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**Correlation of drought traits and the predictability of osmotic potential at full leaf
turgor in vegetation from New Zealand**

Running headline: *Drought traits correlation and osmotic potential*

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Correlation of drought traits and the predictability of osmotic potential at full leaf turgor in vegetation from New Zealand

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Abstract

Scientists do not know precisely how severe will be the impact of climate change on species. Evidence suggests that for some species, their future distributions might be jeopardized by local extinctions and drought-induced tree mortality. Thus, we require models capable of estimating drought tolerance across many species. We can approach this goal by assessing functional traits. The trait osmotic potential at full turgor, π_o , is potentially a good drought indicator; however, few studies address its importance as a drought-tolerance predictor and it is difficult to measure in the field with accuracy. In this work we aim to answer the questions: which drought traits correlate with π_o ?; do morpho-anatomical traits correlate with π_o ?; and which trees and shrubs are more (or less) vulnerable to drought? To achieve this aim, we assessed physiological and morpho-anatomical traits for 14 native species from New Zealand forests. We included leaf- and wood-related traits, π_o , water potential, and stomatal conductance. We examined how these traits correlate with π_o and sought to generate models to predict π_o as a function of other traits. We tested 33 different models and evaluated them using Akaike's information criterion. Unfortunately, none of the morpho-anatomical traits correlated well with π_o . Instead, water potential correlated most strongly with π_o . None of the models using only morpho-anatomical traits produced plausible results. The model with the best predictive performance incorporated the effects of both morpho-anatomical and physiological traits: water potential and wood saturated water content. Of the species analysed, and based on their π_o response, *Lophozonia menziesii* was considered the most vulnerable to drought stress, whereas *Plagianthus regius* was the least vulnerable. Our findings imply that it is potentially valuable to keep exploring the use of π_o as a drought indicator and that the effort required to measure some physiological traits, such as water potential, may be essential to consider plant drought responses and to predict π_o .

Key words. Akaike's information criterion; drought indicator; drought traits; morpho-anatomical traits; physiological traits; water potential; wood saturated water content; stomatal conductance

41 *Abbreviations:* leaf area, LA; leaf relative water content, LRWC; leaf thickness, LT;
42 minimum seasonal water potential, Ψ_w ; osmotic potential at full turgor, π_o ; osmotic
43 potential, Ψ_π ; specific leaf area, SLA; stomatal conductance, g_s ; wood density, WD; wood
44 saturated water content, WC_{sat} .

Introduction

Climate change will affect species and ecosystems differentially and the severity of its impacts will vary according to specific regional and local variations in climate (Lindner *et al.* 2010). Species have different strategies to face climatic changes and respond idiosyncratically to those changes (Esperón-Rodríguez and Barradas 2015; García-Robledo *et al.* 2016; Malyshev *et al.* 2016). Thus, assessing and understanding these strategies is a major challenge. For instance, species can shift their distributions and migrate to areas where conditions are more suitable or they can adapt to new conditions by changing their physiological responses (Engelbrecht *et al.* 2007; Lenoir *et al.* 2008; Pellegrini *et al.* 2017). Further, in some cases, survival of species will depend on their adaptive capacity (Mellilo *et al.* 1996).

As temperature increases and precipitation patterns are altered, drought will become a threat to many species (Field *et al.* 2014). Current species distributions are determined to some extent by the species' drought tolerance. Furthermore, for some species, their future distributions might be jeopardized by possible local extinctions and drought-induced tree mortality (Anderegg *et al.* 2015; Engelbrecht *et al.* 2007; Feeley *et al.* 2011). Therefore, we require models capable of estimating drought tolerance across many species. The assessment of drought-related functional traits provides one approach to estimating this tolerance (Bartlett *et al.* 2012a).

Functional traits include plant attributes that impact fitness via their effects on growth, reproduction, and survival (Violle *et al.* 2007). These traits can be classified as morpho-anatomical and physiological. Physiological traits are tightly linked to plant functions and are known to be indicators of drought resistance and water use efficiency (Cornelissen *et al.* 2003). Some of these traits are evolutionarily linked, show a strong association with water availability, and can be used to predict i) species' distributions with respect to water supply and ii) plant responses to water stress within or across biomes (Bartlett *et al.* 2016; Blum 2005; Buckley 2005; Larcher 2003; Nobel 1999). However, physiological traits are often difficult to measure and to quantify for large numbers of species or individuals (Cornelissen *et al.* 2003; Hodgson *et al.* 1999).

