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ORIGINAL ARTICLE

Genetic variation in *Eucalyptus viminalis* Labill. is limited for drought resistance traits but varies for lignotubers

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Abstract

Key message **Drought and fire stress acted independently in shaping the evolution of a widespread eucalypt species.**

Abstract The mixing of local and non-local seed sources (e.g., climate-adjusted provenancing) for revegetating damaged or degraded ecosystems assumes that the non-local genotypes growing in future climates will harbour genetic variation in traits important for maintaining fitness in drier/hotter environments, but this is rarely validated. To determine the extent to which genetic variation in traits associated with drought and recovery covaries with provenance homesite climate, we sampled multiple provenances of *E. viminalis*, collected from a precipitation gradient and grown in a common garden trial. We hypothesised that provenances from increasingly drier homesite environments will show greater resistance to failure of the hydraulic system and greater resource allocation to recovery traits, compared to provenances from wetter homesite environments. Contrary to expectation, we found no significant difference among provenances for drought traits and carbon resource allocation along the rainfall gradient. Mean xylem cavitation resistance (P50) and turgor loss point (TLP) in leaves did not differ significantly among provenances. However, we did find significant genetic-based variation in the recovery trait (relative lignotuber size) that was associated with the provenance homesite climate, and this trait was also independent of any of the drought traits studied. Relative lignotuber size was larger in individuals from increasingly arid provenances, consistent with selection favouring greater investment in recovery traits in environments where canopy loss is frequent, potentially due to disturbance such as fire or severe drought. These results suggest that recovery traits may represent a stronger or more consistent axis of selection than drought resistance traits in this species.

Keywords Climate-adjusted provenancing · Drought adaptation · Xylem vulnerability · Leaf traits

Introduction

Rapid climate change is causing species distribution contraction and extinction, along with shifts in community composition. Plants are highly susceptible to increasing temperatures and decreasing water availability, and trees, in particular, are impacted significantly by climate change-related mortality (Bauman et al. 2022; Brodribb et al. 2020; De Kauwe et al. 2020; Hartmann et al. 2022). The chances of tree species survival will not only depend on the severity of climate change but also on the extent to which species can respond and adapt to new and changing conditions, but the rate of adaptation might be too slow compared to the velocity of climate change. Rising temperatures and increased frequency and duration of droughts are likely to have a bigger impact on fragmented vegetation due to the stochastic erosion of genetic variation, gene flow limitations, and inbreeding, increasing the risk of tree populations becoming locally extirpated (Aitken et al. 2008).

Genetic variation can result from adaptation to local conditions and one way to explore it is through the study of plant traits that convey functions that impact plant fitness by effects on growth, reproduction, and survival (Diaz et al. 2016; Violle et al. 2007). Traits can be used to compare

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different plant species from the same environment to understand adaptation (Adler et al. 2014; Prober et al. 2022; Skelton et al. 2021), drought resistance (Bartlett et al. 2012a) and competition (Petruzzellis et al. 2019a), trade-offs (Maynard et al. 2022; Petruzzellis et al. 2021), plasticity and genetic variation (Pritzkow et al. 2020). However, given the high number of traits that can be measured in plants (Perez-Harguindeguy et al. 2016), it is crucial to select a subset of traits that can provide as precise and complete information possible about plant function and adaptation, while also being relatively fast to measure. Among these, trait syndromes that provide information about resource investment and allocation (LMA, C content for example), are useful to generalise leaf economy along environmental gradients (Dong et al. 2020; Wright et al. 2004). However, when looking for clear and causal information about specific plant functions, traits that are directly connected to processes causing plant damage may provide particular insights (Brodribb 2017). For example, hydraulic traits like P50, the water potential corresponding to the loss of 50% xylem water transport capacity, provide information about the plant resistance to drought by quantifying plant organ resistance to embolism which sets limits to species distribution (Blackman et al. 2014; Brodribb and Hill 1999; Choat et al. 2012; Hartill et al. 2023; Larter et al. 2017; Nardini and Luglio 2014). At the same time, the turgor loss point (TLP) is correlated with species distribution and tolerance to drought (Bartlett et al. 2012b; Martin et al. 2024; Zhu et al. 2018). The consideration of mechanistic traits such as P50 or TLP, thus clearly inform species climatic preferences and can be used to select provenances that are genetically better suited for future climatic conditions. At the same time, trait syndromes are also useful to have bigger pictures of plant adaptation and evolution to the environment. For example, leaf traits can provide information about trade-offs existing in carbon resource allocation (Dong et al. 2020; Maynard et al. 2022; Wright et al. 2004) and leaf mechanical properties (John et al. 2017).

