climatic gradients, our study builds on a growing body of work that links key functional traits to a species habitat and climatic range and strengthens efforts to predict shifts in forest distribution and function under a changing climate.

A significant proportion of the variability in π_{tlp} was explained by climatic indices based on precipitation (MAP) or climatic water deficit (MAPD). This observation supports the finding of Bartlett *et al.* [10,23] and others [25] that π_{tlp} is an adaptive trait whereby a lower π_{tlp} allows species to tolerate increased aridity in terms of lower precipitation and/or increased evaporative demand. Furthermore, the relationship between π_{tlp} and MAPD was also maintained among the eucalypt spp. ($n = 47$) in the database, supporting the suggestion that turgor maintenance traits explain much of the distribution of the dominant genus in forests across Australia [26]. However, our study furthers our understanding of leaf physiological adaptations to climate by showing a significant interaction between maximum temperature (MHMT) and MAP in influencing variation in leaf turgor maintenance ($R^2 = 0.35$). This result indicates an important role for high temperature in modulating π_{tlp} among species. There is likely to be strong selection for low π_{tlp} in dry climates with high summer temperatures given the potential for additional heat stress if turgor loss triggers stomatal closure. High temperature stress is amplified under water stress when leaf cooling via transpiration ceases after stomatal closure [27]. This could trigger leaf or whole-tree mortality if leaf temperatures exceed ambient air temperatures and reach critical temperatures for maintaining cell function [28,29]. It remains to be tested whether π_{tlp} also co-varies with those leaf traits associated with resistance to high temperature stress. These data support recent studies that highlight the strong interaction of drought and high temperature stress in affecting tree functioning and survival in Australia [21] and globally [30]. Our findings demonstrate a role of both aridity and high temperature in controlling leaf water relations and π_{tlp} presumably because conditions of high evaporative demand and high temperature exert strong selection pressure on species to adequately regulate their physiology over a given range of leaf water potentials and temperatures.

In general, the inclusion of climate indices based on the dry tails of the species distribution (e.g., MAP and MAPD) did not strengthen the relationship between climatic indices and π_{tlp}, compared to climate indices derived from the median (Table 1). It is likely that these climate-trait relationships are maintained at both parts of the distribution because values derived from the median scale linearly with those at the dry or warm tail of the distribution.

This study also elucidates the role of species habitat water availability and water management strategy, in addition to species climatic envelope in driving species leaf water relations. Species that experience lower Ψ_{md} (and lower Ψ_{pd}) tended to have lower π_{tlp}, particularly for those species from more arid environments. Variation in habitat water availability is also reflected in the larger dispersion in π_{tlp} at observed in MAPD between −50 to −150 mm (Figure 2). This suggests that increasing aridity drives greater selection pressure for different strategies to exploit a wider range of potential water sources and ecohydrologic niches [31]. Regulation of water use must also closely align with spatial and temporal patterns in water availability thereby promoting strong divergence in water status, particularly during dry periods [32]. The tendency for larger trait variation in drier climates is consistent with other drought trait databases such as the global analysis of stem embolism resistance (defined using the water potential at 50 percent loss of hydraulic conductivity), that shows increasing trait variation with climatic water availability [33]. In this study, climatic water deficit explained only ~ 30% of the variation in π_{TLP}. These patterns among drought resistance traits indicate the significance of contrasting water management strategies that may diminish the importance of a single trait π_{tlp} in enabling survival under water deficit. Hence, at the whole plant level, species responses to increasing aridity involves the coordination of multiple traits and provide differential responses to drought and rates of recovery following drought.

Shifts in turgor maintenance are a good example of how alternative strategies may bring about similar outcomes for tolerating low water availability. Osmotic adjustment is widely evaluated in order to compare drought tolerance among differing species and genotypes [23], however elastic adjustment or increased elasticity (lower ε) can potentially buffer against steep declines in water status [5,34]. The relatively weak relationship we observed between differential modes of turgor maintenance; osmotic adjustment and bulk tissue elasticity *versus* aridity suggests no consistent shift in determinants of leaf turgor. The negative relationship between π_0 and ε is consistent with the trade-off observed among many species exhibiting either lower elasticity or osmotic potential (less negative) or higher elasticity and osmotic potential [10,25,35]. This trade-off probably originates from a biophysical requirement of tissues and cells to either accumulate solutes accompanied by a decrease in elasticity to avoid cell rupture or increased elasticity without having to incur the cost of producing compatible solutes [35]. Several studies in dry climates show strong divergence in turgor maintenance patterns among sympatric or closely related species that confer resistance to water deficit [13,35,36].

Intra-specific variation in π_{tlp} may also drive adaptation across the species distribution. Evidence for systematic variation in π_{tlp} under well-watered conditions is limited in woody species and most studies included in the database showed non-significant differences in π_{tlp} among genotypes [37–39], whereas variation among genotypes tends to occur in response to seasonal or short-term water deficit suggesting plasticity in ability to adjust π_{tlp} among genotypes [39,40]. Nevertheless patterns in π_{tlp} presented here would suggest that single parameters of species climatic envelope and corresponding mean trait value provide a fairly robust indication of inter-specific patterns in adaptation to aridity.

5. Conclusions

We showed that among the 174 woody species for which there were data for π_{tlp}, a large proportion of the variability in π_{tlp} could be explained by mean annual precipitation or climatic water deficit (precipitation deficit). While similar biome and species-level patterns in π_{tlp} has been demonstrated in global meta-analyses that considered species aridity values from the study site [10,23], our study also confirmed the significance of an interaction between hottest monthly maximum temperature with climatic water availability. This provides evidence for strong selective pressure from both water deficit and high temperature in defining physiological strategies among Australian species. Furthermore, habitat water availability and plant water management patterns as reflected by differences in midday leaf water potential was a slightly better predictor of π_{tlp} across these gradients in aridity, highlighting the fundamental importance of these factors, in addition to the prevailing climatic conditions, in modulating the operating range over which plants may actively sustain turgor. Further research is required to examine the relationship between turgor maintenance parameters and other traits known to exert strong controls on plant performance under water deficit across a broad range of species, e.g., leaf hydraulic conductance. This study suggests that π_{tlp} plays a central role in defining plant performance and could be incorporated in species distribution modelling given its responsiveness to climatic and site-based drivers in water availability.

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Author Contributions

Patrick J. Mitchell and Anthony P. O'Grady compiled the database, Patrick J. Mitchell analysed the data and wrote the paper with significant input from Anthony P. O'Grady.

Conflicts of Interest

The authors declare no conflict of interest.

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