Conversely, some morpho-anatomical traits are easier to measure and are especially useful when assessing large numbers of species or individuals (Cornelissen *et al.* 2003). Some of these traits are correlated to drought tolerance (i.e. leaf size) (Sack *et al.* 2012). However, they are often less tightly linked to plant function (Hodgson *et al.* 1999; Wright *et al.* 2010). Morpho-anatomical traits are often correlated with physiological traits because

differences in morpho-anatomical traits might reflect different physiological responses related to adaptation or evolution processes (Chabbi and Loescher 2017; Cornelissen *et al.* 2003; Dudley 1996).

Recent studies identify osmotic potential (Ψ_w) and osmotic potential at turgor loss point or wilting (π_{tlp}), as important physiological determinants of plant water stress. These traits are widely used to explain the biological basis of drought tolerance and predict species' distributions (Bartlett *et al.* 2012a; Bartlett *et al.* 2012b; Bartlett *et al.* 2014; Callister *et al.* 2008; Lenz *et al.* 2006; Sakthivelu *et al.* 2008). However, the osmotic potential at full turgor (π_o) has been less studied (but see Mart *et al.* 2016; Meinzer *et al.* 2016; Patakas *et al.* 2002; Savi *et al.* 2017), and there is a less understanding of how this trait can be used as an indicator of drought tolerance. Only a few studies have investigated π_o for i) its use as a proxy for drought tolerance and the degree of iso- vs. anisohydry, ii) its correlation with the ability to withstand low leaf water potentials, or iii) tested the relationship between π_o with water availability, and with morpho-anatomical —such as WC_{sat} - and physiological —such as g_s , Ψ_w , π_{tlp} , leaf and stem vulnerability to cavitation, and leaf hydraulic conductance- traits (Bartlett *et al.* 2012b; Bonal and Guehl 2001; Brown *et al.* 1976; Hinckley *et al.* 1980; Jones and Rawson 1979; Lenz *et al.* 2006; Mart *et al.* 2016; Meinzer *et al.* 2016; Turner *et al.* 1986; Tyree *et al.* 2003; Villagra *et al.* 2013). Understanding how π_o changes under water stress conditions can help to predict a plant's hydration level and turgor leaf requirements under different environmental conditions (Vila 2011). Therefore, π_o can provide an assessment of drought tolerance and resistance of the species.

In this work we explore three questions: i) which drought traits correlate with osmotic potential at full turgor, π_o ?; ii) do morpho-anatomical traits correlate with π_o ?; and iii) which trees and shrubs are more (or less) vulnerable to drought? We accomplish this by measuring a range of morpho-anatomical and physiological traits of 14 trees and shrubs species native from lowland, mountain and subalpine forests, and shrublands from New Zealand (Table S1). We determined how strongly the morpho-anatomical traits correlate to the physiological trait π_o , and we propose a model for its estimation.

Methods

Study area and species selection

The study area is located in the Canterbury region in New Zealand (Fig. S1). All sampling was undertaken in the gardens at Landcare Research and Lincoln University located in the

town of Lincoln, 22 km south of Christchurch, New Zealand, at 15 m asl (43°39' S, 172°29' E). These gardens are separated by a distance of around 1 km. Climate is temperate with an annual precipitation of 663 mm. April is the driest month on average with 43 mm (Cox 1978). Lincoln has a mean annual air temperature of 10.8 °C, with January and February the warmest months and June and July the coldest. Mean annual soil temperature at 10 cm depth is 10.7 °, at 30 cm is 11.9 °, and at 91 cm is 12 °C. Annual number of days of frost are 39 (screen frost) and 91 (ground frost) (data from 1881-1970; Cox 1978).

For our study, we selected 14 native trees and shrubs species from a broad range of habitat types of New Zealand. All species are grown in the Lincoln gardens: *Aristotelia serrata*, *Coprosma robusta*, *Dodonaea viscosa*, *Fuchsia excorticata*, *Fuscospora cliffortioides*, *Fuscospora fusca*, *Griselinia littoralis*, *Hoheria angustifolia*, *Kunzea ericoides*, *Lophozonia menziesii*, *Pittosporum eugeniioides*, *Pittosporum tenuifolium*, *Plagianthus regius*, and *Pseudopanax arboreus* (Table S1).