Plant traits can therefore be used to explore and characterize the genetic variation present at the species level and be applied to protect, conserve, and restore those trees that have been particularly endangered by climatic change. In particular, restoration is a mitigation strategy to stem the loss of biodiversity and return the services and functions that humans rely on, and traditionally the recovery of degraded and damaged ecosystems has followed a local-only approach to maintain local adaptations that maximised fitness, as well as maintaining the evolutionary history and interactions (Breed et al. 2013; Hufford et al. 2016). However, climate change is beginning to outpace local adaptations and there is growing momentum to mix local seed sources with non-local seed sources through genetic rescue strategies, such as climate-adjusted provenancing. This assumes populations already growing in future climates to have traits that confer a fitness advantage (e.g., have greater physiological resilience or avoidance given selective pressures) (Harrison et al. 2017; Prober et al. 2015; Ramalho et al. 2017). However, of particular importance is determining how to select those provenances that display adaptation to the predicted environment (Petrík et al. 2022). Provenances in the warmer and drier end of the species distribution should be adapted to the warmer and drier conditions of the future and therefore display trait value in accordance. Thus, plant traits may provide an opportunity to screen for resistance in seedlings.

The studies conducted so far mostly consider leaf economic traits (Costa e Silva et al. 2021; Prober et al. 2016; Walters et al. 2005), while few also considered hydraulic traits (Lucani et al. 2019; Pritzkow et al. 2020). Furthermore, studies reported none (Lobo et al. 2018) or very limited differences among populations (Lucani et al. 2019; Pritzkow et al. 2020).

To explore genetic variation in leaf and hydraulic traits, we chose the tree species manna gum (*Eucalyptus viminalis* Labill.) which has been largely impacted by drought in the last years in Australia (Ross and Brack 2015), raising concern for the future of this ecologically important species. We also consider the belowground lignotubers, given the key role lignotubers play in eucalypts as reserve organs for resprouting and recovery of the main stem in the event it suffers major damage by fire or drought (Zimmer et al. 2021). In this study, we analysed traits associated with drought and recovery of seedlings from six provenances grown in a common garden. We hypothesised that provenances originating from the sites characterised by lower rainfall would have a higher drought resistance while provenances from the wet end had a lower drought resistance and lower leaf carbon allocation. We also hypothesized that provenances from the drier sites would also exhibit greater investment in lignotubers, resulting from a higher fire incidence. This paper studies the correlations between traits and climate in plants grown in a common garden to seek evidence of genetic adaptation in putative function traits associated with drought or fire.

Materials and methods

Plant material

Six provenances of *E. viminalis* distributed along a precipitation gradient (MAP, mean annual precipitation) were sampled in a common garden over the austral spring and summer of 2019. Seeds were collected from 11 open-pollinated families around Tasmania, Australia. *E. viminalis* is

widespread in Tasmania (and mainland Australia), and can be found from 600 m to the sea level (Williams and Potts 1996), and generally forms open and tall forests (up to 90 m height) (Ladiges and Ashton 1977).

Seeds were germinated in a nursery and seedling plugs were grown in 3 L pots filled with potting mix consisting of an 8:4 mixture of composted pine bark and coarse-washed river sand, in a glasshouse facility at the University of Tasmania from January to February 2020. Plants were watered twice daily at field capacity and experienced natural light conditions and an average day and night temperature of 23 °C and 18 °C, respectively. After two months the plants were moved outside into a common garden at the University, still growing in the same pots, where they were watered twice daily (at field capacity). During this study the pots were arranged in a randomised block designed to unify any micro-environmental gradient within the common garden.

Lignotubers ratio was measured once plants were 3 months of age while the physiological measurements and lignotuber number were taken once the seedlings had reached six months of age (ca. 140 cm tall).

Plant traits

To determine differences between provenances, we selected a suite of plant traits that give information about drought resistance turgor loss point, TLP and 50% loss in leaf water transport capacity, P50), leaf economy (leaf dry matter content, LDMC and leaf mass per area, LMA), resource allocation (root density and stem diameter) and vegetative recovery (lignotuber ratio and lignotuber number).

