New Phytologist

Canopy damage during a natural drought depends on species identity, physiology and stand composition

Travis G. Britton[1,2], **Timothy J. Brodribb**[1], **Shane A. Richards**[3], **Chantelle Ridley**[1] and **Mark J. Hovenden**[1,2]

[1]Biological Sciences, School of Natural Sciences, University of Tasmania, Hobart, Tas. 7001, Australia; [2]ARC Training Centre for Forest Value, University of Tasmania, Hobart, Tas. 7001, Australia; [3]School of Natural Sciences, University of Tasmania, Hobart, Tas. 7001, Australia

Author for correspondence:
Travis G. Britton
Email: travis.britton@utas.edu.au

Received: *28 September 2021*
Accepted: *21 November 2021*

New Phytologist (2022) **233:** 2058–2070
doi: 10.1111/nph.17888

Key words: canopy damage, cavitation, competition, density, drought, forest dieback, mortality, tree size.

Summary

- Vulnerability to xylem cavitation is a strong predictor of drought-induced damage in forest communities. However, biotic features of the community itself can influence water availability at the individual tree-level, thereby modifying patterns of drought damage.
- Using an experimental forest in Tasmania, Australia, we determined the vulnerability to cavitation (leaf P_{50}) of four tree species and assessed the drought-induced canopy damage of 2944 6-yr-old trees after an extreme natural drought episode. We examined how individual damage was related to their size and the density and species identity of neighbouring trees.
- The two co-occurring dominant tree species, *Eucalyptus delegatensis* and *Eucalyptus regnans*, were the most vulnerable to drought-induced xylem cavitation and both species suffered significantly greater damage than neighbouring, subdominant species *Pomaderris apetala* and *Acacia dealbata*. While the two eucalypts had similar leaf P_{50} values, *E. delegatensis* suffered significantly greater damage, which was strongly related to the density of neighbouring *P. apetala*. Damage in *E. regnans* was less impacted by neighbouring plants and smaller trees of both eucalypts sustained significantly more damage than larger trees.
- Our findings demonstrate that natural drought damage is influenced by individual plant physiology as well as the composition, physiology and density of the surrounding stand.

Introduction

Increased drought frequency and severity as a result of anthropogenic climate change (Trenberth *et al.*, 2014) can alter tree growth and in extreme cases, cause widespread mortality (Choat *et al.*, 2012; Brodribb *et al.*, 2020). Drought-induced mortality is already well documented in forests globally (Phillips *et al.*, 2009; Millar & Stephenson, 2015; Young *et al.*, 2017; Meakem *et al.*, 2018; Fettig *et al.*, 2019; Powers *et al.*, 2020) and is widely thought to be driven by hydraulic failure of the water transport system (Adams *et al.*, 2017). Physiological characteristics of the plant hydraulic system have been incorporated into models to predict which species, forest types or regions are the most vulnerable to future drought (Anderegg *et al.*, 2015; Martin-StPaul *et al.*, 2017). However, this approach has focussed on individual trees in isolation of the communities in which they persist (Clark *et al.*, 2016). Interactions between neighbouring trees are a critical component of community dynamics and may modify the direct effects of drought (Fichtner *et al.*, 2020). Understanding how neighbours modulate drought-induced mortality is needed to accurately predict how forest systems will be affected by future climate conditions.

The point at which water stress causes tree death is controlled by physiological characteristics of the plant, namely the water transport system and its vulnerability to drought-induced damage (Choat *et al.*, 2018). Tension in the water column increases with water stress causing cavitation, in which gas bubbles (emboli) form in xylem conduits that progressively block water flow and restrict water supply to leaves (Tyree & Sperry, 1989). Functional impairment increases with embolism, ultimately killing the tree if water transport is sufficiently inhibited. Xylem vulnerability to embolism varies widely among species and is a key indicator of their ability to survive sustained drought (Brodribb & Cochard, 2009; Kursar *et al.*, 2009). Hydraulic traits describing xylem vulnerability, such as the water potential causing a 50% loss in conductivity (P_{50}) and hydraulic safety margins, have previously explained mortality patterns during natural drought (Anderegg *et al.*, 2016; Powers *et al.*, 2020). Anderegg *et al.* (2016) and Powers *et al.* (2020) highlighted the importance of physiology in determining species mortality risk to drought, but their studies indicated that substantial variation in mortality rates remains unexplained (*c.* 40–70%) when considering physiology alone. This suggests that other factors are also important in determining which trees suffer during drought, such as the effect of co-occurring neighbours on soil water availability. Differences in xylem vulnerability, stomatal behaviour and root characteristics are likely to produce local variation in soil drying within a forest community (Tardieu & Simonneau, 1998; Klein, 2014). Plants

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

with cavitation resistant xylem are typically anisohydric, meaning that they will continue to lose water for longer into a drought period than those with less resistant xylem. Assuming a degree of root overlap between neighbours (Manoli *et al.*, 2014), vulnerable plants that limit water use to preserve hydraulic function may still experience a strong reduction in soil moisture content by neighbours with more resistant xylem. Increased water stress within the rooting zone can potentially lead to embolism-inducing soil water potentials for more vulnerable plants. Therefore, in forest communities, the severity of the water deficit and the rate at which it will occur should not be dependent on the abiotic environment alone, but also on the composition, physiology and density of the surrounding stand.

Forest stands vary widely in the identity and density of trees they contain. During drought, greater competition for water in high density stands can increase the probability of mortality (Dwyer *et al.*, 2010; Young *et al.*, 2017). The composition of those stands – the identity of neighbours – also influences the strength of competition. Plants have historically been assumed to compete more intensely with conspecific than with heterospecific neighbours due to greater niche overlap (MacArthur & Levins, 1967). Conspecific density effects have decreased survival in many forest systems (Dwyer *et al.*, 2010; Piao *et al.*, 2013; Johnson *et al.*, 2017). Heterospecific density effects on survival have also been documented, albeit less commonly (Zhu *et al.*, 2018). When heterospecific densities are included, they are rarely partitioned into species-specific densities meaning that the strength of their impact, due to differing physiology and ecology, cannot be explored.

Drought susceptibility can be influenced by individual tree size. Numerous studies have linked tree size with drought susceptibility with mixed findings of whether small or large trees are most at risk during drought (Nepstad *et al.*, 2007; Phillips *et al.*, 2010; Peng *et al.*, 2011; Bennett *et al.*, 2015; Fajardo *et al.*, 2018; Brun *et al.*, 2020; Nolan *et al.*, 2021). Size-dependent drought susceptibility can be a result of variation among different size trees in embolism vulnerability (Ambrose *et al.*, 2018), rooting depth (i.e. soil water access; Giardina *et al.*, 2018) or severity of biotic agent attack (Stephenson *et al.*, 2019). However, much of the evidence linking tree size with drought susceptibility in the field is observed in mature forests with little attention paid to small, young trees such as seedlings and saplings (McDowell *et al.*, 2013). While differences in drought tolerance have previously been assessed between juvenile and mature trees (Domec & Gartner, 2001; Rice *et al.*, 2004), studies assessing size-dependent differences among single-age saplings in the field are rare. Single-age forests are common following both natural and managed disturbance and it is therefore necessary to determine which size classes are the most susceptible to drought in these systems and whether such relationships are consistent with that of mature, multi-age forests.