Morpho-anatomical and physiological traits

We measured four physiological and six morpho-anatomical traits. Morpho-anatomical traits included: individual-leaf area (LA); leaf relative water content (LRWC); leaf thickness (LT); specific leaf area (SLA); wood density (WD); and wood saturated water content (WC_{sat}). Physiological traits included: osmotic potential at full turgor (π_o); osmotic potential (Ψ_π); minimum seasonal water potential (Ψ_w); and stomatal conductance (g_s). All traits are considered indicators of drought tolerance (see Table 1)

Data collection

Field and lab work was undertaken from 3 – 15 March 2014, during early autumn when precipitation in the region is lower. In order to reduce the potential effects of tree size and age on the plant responses, the physiological traits were measured for five mature individuals of each species using mature fully expanded canopy leaves without herbivore damage and in good health conditions. We assessed the diurnal temperature variation, finding a peak of temperature after noon; thus, the physiological traits Ψ_w and g_s were measured at 1300 hours (h, local time) when we assumed the individuals were more stressed.

Leaf and wood traits were collected at the beginning of the experiment at 0900 h. For wood traits (WD and WC_{sat}), two small pieces of wood were collected from five individuals of each species. Wood density was calculated using Archimedes' method (Falster and Westoby 2005). The wood density of all samples was determined by taking a 3 cm-long segment cut from one end of each sample at a regular branch thickness (~ 1 cm of diameter);

its fresh volume was measured by water displacement with an analytical balance. We also measured the fresh mass (FM) of these stems. Prior to oven-drying, we immersed the stems in distilled water for 24 h, at which point we assumed they were saturated, and later stems were re-weighed to determine saturation mass (SM) (Borchert 1994a). Using these data, we calculated water content (WC, % FM) = 100 (FM - DM)/FM and saturation water content (WC_{sat}, % DM) = 100 (SM - DM)/DM (Borchert 1994b). Wet mass and volume were determined and stems were dried for 72 h at 100 °C and weighed to determine saturated water content (WC_{sat}). Wood density was estimated as dry mass divided by fresh volume.

For leaf traits, four leaves per individual plant were collected. To measure LA, individual leaf laminae were measured without petiole or rachis by taking photographs of each leaf and using the software *ImageJ* (Version 1.49q 27). Leaves were then dried for 72 h at 70 °C and weighed to determine dry mass. SLA was determined by dividing the surface area of the fresh leaf and dry mass. Leaf thickness was measured using a dial gauge micrometer (0.01 mm; Insize Inc., Cheektowaga, NY) at three points along the lamina on a fresh leaf, taking care to avoid major veins or the midrib. For LRWC, samples were weighed to give fresh mass (FM). Segments were then floated on distilled water for 4 h at room temperature in laboratory lighting that was close to the compensation point for photosynthesis (Barrs and Weatherley 1962). Leaves were then re-weighed to give the ‘fully turgid’ or hydrated mass (HM), after which they were dried for 48 h in an oven at 80 °C to give the dry mass (DM). LRWC was calculated according to Weatherley (1950):

$$\text{LRWC} = (\text{FM} - \text{DM}) / (\text{HM} - \text{DM}) \times 100 \quad (1)$$

Physiological traits were measured for five consecutive days. We measured two leaves from three individuals for each species. We obtained the Ψ_{π} using a vapor pressure osmometer (VAPRO 5520). We collected leaves, which were then submerged in liquid nitrogen, centrifuged for 4 minutes at 12 rpm, and finally, Ψ_{π} was read in an osmometer. Minimum seasonal water potential (Ψ_w) was measured by obtaining the stem water potential from non-stabilized branches using a pressure chamber (PMS, Corvallis, Oregon, USA) (Scholander *et al.* 1964; Turner 1981). Stomatal conductance (g_s) was measured using a leaf porometer (Decagon SC-1, Washington, USA). For the calculation of π_o we used the traits Ψ_{π} and LRWC, with an equation modified from Nguyen-Queyrens *et al.* (2002):