Drought resistance traits

To investigate differences in leaf drought resistance in different provenances of *E. viminalis* we measured leaf turgor loss point (TLP) and 50% loss in leaf water transport capacity (P50) in five individuals per provenances (total 30 individuals).

We measured TLP using the osmometer method (Bartlett et al. 2012a; Petruzzellis et al. 2019b). Juvenile trees were sampled early in the morning (7 am) to ensure that plants were hydrated. Five leaf discs per individual were obtained with punching pliers and discs were immediately wrapped in aluminium foil and immersed in liquid nitrogen for 30 s, before being punctured with fine forceps to rupture cell membranes and release the sap. The leaf discs were then stored in a plastic bag at -20 °C until measurements were performed. The osmotic potential (π_0) was measured with a psychrometer and then corrected according to Bartlett et al. (2012a) with the modification from Petruzzellis et al. (2019b), using the equation:

$$\pi_0 = (0.5303 \times \pi_{psy}) + (0.0019 \times LDMC) - 0.001306.$$

where π_{psy} is the raw value obtained with the psychrometer and LDMC (Leaf Dry Matter Content, mg g^{-1}) was calculated as leaf dry weight/ leaf turgid weight.

TLP was derived from the previous equation and estimated following Petruzzellis et al. (2019b):

$$TLP = (1.31 \times \pi_0) - 0.03.$$

Leaf vulnerability to cavitation was measured with the Optical Vulnerability Technique (Brodribb et al. 2016) while stem water potential (Ψ_{stem}) was monitored during dehydration. A psychrometer (ICT Armidale, NSW, Australia) was installed 50 cm above the root collar by gently removing part of the bark and washing the surface with distilled water. Once the psychrometer sensor was attached, it was sealed with parafilm and Ψ_{stem} logged every 10 min. The accuracy of water potential measurements was double-checked with a Scholander pressure chamber, twice a day.

Before dehydration, the roots of fully hydrated *E. viminalis* seedlings were gently rinsed in water to remove all the soil to ensure that dehydration to the point of leaf death occurred within ca. 5 days. Plants were then transferred to the laboratory where the average temperature and relative humidity were 23 °C and 35%, respectively.

Plants were then allowed to dehydrate until the leaves became visibly damaged (i.e. discoloured and desiccated). To capture the temporal and spatial pattern of cavitation spread in the leaf, we used custom-built cameras (Cavicam, Hobart, Tasmania) that were attached to the distal quarter of the leaf, covering an area of ca. 1 cm^2. Images were captured during dehydration every five minutes until no cavitation was recorded for at list 12 h. Image sequences were then analysed to quantify differences in light transmission caused by xylem cavitation using image subtraction in IMAGEJ (for details, see Brodribb et al. 2016 and www.opensourceov.org). Combining data from the dynamics of declining water potential with cavitation data for each leaf enabled the accumulation of cavitation events to be plotted as a function of Ψ_{stem}. A cumulative projection of all the threshold images produced a map of all embolism events.

Resource allocation and leaf economy traits

Leaf Mass per Area (LMA) was calculated as Leaf dry weight/Leaf area from five fresh leaves for each individual. Leaves were scanned with a flatbed scanner and leaf area

was measured with IMAGEJ (National Institutes of Health, Bethesda, MD, USA). Leaves were then dried at 70 °C for 48 h and leaf dry weight was measured with an analytical balance (±0.0001 g, model MS204S; Mettler Toledo, Columbus, OH, USA). Leaf Dry Matter Content (LDMC) was determined as explained above for TLP determination.

Root dry weight was determined once the plants were completely dehydrated and cavitated by cutting at the root collar and roots were dehydrated in an oven for 48 h at 70 °C, after which the weight was taken with an analytical balance.

The stem diameter was measured with a calliper at the plant base just above the lignotubers.

Lignotuber traits

Lignotuber width was measured as the diameter (mm) across the lignotubers developed in the axils of the cotyledons, while the lignotuber ratio was expressed as mean lignotubers width divided by stem diameter (measure at the base of each individual). The maximum number of lignotubers was counted at the end of the dehydration experiment before removing the roots.