Here, we explore canopy foliage damage in four co-occurring species following a significant drought in the 2018/2019 austral summer. The summer was the hottest on record for south-eastern Tasmania (Bureau of Meteorology, 2020) and included the driest January on record at the closest weather station (Bushy Park, Tasmania; *c.* 10 km from the study site). The study was conducted in the Australian Forest Evenness Experiment (AFEX; Gerwin *et al.*, 2020); an experimental forest in south-east Tasmania, Australia, 6 yr old at the time of the study. The AFEX consists of four species, *Eucalyptus regnans*, *Eucalyptus delegatensis*, *Pomaderris apetala* and *Acacia dealbata*, sown experimentally to create a range of community compositions over a small geographical area where, unlike in natural systems, abiotic factors such as rainfall do not vary substantially. Therefore, the AFEX provides a rare opportunity to explore how the effects of a natural drought event are simultaneously influenced by both physiological (vulnerability to cavitation) and ecological (stand composition) processes. We first explored how drought-induced canopy damage correlated with species' vulnerability to cavitation and, secondly, if neighbour species and density, and tree size influenced the severity of damage within species. Specifically, we posed the following questions:

(**1**) Does natural drought damage correlate with species' vulnerability to cavitation?

(**2**) How does the density and identity of neighbours impact drought damage?

(**3**) Is drought damage size-dependent in the early stages of stand regeneration?

We hypothesised that (1) species that are most vulnerable to cavitation will experience the highest levels of damage; (2) the degree of damage will be exacerbated in trees co-occurring with a high density of neighbours with more resistant xylem; and (3) smaller trees will suffer the most damage.

Materials and Methods

Study site and species

The AFEX (Gerwin *et al.*, 2020) occupies a 5 ha site in the Styx Valley, southern Tasmania (42°46′49″S, 146°49′01″E; Fig. 1) at an altitude of 530–590 m above sea-level on a north-west facing slope. The site receives 984 mm average rainfall annually with mean minimum and maximum temperatures of 3.28°C and 13.18°C, respectively. The AFEX is surrounded by production eucalypt forest and *Pinus radiata* plantations and, before establishment, was a native forest dominated by *E. delegatensis* and *E. regnans*. In April 2013, the site was burnt in a high intensity regeneration fire following clear-felling, resulting in complete removal of all pre-existing vegetation.

At 2 d after the regeneration burn, locally sourced seeds of four native tree species (*E. delegatensis* R.T.Baker, *E. regnans* F.Muell., *Acacia dealbata* Link and *Pomaderris apetala* Labill.) were hand sown to create an orthogonal evenness × species design of five evenness levels for each species, creating 20 treatments replicated four times across eighty 25 × 25 m plots (Supporting Information Table S1). The four species are common in wet sclerophyll forest and locally abundant. *Eucalyptus regnans* and *E. delegatensis* are fast-growing, light-dependent dominant tree species reaching mature heights up to 100 m (Hickey *et al.*, 2000). The two eucalypts are closely related, belong to the *Monocalyptus* subgenus (Williams & Potts, 1996) and occur as co-dominants in

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

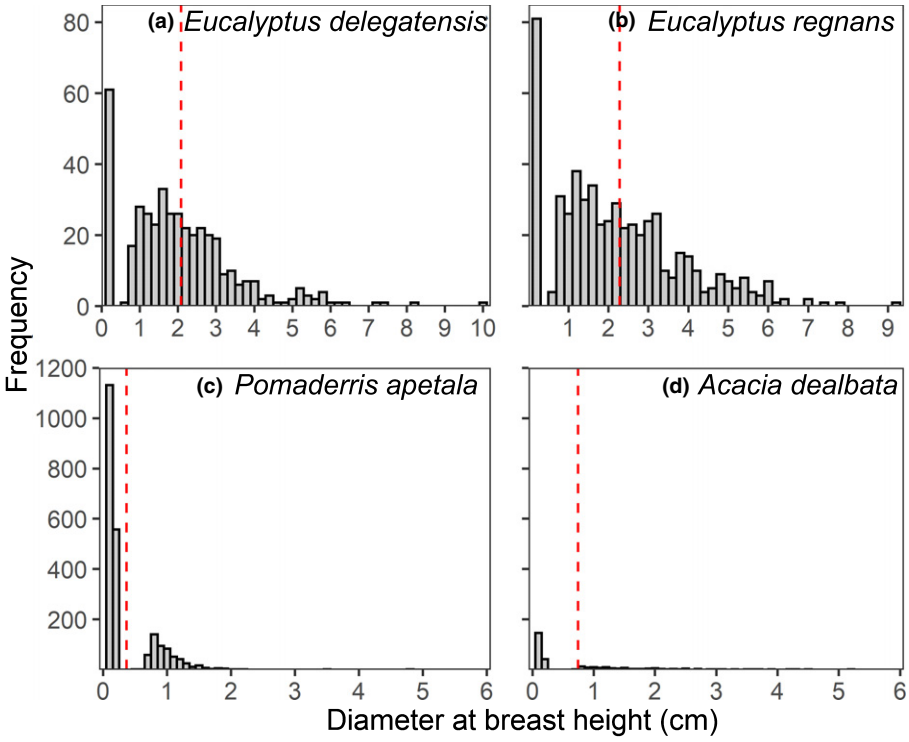


Fig. 1 Size–frequency distributions in diameter at breast height (DBH; cm) of the four species in the Australian Forest Evenness Experiment (AFEX): (a) *Eucalyptus delegatensis*, (b) *Eucalyptus regnans*, (c) *Pomaderris apetala* and (d) *Acacia dealbata*. The red, vertical dashed line shows the mean size for each species. Treatment-specific size distributions are provided in Supporting Information Figs S1, S2.

surrounding native forest. *Acacia dealbata* and *P. apetala* are nitrogen fixing, moderately shade-tolerant, subcanopy tree species reaching mature heights of 30 and 15 m, respectively (Walsh & Entwisle, 1999; Maslin, 2001).

To initiate germination before sowing, *P. apetala* seeds were heated to 120°C for 10 min and *A. dealbata* seeds were steeped in boiling water for 15 min and then rinsed. Eucalypt seeds were not pretreated before sowing due to already high germination rates. Seeds were sown at a target community density of 20 potential germinants m^{-2} but some variation exists between the realised and sown composition of each treatment (Table S1; Gerwin *et al.*, 2020). *Acacia dealbata* is under-represented due to lower-than-expected germination success and severe browsing of seedlings in the first year. *Pomaderris apetala* is over-represented, probably due to successful germination from a persistent soil seedbank in addition to sown seed.