$$\pi_o = (\Psi_{\pi} \times \text{LRWC}) / 100 \quad (2)$$

Statistical analysis

All individual trait values were averaged to obtain a mean value for each species. The

correlation among traits across the 14 species was evaluated using a Spearman correlation (Legendre and Legendre 2012) ($P \leq 0.05$ level of significance). P -values were corrected for family-wise error (Zar 1999). After assessing correlation, we developed a set of hypotheses about how the selected traits are likely to influence π_O and based on their relevance as drought predictors (Table 1). We tested models with less than four predictor variables to avoid overparameterized models (in relation to our total n used, 14 species). We took this approach because over-parameterization can cause insensitivity of the response variable to fitted parameters (Bolker 2008; Zuur *et al.* 2010). The traits Ψ_π and LRWC were not included in any of the models because they are directly involved in the calculation of π_O and therefore, are not independent. Additionally, we did not include within models highly correlated variables (correlation coefficient ≥ 0.7).

For our model analysis, values of traits were log transformed. For Ψ_w , we used the transformation $\log(Y+a)$ where a is the constant and Y is the trait. We chose a so that $\min(Y+a) = 1$ (Zar 1999). All models were fitted using linear regression, and model performance was evaluated using corrected Akaike's information criterion (AICc) (Akaike 1974). AICc was selected over Akaike's information criterion (AIC) as the total sample size was low and AIC can perform poorly when there are too many estimated parameters (Anderson 2008). Not all traits contributed to all models. The calculation of AICc also enabled the ranking of the importance of each trait to the overall set of models. To do so, the AICc weight values were summed for all models containing a given trait and the totals for each trait were then ranked (Burnham and Anderson 2001). AICc weights reflect the relative likelihood of each model: the bigger the Delta AICc (Δ_{AICc}), the smaller the weight and the less plausible the model given the data. Model performance was evaluated through leave-one-out cross-validation, leading to the estimation of the root mean squared error (RMSE) produced by each model, and to the calculation of the R^2 .

All statistical analyses were conducted using the statistical environment software R (R Development Core Team 2014), specifically the package AICcmodavg (Mazerolle 2013).

Results

Which traits and trait combinations are most correlated with π_O ?

Correlation among traits is in general weak (mean = 0.25, SD = 0.18; $P \leq 0.05$). We found that Ψ_w has the highest correlation with π_O (0.49). The traits g_s , WD, and LT correlated negatively with π_O . None of the morpho-anatomical traits selected has a high correlation with

π_O . The highest correlation was between π_O and LA (0.16) (Table 2; Fig. 1).

Thirty-three models were evaluated to predict π_O considering different trait combinations (the best 10 models are presented in Table 3, but see the complete list in Table S2). Δ_{AICc} values were used to evaluate models' relative strength. The AICc weight of each trait in the overall model set (Tables 3 and S2) was used to rank the importance of each trait as follows: $\Psi_w > WC_{sat} > LA > g_s > WD > LT > SLA$ (Table S3).

The most parsimonious model to predict π_O was $\Psi_w + WC_{sat}$, which had the highest AICc and R^2 , and the lowest RMSE (Table 3; Fig. S2). The model including $\Psi_w + LA + WC_{sat}$ was ranked second, suggesting that the combination of these three traits is also a good predictor of π_O (Table 3). The models with the best performance ($\Delta_{AICc} < 12$) included a trait combination of Ψ_w and all the other traits (Tables 3 and S2). For the best predictor model, π_O decreases when Ψ_w decreases and WC_{sat} increases (Fig. 2; equation 3):

$$\pi_O = -1.78587 + 0.39389 (\log (3 + \Psi_w)) - 0.07894 (\log WC_{sat}) \quad (3)$$

Interestingly, the best-ranked model including only morpho-anatomical traits was ranked in the position 20 ($\Delta_{AICc} > 12$) and included only SLA (Table S2). The other models including only morpho-anatomical traits were ranked below position 20 (Table S2).