Statistical analysis

Data were analysed using R version 3.6.2 (R Core Team, 2016). To test for associations between traits and climate of origin, we fitted linear models with mean annual precipitation (MAP) as a continuous predictor. These models were used to evaluate whether trait variation followed a precipitation gradient across provenance origins. Seedlings originated from open-pollinated families nested within provenances; however, due to the labour-intensive nature of physiological measurements, each family was represented by a single individual. As a consequence, family-level variance could not be estimated, and mixed-effects models including family as a random effect resulted in singular fits. Individuals were therefore treated as independent genetic samples, and linear models were retained for all analyses.

Results

Traits variation along the rainfall gradient

To determine whether the provenances of *E. viminalis* displayed any difference in drought adaptation, we first analysed drought related traits, such as P50 and TLP (Fig. 1). Neither P50 nor TLP were related to MAP (P50: $R^2=0.03$, p-value=0.21; TLP: $R^2=0.02$, p-value=0.21). The provenance from the driest site ("Swansea") had a mean P50 of -3.58±0.22 MPa and mean TLP of -2.12±0.11 MPa. Whereas the provenance from the wettest site ("Liffey") had a mean P50 of -3.42±0.31 MPa and a mean TLP of -2.02±0.08 MPa. When we considered traits related to carbon investment (i.e., LDMC, LMA, stem width and root dry weight; Fig. 2), we did not find any relationship with the climate of origin (LDMC: $R^2=0.03$, p-value=0.68; LMA: $R^2\approx0$, p-value=0.91; stem width: $R^2=0.05$, p-value=0.13; root DW: $R^2=-0.03$, p-value=0.59). For example, leaves sampled off plants from the driest provenance were only 0.59% thicker than the ones from the wettest site.

By contrast, traits related to vegetative recovery showed correlation with climate of origin (ligno ratio: $F_{1,28}=20.03$, $R^2=0.39$, p-value<0.001). Mean provenance lignotuber ratio changed along the rainfall gradient (Fig. 3A). In particular, provenances from drier sites had higher lignotuber ratio compared to those populations from wetter sites. The driest population ('Swansea") had the highest lignotuber ratio (0.96±0.17) while the wettest population had the lowest (0.24±0.21). Lignotuber number was not related to MAP (ligno num: $R^2=0.02$, p-value=0.23) but differed significantly among provenances ($R^2=0.38$, p-value=0.01; Fig. 3B).

Discussion

Genetic variation in leaf traits

The six provenances of *E. viminalis* originating from a broad rainfall gradient in Tasmania showed no genetic variation in traits related to drought resistance and leaf carbon resource allocation. However, we found significant differences in traits related to the ability to vegetatively recover after fire and drought stress (lignotubers).

In particular, provenances from drier sites did not show evidence of trait adaptations associated with higher drought tolerance (TLP and P50) (Bartlett et al. 2014; Nardini and Luglio 2014). Turgor loss point is a powerful mechanistic trait that is often used to understand variation and predict plant response to different environments. Many studies have identified low (more negative) TLP as an indicator of water stress as cells can withstand lower water potential during dehydration before losing their turgor and therefore sustaining leaf functions for longer (Bartlett et al. 2014; Maréchaux et al. 2015; Zhu et al. 2018). Thus, lower values of TLP are associated with species adapted to arid environments (Hannus et al. 2021).

P50 is also another trait often used to compare the drought tolerance of different species growing in diverse environments (Blackman et al. 2014; Larter et al. 2017). P50 is a