In this study, *E. regnans* was the largest species with a mean diameter at breast height (DBH) of 2.3 cm and height of 3.45 m (Fig. 1). *Eucalyptus delegatensis* plants were slightly smaller with a mean DBH of 2.1 cm and height of 3.07 m (Fig. 1). The maximum tree size recorded for each eucalypt was 9.2 cm DBH in *E. regnans* and 10 cm in *E. delegatensis*. *Acacia dealbata* were substantially smaller than the eucalypts at 0.8 cm DBH and 1.66 m height (Fig. 1). *Pomaderris apetala* trees were the smallest: 0.4 cm DBH and 1.31 m height (Fig. 1).

Drought event

In 2018/2019, an exceptionally hot and dry austral summer resulted in a severe drought episode at the AFEX. January 2019 received a total rainfall of 2.6 mm; just 6.5% of the 40.5 mm monthly average for the region, making it the driest January on record (since 1874). Concurrently, the mean maximum temperature was 4.3°C warmer than average and the mean daily evaporation was 7.7 mm, 51% higher than average. The 4 months preceding the January 2019 drought event were 1.47°C warmer than average and recorded 24.5% less rainfall than the long-term average. We determined the standardised precipitation evapotranspiration index (SPEI; Vicente-Serrano *et al.*, 2010) using temperature and rainfall data from the Bushy Park weather station. The SPEI is a commonly used drought index ranging from −3 to +3, in which negative and positive values indicate dry and wet weather conditions, respectively. The SPEI was calculated over a 3-month analysis period to capture seasonal patterns (Fig. 2a) and, therefore, represents the accrual of deficit/surplus of a given month, as well as the preceding 2 months. January and February 2019 SPEI values were −2.13 and −2.58, respectively, making February 2019 the lowest SPEI value recorded at the Bushy Park weather station since temperature data were recorded (1963; Fig. 2a). Therefore, the 2018/2019 austral summer was the most extreme seasonal drought episode since at least 1963 (Fig. 2a) and well past the dieback threshold (SPEI value of −2) common across a range of Australian vegetation types (Mitchell *et al.*, 2014). The drought ended in February following a significant rainfall event (13 mm), however, both February and March 2019 still experienced below average rainfall and above average temperatures.

Species vulnerability to cavitation

To determine the hydraulic vulnerability of the four study species, we investigated the relationship between leaf cavitation

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

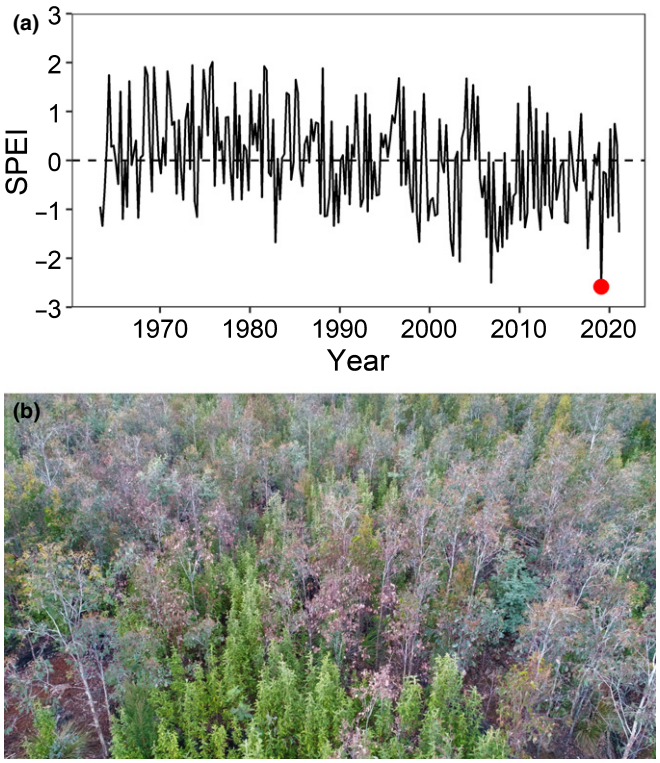


Fig. 2 (a) Time series of seasonal, 3-month standardised precipitation evapotranspiration index (SPEI) at Bushy Park Estates weather station *c*. 10 km from the Australian Forest Evenness Experiment (AFEX) field site (data obtained from the Australian Bureau of Meteorology; http://www.bom.gov.au/climate/data/). The line depicts the SPEI value of the last month of each season, indicating the accrual of deficit/surplus over the entire season. The red point indicates the 2018/2019 austral summer drought episode. (b) Image of canopy drought damage in the AFEX forest community. Shown in the foreground are light green *Pomaderris apetala* trees, surrounded by canopy damage in *Eucalyptus delegatensis* and *Eucalyptus regnans* trees, and a glaucous *Acacia dealbata* tree on the mid-right of the image.

and stem water potential (Ψ_{stem}) on cut branches. We measured cavitation in leaves rather than stems, which is more common, because canopy foliage damage was evident throughout the site, but complete tree death was rare, suggesting that leaves had cavitated during the drought but the main stem had not. During water stress, leaves generally embolise before stems because the distal xylem is typically more vulnerable to embolism than the basal region of the plant (i.e. the hydraulic vulnerability segmentation hypothesis; Johnson *et al.*, 2016; Losso *et al.*, 2019; Bourbia *et al.*, 2020). Therefore, we considered hydraulic vulnerability of the leaf the most relevant measure for explaining canopy drought damage patterns in the field.

Branches were collected early in the morning (before *c.* 08:00 h) during winter and spring 2020, both of which experienced typically wet weather of 167.8 and 154.8 mm of rainfall, respectively. SPEI values for each season were 0.75 and 0.33, respectively (Fig. 2a), meaning plants were well hydrated and native embolism should be minimal. Branches *c.* 1 m long were collected from the upper canopy of 3–5 similarly sized plants per species. Branches were sealed separately in two plastic bags with damp paper towels to avoid water loss and transported to the laboratory (< 1.5 h). Before beginning measurements, branches were placed in the dark for at least 30 min to allow the water potential of the whole branch to equilibrate.