Trait differences among species

For the morpho-anatomical traits, the species with the highest WD was *D. viscosa*, whereas *P. arboreus* had the lowest WD. In contrast to the relationship involving WD, *P. arboreus* had the highest values of WC_{sat} , and *D. viscosa* had the lowest. *Pseudopanax arboreus* had the highest LA and *K. ericoides* the lowest; *F. excorticata* had the highest SLA and *K. ericoides* the lowest. For LRWC, *H. angustifolia* had the highest and *K. ericoides* the lowest values. LT was highest for *G. littoralis* and lowest for *F. fusca*. Concerning the physiological traits, the highest Ψ_π and π_O was observed in *L. menziesii* and the lowest in *P. regius*. For Ψ_w , *P. arboreus* had the highest and *H. angustifolia* the lowest values. *Plagianthus regius* had the highest g_s and *P. arboreus* the lowest (Fig. 3; Tables S4 and S5).

Discussion

The main questions of our research were: i) which drought traits correlate with osmotic potential at full turgor, π_O ?; ii) do morpho-anatomical traits correlate with π_O ?; and iii) which trees and shrubs are more (or less) vulnerable to drought?

For our study, we found that the physiological trait water potential, Ψ_w , is a good correlate of π_O , and the model $\Psi_w + WC_{sat}$ is the best predictor. The morpho-anatomical traits

selected in this study did not individually have a strong correlation with, or were good surrogates to, π_O . The model that produced the best predictions included both physiological and morpho-anatomical traits. Of the drought traits evaluated, we found differences among species, which might have implications for changes in forest composition under various climate change scenarios. Based on the physiological traits π_O and Ψ_w we identified *L. menziesii* as the most vulnerable to drought stress, whereas *P. regius* was the least vulnerable. These species have the highest and lowest π_O and Ψ_w , respectively, reflecting their capacity to maintain the full turgor and water potential at different stress levels.

The best predictor model

In this work, we provide some insights about the correlation and estimation of π_O using other traits. Unfortunately, models using morpho-anatomical traits were not considered accurate ($\Delta AIC_c > 12$) (Anderson 2008). Thus, we conclude that the commonly used morpho-anatomical traits that we measured are not suitable surrogates for π_O . However, combinations of physiological and morpho-anatomical traits are good predictors, and all of them included Ψ_w . Here, π_O was most strongly correlated with Ψ_w , with π_O decreasing when Ψ_w decreases and WC_{sat} increases (Fig. 2).

Previous work highlights the importance of WC_{sat} . The water stored in the stems helps to maintain the water status and carbon gain (Villagra *et al.* 2013). Also, in early life stages, a plant depends on its sapwood water reserves to survive because the root ability to obtain water can be limited (Pineda-García *et al.* 2013). In water-limited environments, plants with high WC_{sat} have a more efficient water transport, present higher maximum photosynthetic rates, lose turgor at higher Ψ_w , and have smaller diurnal variations of Ψ_w (Stratton *et al.* 2000; Villagra *et al.* 2013). Conversely, species with low WC_{sat} have low Ψ_w associated with lower leaf turgor loss point and higher leaf solute content (Stratton *et al.* 2000). This is the case of *P. tenuifolium*. Low WC_{sat} and Ψ_w recorded in this species might be an adaptation for its tolerance to inhabit dry soils in full sun exposition (Mugnai *et al.* 2005; Williams and Buxton 1989). Conversely, *F. excorticata* is usually found alongside creeks and rivers (Dawson and Lucas 2000) where water might not be a limited factor reflected in higher WC_{sat} .

Regarding Ψ_w , its importance as a drought tolerance trait and correlation with other traits have been broadly studied (Bartlett *et al.* 2016). Some species are able to maintain their turgor potential by decreasing their leaf water potential, thus maintaining g_s , photosynthesis, and production under severe water stress (Katerji *et al.* 1997). Conversely, rapid stomatal

closure can prevent water loss and embolism, and maintain high water potentials (Benzing 1998; Graham and Nobel 2005; Martin-StPaul *et al.* 2017; North and Nobel 1994). For our species, *P. regius* can be considered less vulnerable to drought, as it has low g_s and Ψ_w , a characteristic that prevents water loss. Again, high g_s and Ψ_w reported for *F. excorticata* might be correlated to its non water-limited habitat (Dawson and Lucas 2000) where species can keep high g_s and transpiration without representing a risk for desiccation.