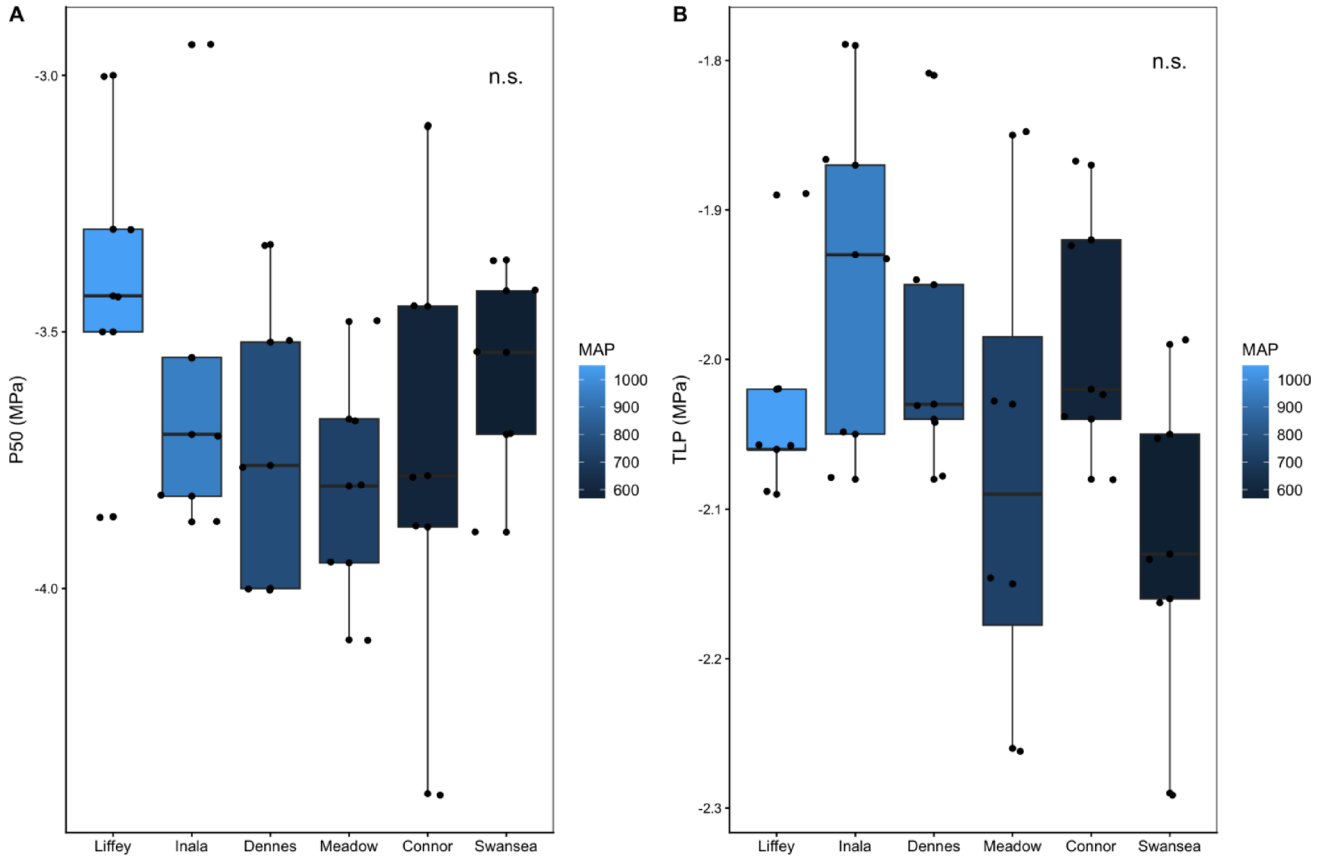


Fig. 1 Distribution of drought resistance traits across *Eucalyptus viminalis* provenances. Boxplots show (**A**) 50 % loss in leaf water transport capacity xylem cavitation resistance (P50) and (**B**) turgor loss point (TLP) for juvenile plants originating from six provenances. Box colours indicate mean annual precipitation (MAP) at provenance origin (mm). Neither trait was related to MAP (all $p > 0.05$; n.s.)

highly adaptive trait correlated with the capacity of plant tissues to withstand xylem embolism formation. Contrasting results show that P50 can either change between provenances (Kavanagh et al. 1999; Lucani et al. 2019; Pritzkow et al. 2020; Schuldt et al. 2016) or not (Lamy et al. 2014; Li et al. 2019), especially when growing in a common garden (Skelton et al. 2019; Torres-Ruiz et al. 2019; Wortemann et al. 2011). This is possibly due to either high gene flow between populations (Skelton et al. 2019) or intraspecific variation and plasticity (Torres-Ruiz et al. 2019). In case of *E. viminalis*, there is a low level of genetic differentiation (data unpublished), suggesting that gene flow might be diluting local adaptations. We here have not focused on the plasticity of the different provenances and a reciprocal common garden will be needed to investigate this important aspect further (Bailey et al. 2021).

At the same time, we did not find any trend along the precipitation gradient for the carbon allocation traits. Provenances from the drier sites did not display tougher leaves (higher LMA and LDMC), and neither did those from the wetter sites have bigger stems (Fig. 2). Often trees from drier populations have smaller leaves (Nardini 2022; Salazar et al. 2018; Torres-Ruiz et al. 2019; Wright et al. 2004), and lower values of LMA are typically a syndrome of other traits, such as leaf thickness, leaf density and vein density (Nardini 2022).