The optical vulnerability technique (OVT; Brodribb *et al.*, 2016) was used to visualise cavitation in leaves of the dehydrating branches. The OVT is a noninvasive method using cameras to detect changes in light transmission when xylem vessels embolise and transition from water filled to air filled. We conducted measurements on a new, fully expanded, undamaged leaf attached to the branch, using purpose-built, high-resolution micro-cameras (www.cavicam.co) positioned on the midrib of *E. delegatensis*, *E. regnans* and *P. apetala* leaves and the rachis of *A. dealbata*. We used changes in transmitted light to capture cavitation events for all species other than *A. dealbata* for which we used reflected light (Brodribb *et al.*, 2017) due to woody tissue blocking transmitted light. This technique quantifies embolism formation in 2D, but produces results that agree very strongly with 3D imagery and flow-based methods (Gauthey *et al.*, 2020). For the entire dehydration process (*c.* 24 h), images were captured at 5-min intervals and Ψ_{stem} recorded at 10-min intervals using a psychrometer (ICT PSY, Armidale, NSW, Australia) attached to each branch, until no new cavitation events were recorded for *c.* 4 h. We measured leaf water potential (Ψ_{leaf}) periodically using a Scholander pressure chamber (PMS Instrument Co., Albany, OR, USA; Scholander *et al.*, 1965) to verify psychrometer readings. The entire process was conducted under ambient laboratory air and lighting conditions (*c.* 20°C and 40% relative humidity).

Embolism was quantified using image analysis in Fiji processing software (Schindelin *et al.*, 2012) following the methods described in detail at www.opensourceov.org. In brief, we calculated pixel differences between all neighbouring images, indicating changes in light transmission/reflection due to cavitation events (embolism) evident as darker lines. Changes in pixel intensity that were not associated with cavitation events (e.g. leaf shrinkage during dehydration) were removed using outlier removal in Fiji or manually when required. Once the image sequence contained only pixels of cavitation events, the embolised pixel area in each image was divided by the total embolised area calculated from all images and expressed as a percentage of total embolism. This was plotted against Ψ_{stem} and we extracted the point at which the water potential caused 50% of the xylem area to be embolised (leaf P_{50}) as a critical threshold for loss of xylem function.

Canopy damage assessments

Following the austral summer drought, we assessed canopy drought damage in April 2019 (Fig. 1b). To capture the range of canopy damage across the site in varying community compositions, we focused on a subset ($n = 14$) of 25 × 25 m plots (Table S1), selected as a combination of different treatments and levels of obvious canopy dieback severity. Within these plots, we randomly established 20 m transects 2.5 m from the plot edge to avoid edge effects with a 1 m boundary on either side of the transect. The transect was then divided into 10 2 × 2 m quadrats.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

We visually assessed canopy damage for each plant > 1.5 m in height as the percentage of canopy with leaf discoloration/browning in 10% increments from 0 to 100%. Damage assessments were conducted before leaf shedding occurred to ensure that canopy foliar damage could be confidently attributed to the recent drought. Only *E. delegatensis* and *E. regnans* suffered substantial damage, so the effect of neighbour density and size were determined for these two species only.

Neighbour density

To assess how neighbour density influences canopy damage, we counted the number of plants of each species in each quadrat and summed quadrat counts to obtain a transect-level count (Fig. 3). Because transects were inside treatments plots that were sown to create a specific community composition, the transect scale is highly indicative of the overall plot community. Each count was converted to a plant density per square metre (mean 5.7 plants m^{-2}). We focused on species densities rather than estimates of tree biomass as the two were highly correlated in this single-age system (Figs S3, S4), in which the range of sizes was relatively small (Fig. 1). Therefore, we opted to use the simpler measurement to determine neighbour influences on drought damage.

Relative tree size

To test how tree size influences drought damage, we calculated DBH (measured at 1.35 m) individually for all *E. regnans* and *E. delegatensis* trees taller than a 1.5 m height pole. Trees shorter than 1.5 m were awarded a constant diameter value of 0.25 cm. Diameter measurements were used to determine individual stem basal area.

Predawn water potential

We measured predawn water potential ($\Psi_{predawn}$), as a proxy for rooting depth, to determine whether species differed in their ability to access soil water resources. $\Psi_{predawn}$ is a robust estimate of soil water availability around a tree's root system because, assuming no night-time transpiration (but see Kavanagh *et al.*, 2007), the absence of leaf water loss creating xylem tension allows the plant and soil water potential to reach equilibrium by dawn (Waring & Cleary, 1967). $\Psi_{predawn}$ has been previously correlated with rooting depth (Bucci *et al.*, 2009; Scholz *et al.*, 2012) and used extensively to examine soil water access in which higher (less negative) values indicate greater water availability (Simonin *et al.*, 2006; Ward *et al.*, 2006; Ambrose *et al.*, 2018). To minimise variation in $\Psi_{predawn}$ values due to tree size and belowground heterogeneity, we selected trees of the three most abundant species (*E. delegatensis*, *E. regnans* and *P. apetala*) that were as similar in size and proximity to one another as possible. *Acacia dealbata* was not sampled because this species was relatively rare in comparison, and because it was also relatively rare in density surveys. Trees were sampled following an extended period of dry weather in March 2021 when the closest weather station had received < 5 mm of rain in the preceding 33-d period and the 3-month SPEI value was −1.52. Tree height was measured using a height pole and leaves were collected before dawn (05:30 h) from 10 plants of each of the three species. Leaves were sealed in two zip-lock bags, wrapped in moist paper towels, returned to the laboratory and Ψ_{leaf} measured using a Scholander pressure chamber.

Stomatal behaviour

We investigated stomatal sensitivity to water potential in the same three species (*E. delegatensis*, *E. regnans* and *P. apetala*) to assess whether differing stomatal behaviour (i.e. anisohydric vs isohydric) explained differences in drought damage patterns. Using cut branches, we measured the relationship between stomatal conductance (g_s) and Ψ_{leaf} as branches dried and compared the slope of the function $g_s = f(\Psi_{leaf})$ among species to determine whether species were more or less capable of maintaining static Ψ_{leaf} as the source (soil) water potential decreased (Brodribb & Holbrook, 2004). A metre-long branch was collected from two or three trees per species at the AFEX before 07:00 h during spring and after a period of wet weather to ensure plants were well hydrated. Branches were collected from similarly sized,

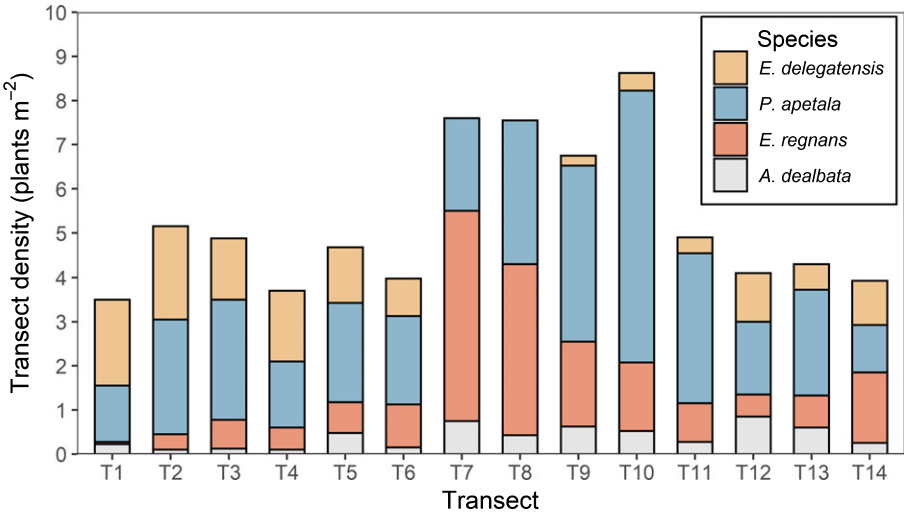


Fig. 3 Species densities (plants m^{-2}) in each of the 14 transects in this study. Other species made up just 2.3% of all plants surveyed and are not presented here.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