To avoid desiccation and death, plants can use stored water from stem tissues (Stratton *et al.* 2000) or increase the osmotic adjustment as a water-saving strategy —osmotic adjustment modifies water potential by decreasing π_o - (Beck *et al.* 2007). As water is transpired through stomata, Ψ_w decreases to avoid water loss (Esperón-Rodríguez and Barradas 2015). Conversely, if g_s decreases, producing increased stomatal resistance when stomata close, plants might save water, therefore Ψ_w and π_o increase. Our results suggest that water storage as WC_{sat} —taken as a surrogate of relative stem water storage capacity (Stratton *et al.* 2000)- might represent an additional source of water that plants can use to maintain high π_o . In water-limited environments, high WC_{sat} might represent an advantage to keep the full turgor of leaves and high Ψ_w .

Another strategy to prevent water loss can be related to leaf size. This trait is of interest in our study. Among individual morpho-anatomical traits, LA has the highest correlation with π_o (Table 2) and the second best predictor model included LA with Ψ_w and WC_{sat} (Table 3). Larger leaves have thicker boundary layers, which provide significant resistance to transpiration (Raschke 1960). Thus it can be suggested that the increased boundary layer resistance of larger leaves saves water under these conditions, and therefore there is less need for osmotic adjustment, and hence π_o is higher. However, caution is suggested when assessing individual species. *Pseudopanax arboreus*, for instance, has quite large leaves, and although it has the highest its Ψ_w and lowest g_s , π_o is not the highest among the species in this study.

Which trees and shrubs are more (or less) vulnerable to drought?

We assessed species' vulnerability according to different drought traits responses. The species selected in this study are distributed in different ecosystems and elevations from New Zealand (Table S1). Therefore, differences in responses to water deficits might reflect differences in climate regimes (Read *et al.* 2010).

Species that survive longest in dry conditions are those able to tolerate low levels of leaf water content and leaf water potentials and possess the physiological ability to keep alive cells and meristems in water-limited environments (Esperón-Rodríguez and Barradas 2015;

Poorter and Markesteijn 2008; Tyree *et al.* 2003). Species that grow in well-hydrated conditions tend to have higher π_o and tissues with full turgor that prevent them from suffering water stress (Levitt 1980). In contrast, low π_o is often found in drought-tolerant plants as an adaptation strategy to maintain the full turgor under dry conditions (Levitt 1980; Shackel *et al.* 1997; Tschaplinski *et al.* 1998). For our study, species with the highest Ψ_π and π_o appeared to be the most vulnerable to drought, *L. menziesii* and *P. arboreus*, both species from relative drier habitat, mountain and subalpine forest and shrublands (Dawson and Lucas 2000).

However, it is important to consider that assessing vulnerability differs depending on the traits used. In our study, we considered as less vulnerable the species capable of reaching the lowest π_o and Ψ_w : *P. regius* and *H. angustifolia*; whereas species such as *L. menziesii* and *P. arboreus* were considered the most vulnerable (higher π_o and Ψ_w). However, if we consider morpho-anatomical traits, species with low values of leaf traits (LA, SLA and LT) are expected to be less vulnerable (Curran *et al.* 2010; Deines *et al.* 2011; Mitchell *et al.* 2008). In accordance with these leaf traits, *K. ericoides* was the least vulnerable species (Fig. 3; Tables S4 and S5). The drought tolerance of *K. ericoides* has been studied previously, and it appears that this species survives in dry locations by having the ability to reach low water potentials (Innes and Kelly 1992). Interestingly, *F. excorticata* and *P. arboreus* were the most vulnerable species regarding leaf traits, but if we use WC_{sat} to assess vulnerability, these two species have the highest wood water content and thus can be considered as less vulnerable (Stratton *et al.* 2000).

What are the caveats of our study?

We found that the traits selected in our study did not have a strong correlation with π_o . Future studies can explore the correlation between π_o with other morpho-anatomical traits and explore more broadly the relationship among π_o , Ψ_w , and WC_{sat} . Although the relationship between Ψ_w and WC_{sat} has been explored previously (Villagra *et al.* 2013), our understanding on how π_o is affected by the stem water content and how this relationship can be beneficial for plants under drought stress periods is still limited. We encourage future experimental (drought-induced) studies to assess these questions. Also, as our species were sampled in common gardens where water supply might not be a limiting factor, further studies in the field can highlight the vulnerability, particularly of those species that are distributed in drier regions.