Eucalypt species have been reported to follow the global pattern of trait covariation (mostly carbon allocation traits) along rainfall gradients, reflecting long-term environmental adaptation (Blackman et al. 2024; Bourne et al. 2017; Hartill et al. 2023; Li et al. 2018; Lucani et al. 2019; Merchant et al. 2007) and previous works have highlighted that eucalypts have a high level of intra-specific variation according to carbohydrate reserves and resprouting ability (Walters et al. 2005). However, other studies report very few differences among provenances, for example in *E. camaldulensis* (Asao et al. 2020). Interestingly, results from Pritzkow et al. (2020) also confirmed what is shown here: despite climate associated trait variation in the field, provenances grown in a common garden did not show differences in drought tolerance. Previous work on *E. viminalis* has highlighted differences between provenances in tree height (Ladiges and Ashton 1974), however, relative water content (RWC) and

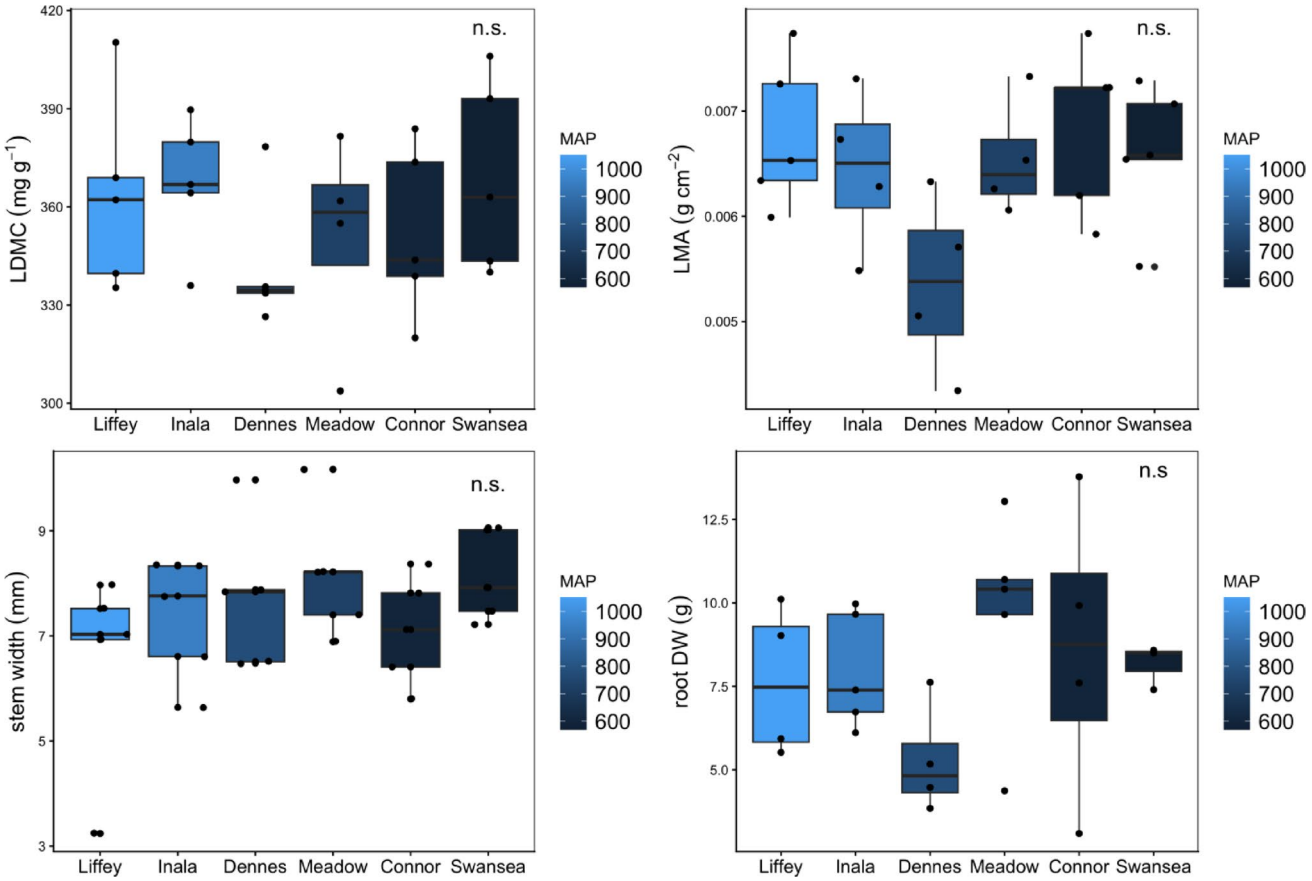


Fig. 2 Variation in leaf economic and growth traits among juvenile *Eucalyptus viminalis* provenances. Boxplots show (**A**) leaf dry matter content (LDMC), (**B**) leaf mass per area (LMA), (**C**) stem diameter, and (**D**) root dry weight. Box colours correspond to mean annual precipitation (MAP) at provenance origin (mm). None of these traits were related to MAP (all $p > 0.05$)

osmotic potential (π_0) were found not to differ between populations (Ladiges 1975).

Another important aspect highlighted by these results is the large variability that presently exists within populations, where the variation among individuals within a population is larger than the one existing among provenances (Lobo et al. 2018).

Genetic variation in fire recovery-related traits