healthy individuals, sealed separately in two plastic bags with damp paper towels to minimise water loss and immediately transported to the glasshouse. Branches were kept in the dark for 30 min before measurement and g_s was measured on a single fully expanded leaf using a LI6400 Portable Photosynthesis System (Li-Cor, Lincoln, OR, USA) at a photosynthetically active radiation (PAR) of 1000 µmol quanta $m^{-2}\,s^{-1}$ and a CO_2 concentration of 400 µmol mol^{-1}. Temperature and vapour pressure deficit (VPD) were monitored to ensure values remained constant and within the ranges 21–25°C and 0.8–2 kPa, respectively. Gas exchange was recorded at 30 s intervals on the same leaf for the duration of the dry-down period between 09:00 h and 14:00 h. Additional leaves were removed from the branch to estimate Ψ_{leaf} (using a Scholander pressure chamber as above) every 15 min to begin with, but more frequently when g_s decreased rapidly.

Statistical analysis

All data analysis was performed using the R programming language (v.4.0.4; R Development Core Team, 2021). Four sets of statistical analyses were performed to identify how canopy drought damage was related to neighbours and tree size in the field, species vulnerability to cavitation, $\Psi_{predawn}$ (rooting depth) and stomatal behaviour. First, species' differences in vulnerability to cavitation were determined by fitting a one-way analysis of variance (ANOVA) using the calculated leaf P_{50} values as the response variable and included species as a fixed effect.

Second, we determined how canopy drought damage differed between and within species in the field using generalised linear mixed-effects models (GLMMs) with the *glmer* function from the LME4 R package (Bates *et al.*, 2014). The proportion of canopy damaged was the response variable, and quadrat, nested within transect, was included as random factors to capture unmeasured environmental differences among quadrats and transects. Canopy damage was binned into 10% intervals and our GLMMs assumed a binomial distribution with a logit link function. All models included a plant-level random effect to account for the overdispersion observed with respect to the binomial distribution.

We first determined if the degree of canopy drought damage differed between the four study species using a likelihood-ratio test (LRT; 'drop1' function). This test compared the null GLMM, which included only random effects, with an identical model that also included species as a fixed factor. Having identified species differences, we assessed the effect of tree size and the four species transect densities on eucalypt canopy damage only. We explored species-specific density rather than total density to address our core research questions of whether neighbouring plants had differential impacts on drought damage based on their identity and associated physiology. The random effects structure and all other model parameters followed the same form as the null model. Tree basal area was log transformed and all predictors were standardised by a *z*-transformation. We estimated maximum likelihood estimates and 95% confidence intervals for each predictor.

Third, species' differences in $\Psi_{predawn}$ were investigated using a fourth root transformation on water potential values to improve normality. We performed an ANOVA using the transformed water potential as the response variable and included species as a fixed factor, tree height as a covariate and an interaction between the two predictors.

Fourth, to investigate differences in stomatal regulation among species we used the technique described in Skelton *et al.* (2015). We converted g_s relative to its maximum value (g_s max) and fitted a Weibull function response curve to the relationship between relative g_s and declining Ψ_{leaf} for each branch. We determined the slope of the line tangential to the response curve at 50% of g_s max and obtained P_{g12} values at the Ψ_{leaf} where the tangent line intersects the *x*-axis. The P_{g12} metric represents the Ψ_{leaf} where g_s is *c.* 12% of g_{max} and reflects the point of stomatal closure (Skelton *et al.*, 2015). We therefore used P_{g12} values to test whether species differed in the Ψ_{leaf} causing stomatal closure using an ANOVA, in which P_{g12} was the response variable and species was a fixed factor. In all ANOVAs, we conducted pairwise comparisons between species using Tukey's honest significant difference (HSD) *post hoc* test when required (multcomp R package; Hothorn *et al.*, 2008).

Results

Vulnerability to cavitation

The four species differed significantly in leaf vulnerability to cavitation ($F_{3,12} = 86.7$, $P < 0.001$), as seen by the water potential causing 50% embolism (leaf P_{50}; Fig. 4). *Eucalyptus regnans* and *E. delegatensis* were the most vulnerable to cavitation with mean P_{50} values of -3.21 ± 0.16 and -3.42 ± 0.16 MPa (mean ± 1SE), respectively, although these were not significantly different ($P = 0.886$). *Pomaderris apetala* was significantly more resistant to cavitation than both eucalypts (*E. regnans*: $P = 0.009$; *E. delegatensis*: $P = 0.014$) with a mean P_{50} of -4.52 ± 0.08 MPa. *Acacia dealbata* was the most resistant to cavitation, with a significantly more negative mean P_{50} value (-7.06 ± 0.26 MPa) than all other species (Fig. 4).

Canopy foliar damage

The degree of canopy damage differed significantly between the four species (LRT; $G_3 = 92.86$, $P < 0.001$; Fig. 5). Both eucalypts experienced substantial levels of canopy damage, while the degree of damage was very minor for both *P. apetala* and *A. dealbata* (Fig. 5). *Eucalyptus delegatensis* suffered the greatest mean damage (34.7%), as well as the greatest proportion of trees with some degree of damage (0.53) and half or more of their canopy damaged (0.36). *Eucalyptus regnans* suffered a lower mean damage (25.3%) than *E. delegatensis*, as well as a lower proportion of trees displaying some damage (0.36), or more than half of their canopy damaged (0.23; Fig. 5).

Neighbour and size effects

The degree of canopy damage in the two eucalypts was influenced by neighbour plant density and associated with tree size (Fig. 6). Both *E. delegatensis* and *E. regnans* damage was negatively related to tree size, whereby damage was on average higher