Finally, our results are related to the species selection and environmental conditions.

We advise caution in the extrapolation of our results to different species and locations. This issue is particularly important because plant responses and traits can vary depending on differences in phenology, plant age, nutrient availability, soil, and stress exposure (Borchert 1994a; Chirino *et al.* 2017; Esperón-Rodríguez and Barradas 2015; Lieberman 1982; Reich and Borchert 1982; Thomas and Winner 2002; Villagra *et al.* 2013).

Conclusions

We conclude that the selected morpho-anatomical traits alone are not good correlates of π_O . We propose Ψ_w as a good surrogate of π_O and the model $\Psi_w + WC_{sat}$ to be the best predictor. We found that the assessment of vulnerability can vary depending on the traits analysed. Nevertheless, the physiological trait π_O has potential to be used to evaluate which species might be most vulnerable to future droughts. Our results imply that it is potentially valuable to keep exploring the use of π_O as a drought indicator and to estimate other physiological traits such as osmotic adjustment, osmotic potential, osmotic potential at loss point, and turgor pressure. We encourage future research on the correlation between other morpho-anatomical traits and π_O .

Conflict of interest

The authors declare that they have no conflict of interest to disclose.

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Tables and Figures

Table 1. List of traits measured, their units, and description of their relevance to drought tolerance.

Symbol/ abbreviation	Trait	Units	Relevance	References
Physiological traits				
π_o	Osmotic potential at full turgor	MPa	Key trait driving π_{tlp} (permanent wilting point) across species during seasonal and experimental droughts; hence, powerful trait for predicting drought tolerance and distributions with respect to water supply	(Bartlett <i>et al.</i> 2012a; Bartlett <i>et al.</i> 2012b; Bartlett <i>et al.</i> 2014; Lenz <i>et al.</i> 2006)
Ψ_π	Osmotic potential	MPa	Recognized as an indicator of drought resistance and water use efficiency, also shows a strong association with water availability within and across biomes	(Blum 2005; Jongdee <i>et al.</i> 2002)
Ψ_w	Minimum seasonal leaf/steam water potential	MPa	Reflection of the water availability in the soil in the season when water is most limited – hence indicator of drought tolerance	(Ackerly 2004; Esperón-Rodríguez and Barradas 2015; Esperón-Rodríguez and Barradas 2014; Scholander <i>et al.</i> 1964; Turner 1981; Wyse <i>et al.</i> 2013)
g_s	Stomatal conductance	$\text{mmol m}^{-2} \text{s}^{-1}$	Recognized as an indicator of plant water stress and	(Buckley 2005; Buckley and Mott

			drought avoidance. High g_s represent high water loss through transpiration. Some plant species close stomata to prevent water loss	2013; Esperón-Rodríguez and Barradas 2015; Esperón-Rodríguez and Barradas 2014; Rice <i>et al.</i> 2004; Wyse <i>et al.</i> 2013)
Morpho-anatomical traits				
LA	Leaf area	cm^2	Correlated with rainfall. It is recognized that plants occurring in areas of low rainfall tend to have smaller leaves than those in more favourable regions. Small leaves have the capacity to shed heat without using evapotranspiration. Also, smaller leaves have denser venation, which can increase drought tolerance by providing an efficient water transport that contributes to drought tolerance by routing water around blockages caused by drought-induced xylem embolism	(Cornelissen <i>et al.</i> 2003; Sack and Scoffoni 2013; Sack <i>et al.</i> 2012)
SLA	Specific leaf area	$\text{cm}^2 \text{mg}^{-1}$	Index of sclerophylly. Linked with drought tolerance	(Cornelissen <i>et al.</i> 2003; Cunningham <i>et al.</i> 1999; Salleo <i>et al.</i> 1997)
LRWC	Leaf relative water content	% fresh mass	Indicator of plant water status and water content	(Saura-Mas and Lloret 2007)