An important consideration when viewing the evolution of *Eucalyptus* in the Australian landscape is that drought may not be the predominant selective pressure-driving adaptation. Fire also represents a key element in the Australian landscape (Bowman 1998; Press 1988; Yibarbuk et al. 2001). One of the traits that best highlights this evolutionary history are lignotubers, which can vary significantly among provenances, especially in seedlings (Noble 2001), and have been linked with greater survival chances to fire and drought stress. Lignotubers are reserve organs that allow plants, in particular eucalypts, to resprout rapidly after fire and/or drought damage (Ammitzboll et al. 2020; Costa e Silva et al. 2021). Indeed, we found the lignotuber ratio to be strongly and inversely correlated with the provenance mean annual rainfall, consistent with other eucalypt studies (Gauli et al. 2015; Harrison 2017; Prober et al. 2016). Genetic variation in lignotuber size has also been previously reported for other species of eucalypts, such as *E. obliqua* (Walters et al. 2005), E. *pauciflora* (Costa e Silva et al. 2021), E. *globulus* (Whittock et al. 2003).

Surprisingly, we did not find any trade-off between lignotubers and carbon allocation traits (LDMC, LMA, stem diameter and root dry weight). Contrary to what was shown by Costa e Silva et al. (2021), provenances from the wetter sites which displayed smaller lignotuber and lower lignotuber ratios did not show differences in LMA, compared to the provenances from the drier sites (Figs. 2 and 3).

Here we show that the genetic variation in fire-related traits suggests a more important role in the evolutionary response in *E. viminalis* than drought-related traits, and specifically that lignotuber development and thus the capacity for vegetative recovery is independent from drought adaptation, as also found in *E. globulus* (Ammitzboll et al. 2020). Wildfire has been shown to change the genetic structure of