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

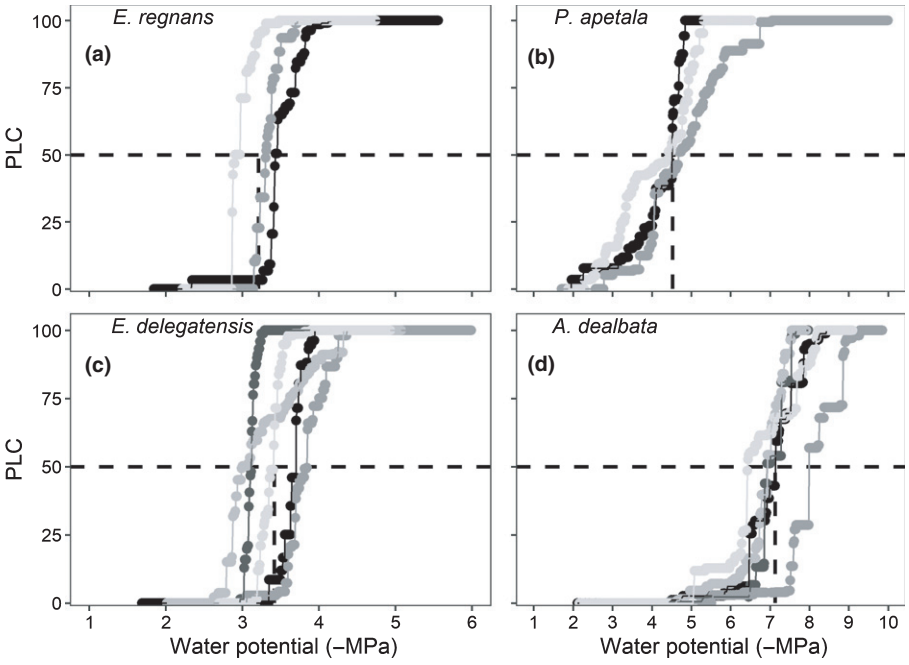


Fig. 4 Leaf vulnerability curves of *Eucalyptus regnans, Eucalyptus delegatensis*, *Pomaderris apetala* and *Acacia dealbata* in the Australian Forest Evenness Experiment, Tasmania, Australia. Curves show the relationship between percentage loss of xylem conductivity (PLC) to declining water potential (MPa). Shaded points represent different plants; dashed lines indicate the average water potential (−MPa) causing a 50% of leaf xylem to become embolised.

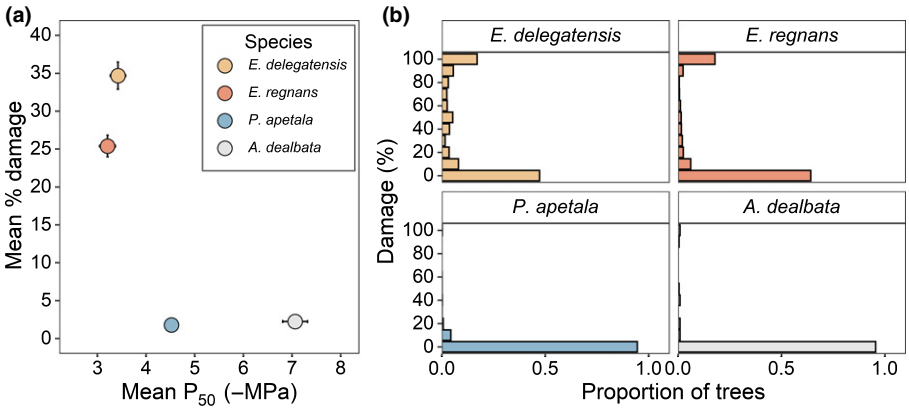


Fig. 5 (a) Relationship between mean % canopy damage ($n = 2944$) and mean 50% loss in conductivity (P_{50}; $n = 16$) values (±SE) of the four species in the Australian Forest Evenness Experiment, Tasmania, Australia: *Eucalyptus delegatensis* ($n = 511, 5$), *Eucalyptus regnans* ($n = 761, 3$), *Pomaderris apetala* ($n = 1453, 3$) and *Acacia dealbata* ($n = 219, 5$). (b) Frequency distribution of the percentage of canopy damage of plants of the four species in 14 20-m transects.

for smaller plants (Figs 6, S5). The impact of neighbouring plants on drought damage, however, differed in strength between the two species (Fig. 6).

Damage in *E. delegatensis* was strongly related to the density of *P. apetala* and was largely unaffected by the density of conspecific, *E. regnans* or *A. dealbata* neighbours (Figs 6, S6). *Eucalyptus delegatensis* plants growing with more *P. apetala* neighbours had a higher degree of damage compared with those in low density transects (Fig. 7a). Damage in *E. regnans* was positively related to the density of all neighbouring species, but similar to *E. delegatensis*, the only species that had a significant effect was *P. apetala* (Figs 6, S7). The effect of *P. apetala* was weaker for *E. regnans* (Figs 6, 7b) but both eucalypts showed the same relationship of greater damage in plants growing in transects with high *P. apetala* density.

Predawn water potential

Predawn water potential ($\Psi_{predawn}$) values varied widely within all three species sampled, ranging from *c.* −0.2 to −0.75 MPa (Fig. 8). $\Psi_{predawn}$ did not significantly differ between species ($F_{2,24} = 1.47$, $P = 0.249$), nor was it influenced by tree height ($F_{1,24} = 1.987$, $P = 0.171$). Water potential values tended to be higher (less negative) in *E. regnans* trees (mean -0.35 ± 0.04 MPa) than either *E. delegatensis* (-0.47 ± 0.06 MPa) and *P. apetala* (0.43 ± 0.05 MPa) (Fig. 8). Therefore, *E. delegatensis* and *P. apetala* had a greater degree of overlap in $\Psi_{predawn}$ than with *E. regnans*.

Stomatal behaviour

The three species (*E. delegatensis, E. regnans* and *P. apetala*) did not differ significantly in their Pg_{12} values ($F_{2,4} = 0.79$, $P = 0.515$) and, therefore, showed relatively similar stomatal behaviour in response to declining Ψ_{leaf} (Fig. 9). However, *E. regnans* stomatal regulation was somewhat less sensitive to declining Ψ_{leaf} than the other two species, having the lowest Pg_{12} (-2.34 ± 0.05), followed by slightly higher Pg_{12} values in *P. apetala* (-2.16 ± 0.22) and *E. delegatensis* (-2.01 ± 0.195).

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

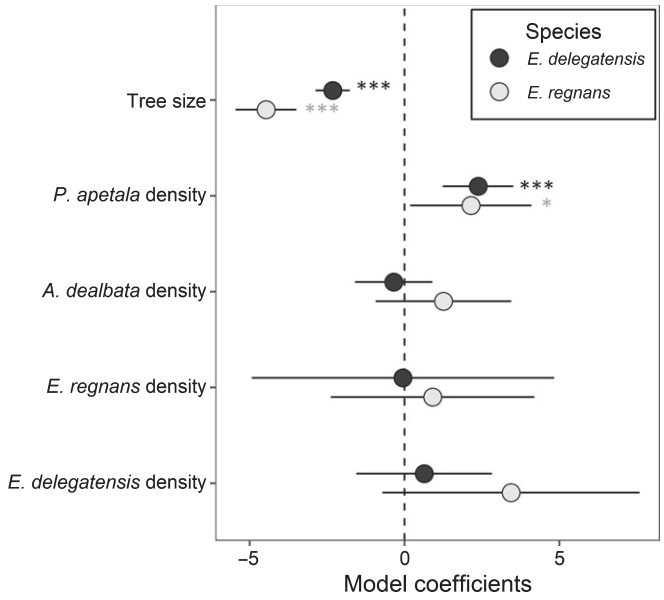


Fig. 6 Standardised coefficient estimates of canopy drought damage in *Eucalyptus delegatensis* and *Eucalyptus regnans* in relation to individual tree size (basal area; cm^2) and density of neighbouring species in the AFEX, Tasmania, Australia. Points are the fixed effects model coefficients from the binomial regression and solid lines are 95% confidence intervals (CIs) in which CIs that exclude zero (dashed vertical line) indicate a significant effect of the predictor on the damage in that species. Statistically significant effects at: ***, $P < 0.001$, *, $P < 0.05$.