LT	Leaf thickness	μm	Indicator of water deficit and used to observe changes in water content dehydration. During water deficit stress, leaf thickness decreased dramatically by as much as 45%	(Marenco <i>et al.</i> 2009; Seelig <i>et al.</i> 2012)
WD	Wood density	mg mm^{-3}	Correlated with xylem resistance to cavitation and hence drought tolerance	(Maherali <i>et al.</i> 2004; Rice <i>et al.</i> 2004; Tyree and Sperry 1989)
WC _{sat}	Wood saturated water content	% dry mass	Measure of stem water storage capacity. It is an indicative of higher water transport efficiency and leaf turgor loss point, smaller diurnal variation in leaf water potential and higher maximum photosynthetic rate	(Blum 2011; Borchert 1994a; b; Villagra <i>et al.</i> 2013)

Table 2. Spearman correlation coefficients of the physiological traits osmotic potential at full turgor (π_o), minimum seasonal water potential (Ψ_w), and stomatal conductance (g_s), and the morpho-anatomical traits wood density (WD), wood water saturated content (WC_{sat}), leaf area (LA), specific leaf area (SLA), and leaf thickness (LT) for 14 trees and shrubs species native from New Zealand. Significance levels were corrected for family-wise error.

Trait	Ψ_w	g_s	WD	WC_{sat}	LA	SLA	LT
π_o	0.49	-0.24	-0.04	0.034	0.16	0.11	-0.04
Ψ_w		-0.26	-0.4	0.31	0.47	0.11	0.12
g_s			0.22	-0.34	-0.23	0.11	-0.03
WD				-0.74	-0.45	-0.21	-0.2
WC_{sat}					0.67	0.15	0.32
LA						0.27	0.29
SLA							-0.12

Table 3. AICc model selection statistics and proposed predicting models for the osmotic potential at full turgor (π_o), considering the physiological traits minimum seasonal water potential (Ψ_w) and stomatal conductance (g_s), and the morpho-anatomical traits leaf area (LA), specific leaf area (SLA), leaf thickness (LT), wood density (WD), and wood water saturated content (WC_{sat}). Values of the Akaike information criterion (AICc), the AICc accumulated change (Δ_{AICc}), the root mean squared error (RMSE), the error rate for each model (% error) and the R^2 associated to each model are presented. AICc weights are the relative likelihood of each model: the bigger the Delta AICc (Δ_{AICc}), the smaller the weight and the less plausible the model. The full list of models is presented in supporting material Table S2.

Model	AICc	Δ_{AICc}	AICcWt	RMSE	% error	R^2
$\Psi_w + WC_{sat}$	-164.57	0.00	0.3310	0.134	0.178	0.301
$\Psi_w + LA + WC_{sat}$	-163.91	0.66	0.2378	0.135	0.179	0.299
$\Psi_w + LA + WD$	-161.58	2.99	0.0742	0.135	0.180	0.290

$\Psi_w + \text{WD}$	-161.49	3.08	0.0711	0.135	0.180	0.284
$\Psi_w + \text{LA} + \text{SLA}$	-161.41	3.15	0.0684	0.135	0.179	0.289
$\Psi_w + \text{LA}$	-161.10	3.47	0.0585	0.135	0.180	0.282
$\Psi_w + \text{LT}$	-160.48	4.08	0.0430	0.135	0.180	0.278
$\Psi_w + \text{LA} + \text{LT}$	-160.38	4.19	0.0408	0.135	0.180	0.284
Ψ_w	-159.81	4.76	0.0306	0.136	0.181	0.269
$\Psi_w + \text{LA} + g_s$	-159.07	5.50	0.0212	0.137	0.183	0.277

Figure 1. Correlation between the osmotic potential at full turgor (π_0) and leaf area (LA), specific leaf area (SLA), leaf thickness (LT), wood density (WD), wood saturated water content (WC_{sat}), stomatal conductance (g_s) and minimum seasonal water potential (Ψ_w). Points represent averages with standard deviations for 14 trees and shrubs species native from New Zealand.

Figure 2. Graphical representations of the model $\Psi_w + WC_{sat}$ (minimum seasonal water potential + wood water saturated content) to predict the osmotic potential at full turgor (π_o).

Figure 3. Averages and standard deviation of the osmotic potential at full turgor (π_0), osmotic potential (Ψ_π), minimum seasonal water potential (Ψ_w), stomatal conductance (g_s), leaf area (LA), specific leaf area (SLA), leaf thickness (LT), leaf relative water content (LRWC), wood density (WD), and wood saturated water content (WC_{sat}) for 14 trees and shrubs species native from New Zealand.

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