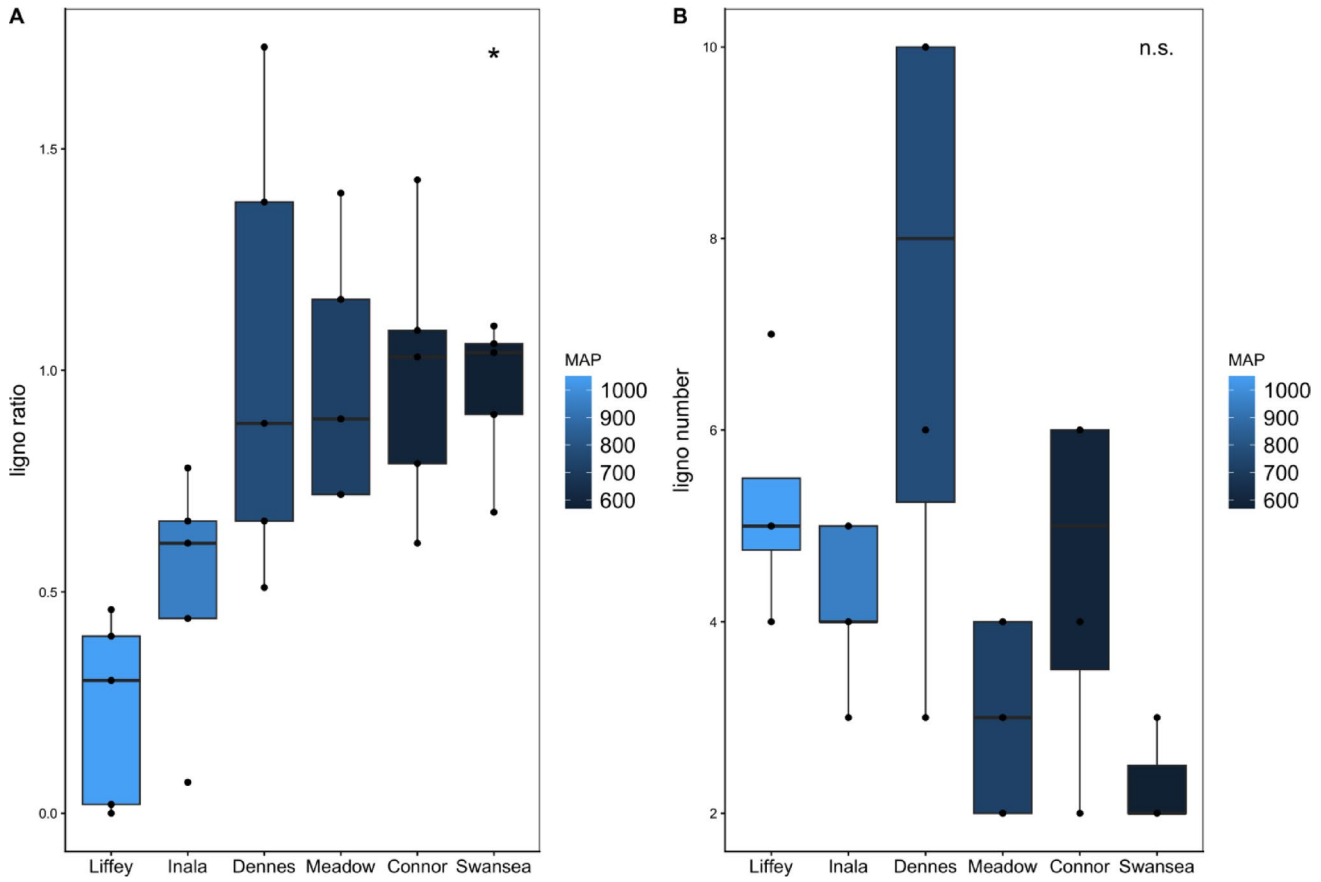


Fig. 3 Variation in vegetative recovery traits among juvenile *Eucalyptus viminalis* provenances. Boxplots show (**A**) lignotuber ratio and (**B**) lignotuber number. Box colours correspond to mean annual precipitation (MAP) at provenance origin (mm). Lignotuber ratio decreased significantly with increasing MAP ($p<0.05$), while lignotuber number was not related to MAP (n.s.), but differed significantly among provenances

trees community and favour those with enhanced recovery ability (Hernández et al. 2022). Lignotubers could therefore provide a mechanism for resprouting after a drought event when plants have sustained loss of canopy.

Conclusions

This work highlighted that for *E. viminalis* in Tasmania, leaf traits might be under genetic control, given the large variability existing in the species. These results suggest that recovery traits related to resprouting may have been subject to stronger or more consistent selection than drought resistance traits in this species, potentially reflecting the importance of disturbance-related processes such as fire. Lignotubers can favour resprouting after drought damage, but the lack of adaptation to drought conditions raises concerns for the future distribution of this species that might contract with climatic changes. This study provides an important look at trait syndromes, however further work is needed to understand if the adult populations are showing the same behaviour and if limited genetic variation in physiological traits is common in the *Eucalyptus* genus. At the same time, this study only tested genetic variation in well-watered conditions while it would also be informative to investigate the response of provenances grown under drought conditions (e.g., a dry-down manipulative study). Moreover, this study was limited to assess the influence of MAP which captures long-term water supply but does not account for VPD or fire, which should be included in further studies. We also acknowledge that root binding, due to the limited pot size, may influence later biomass allocation and growth-related traits; future studies using field-grown plants will be important to further disentangle developmental plasticity from genetic differentiation in recovery traits.

The information here presented paves the road to inform reforestation policy and at the same time broaden our understanding of populations response to climate change. In this paper we show that despite drought and fire being linked, they acted independently in shaping the evolutive history *E. viminalis*.

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Author contributions VT, TB and PH designed the experiment, VT collected the data, VT performed the analysis, VT wrote the manuscript with revisions from all the co-authors.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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