Discussion

In this study, we demonstrate that drought-induced canopy damage in the AFEX was the combined result of both physiological and ecological processes. In line with our first hypothesis and previous studies linking natural drought damage with hydraulic traits (Breshears *et al.*, 2009; Anderegg *et al.*, 2016; Powers *et al.*, 2020), we found that the two species most vulnerable to cavitation (*E. delegatensis* and *E. regnans*) also suffered the most drought damage. Unlike any previous studies, however, and in support of our second hypothesis, we found that damage in the two eucalypts was greater when co-occurring with a higher density of neighbours with more resistant xylem. The impact of neighbouring plants on the two co-occurring eucalypts differed in strength, explaining differences in the degree of damage between the two species. Finally, we found smaller trees to be more susceptible to damage than larger trees, supporting our third hypothesis. Taken together, these results showed that characteristics of the plant hydraulic system describe both the susceptibility of a plant to hydraulic failure during water stress, as well as the strength of its competitive effect on co-occurring plants. This finding highlights the importance of plant–plant interactions in determining the extent of natural drought damage in forest communities.

Species physiology

Our study contributes to growing evidence that drought-induced damage is governed by the plant hydraulic system (Anderegg *et al.*, 2015; Rowland *et al.*, 2015; Adams *et al.*, 2017; Powers *et al.*, 2020). A common hydraulic trait – the xylem water potential causing 50% loss of leaf hydraulic conductivity (leaf P_{50}) – correctly predicted the susceptibility of the two eucalypts and the tolerance of *A. dealbata* and *P. apetala* to natural drought damage in this study. However, damage patterns were not fully explained by this trait alone, as damage in *E. delegatensis* was significantly greater than in *E. regnans,* despite similar leaf P_{50} values. While P_{50} is the most common metric used to explain vulnerability (Brodribb & Cochard, 2009; Choat *et al.*, 2012; Fichtner *et al.*, 2020), other possible reference points (e.g. P_{88}) have been proposed to better represent the point of hydraulic failure in angiosperms (Urli *et al.*, 2013). In our study, however, using either P_{50} or P_{88} led to the same conclusions in the order of species' vulnerability to cavitation and was therefore accurately described by leaf P_{50} values.

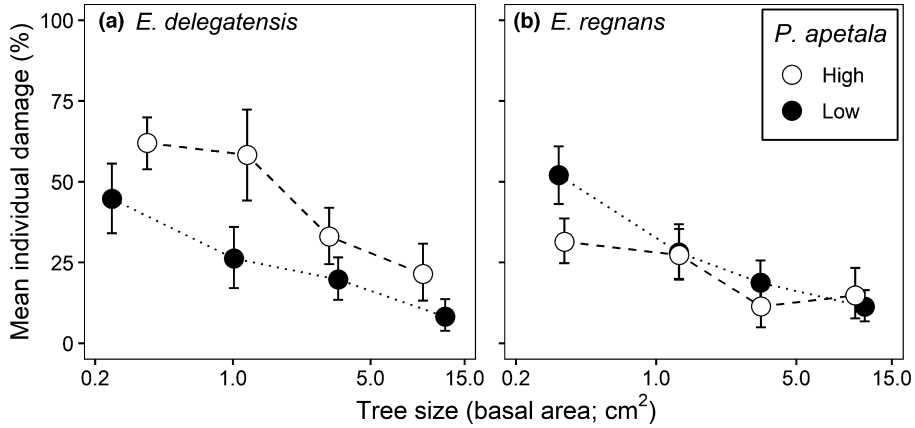


Fig. 7 Observed relationship between mean individual canopy damage and four approximately equal groupings of tree size for (a) *Eucalyptus delegatensis* and (b) *Eucalyptus regnans* in the Australian Forest Evenness Experiment, Tasmania, Australia. Means are provided for each of the four groupings and mean damage is also presented at above and below the median *Pomaderris apetala* transect density experienced by both species (*E. delegatensis*: 2 plants m^{-2}; *E. regnans*: 2.4 plants m^{-2}). Error bars depict 95% confidence intervals of the mean and were calculated using 10 000 bootstrapped samples. Note the log scale on the *x*-axis. Raw data are presented in Supporting Information Figs S6, S7.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

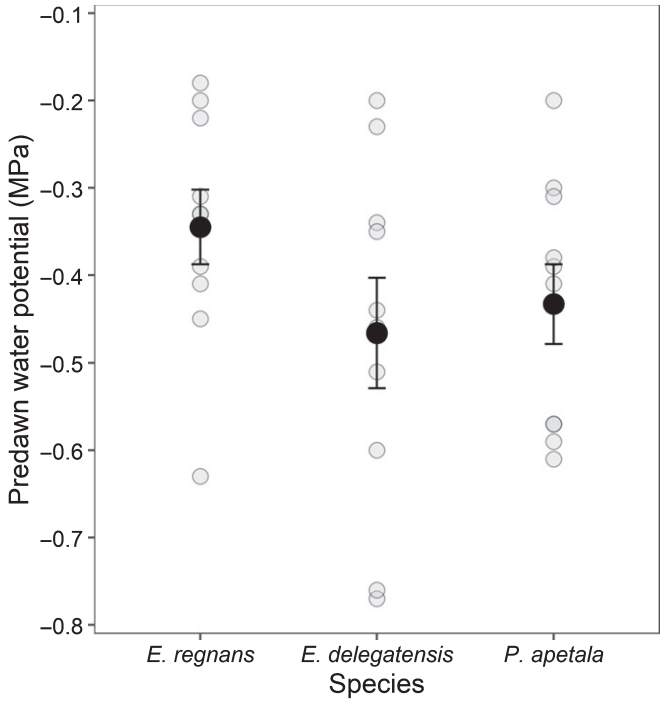


Fig. 8 Predawn water potential (MPa; $n = 10$ per species) of the three most common species at the Australian Forest Evenness Experiment, Tasmania, Australia: *Eucalyptus regnans*, *Eucalyptus delegatensis* and *Pomaderris apetala*. Black points and error bars indicate the mean and standard error for each species, grey points show the raw water potential values.

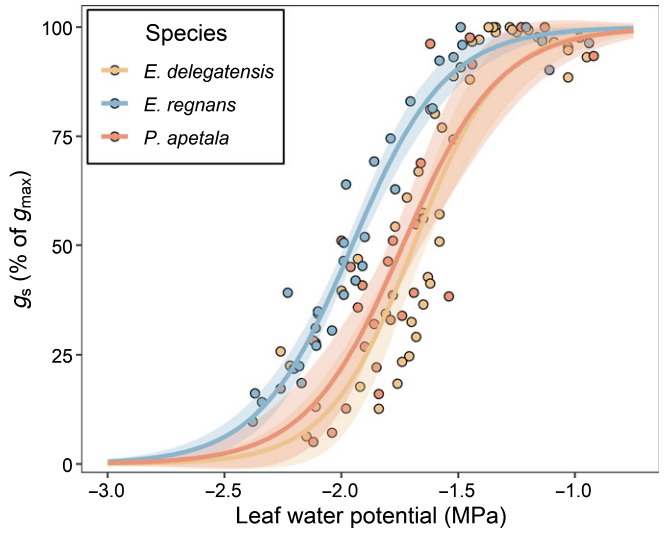


Fig. 9 The relationship between relative stomatal conductance (g_s; % of maximum g_s) and leaf water potential (Ψ_{leaf}) in three species in the Australian Forest Evenness Experiment (AFEX): *Eucalyptus delegatensis* ($n = 3$), *Eucalyptus regnans* ($n = 2$) and *Pomaderris apetala* ($n = 2$). Points show the raw data and curves depict a Weibull function fitted to the relative g_s and leaf water potential relationship. Shading of each curve indicates 95% confidence intervals. Unnormalized g_s data are shown in Supporting Information Fig. S8.

Differences in canopy damage between the two eucalypts might be due to variation in heat tolerance as the 2018/2019 austral summer was also unusually warm. This was supported by the fact that *E. delegatensis* occurs at higher altitudes than *E. regnans* and the AFEX site is close to the minimum elevation limit of *E. delegatensis* (Williams & Potts, 1996). However, the period in question was an extended warm period, rather than a heatwave, as air temperatures never exceeded 34.8°C. As this temperature was below the threshold causing heat damage in other Australian temperate species (Cunningham & Read, 2006), it is unlikely that the damage observed here was solely due to heat injury. Furthermore, higher air temperatures were recorded at the site several times in preceding summers with no apparent consequent canopy damage. Therefore, it is more likely that the warmer and drier conditions simultaneously increased xylem tension within the plant and created embolisms in leaf veins, leading directly to tissue damage through dehydration (Brodribb *et al.*, 2021). This proposal is supported by a recent study that found foliar damage in other eucalypts to be strongly associated with hydraulic failure during drought (Nolan *et al.*, 2021).

Differences among species in the degree of damage were not related to stomatal behaviour. Stomatal sensitivity to declining water potential is a key response to drought stress, determining the rate of plant dehydration (Tardieu & Simonneau, 1998; Wyse *et al.*, 2013; Klein, 2014). Plants typically close their stomata before cavitation (Brodribb & Holbrook, 2004), but those with more sensitive stomata are better able to slow dehydration (Buckley, 2019) and prolong the onset of damaging cavitation (Martin-StPaul *et al.*, 2017; Li *et al.*, 2018). We found only minor evidence that our species differed in the sensitivity of stomata to declining water potential and no statistical differences among species in a key indicator of stomatal sensitivity (P_{g12}). In contrast with expectations if the observed damage patterns were linked to differing stomatal regulation, we found that *E. regnans* had the least sensitive stomatal regulation and a lower degree of damage when compared with *E. delegatensis*, which had the most sensitive regulation and a higher degree of damage. Furthermore, *E. regnans* also had the highest P_{50} value and, therefore, had a narrower hydraulic safety margin (Skelton *et al.*, 2015). Therefore, the minor differences in stomatal regulation strategy of the species examined here do not explain the degree of drought damage in each species. Our results instead provide compelling evidence that differences in damage between the two co-occurring eucalypts result from differential impacts of neighbouring plants.

Neighbour density

Neighbour plant density strongly impacted the degree of damage in *E. delegatensis* but less so in *E. regnans*. Although previous studies have found general community predictors, such as conspecific and heterospecific densities or total basal area, to influence drought-induced mortality (Dwyer *et al.*, 2010; Young *et al.*, 2017; Pillet *et al.*, 2018), our study showed that species-specific densities had distinct effects on drought damage in the two eucalypts. Specifically, damage in both *E. delegatensis* and *E. regnans* was more strongly impacted by the density of a heterospecific neighbour, *Pomaderris apetala*, than it was by the density of

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

conspecific neighbours. This is in contrast with theoretical expectations that intraspecific competition should always be stronger than interspecific competition, because greater niche overlap infers greater similarity in resource capture and requirements (Gause, 1934). Support for this theory in the literature is mixed (Goldberg & Barton, 1992; Gurevitch *et al.*, 1992; Adler *et al.*, 2018), emphasising the need for a more mechanistic approach to examining how plants interact (Trinder *et al.*, 2013; Aschehoug *et al.*, 2016).

The mechanisms of plant competition for water – the use of this common resource by neighbouring individuals – is relatively understudied compared with nutrient and light competition (Craine & Dybzinski, 2013; Aschehoug *et al.*, 2016). Although our study did not directly estimate plant water use in the field, the physiological characteristics of *P. apetala* provide a mechanistic, albeit indirect, explanation for the stronger influence of this species on *E. delegatensis* and *E. regnans* damage than conspecific neighbours. In the early stages of drought, all plants compete for soil water but, as the soil dries, species with more vulnerable xylem (higher P_{50}) are the first to experience damaging embolisms. Embolised leaves reduce the functional leaf area of a plant and, therefore, its water use (Hochberg *et al.*, 2017), increasing the availability of water to more resistant neighbours. In our system, as the soil water potential approached *c.* −3 MPa, both eucalypts began to suffer substantial embolism and reduced ability to transport water, while *P. apetala* was relatively unaffected. As soil drying continued, eucalypt water use and their effect on soil water availability became progressively less as leaves became damaged or were shed. Eucalypts are well known to shed leaves during drought, reducing transpiration and soil drying (Blackman *et al.*, 2019), but this strategy is futile when co-occurring with more drought-resistant species such as *P. apetala*. Because *P. apetala* plants are not inhibited by embolisms until more negative soil water potentials (< −4 MPa), they should have a stronger, prolonged effect on soil drying. Therefore, sites with higher densities of *P. apetala* should also have a higher degree of damage in the two eucalypts. Similarly, we would expect *A. dealbata* to have the same, but even stronger effect, due to the very high xylem resistance in this species. However, due to the relatively low density of *A. dealbata* plants (mean 0.4 plants m^{-2}) in our field surveys compared with the other three species, particularly *P. apetala*, we did not detect an effect of this species.

The effect of neighbour density on *E. regnans* differed slightly to that of *E. delegatensis*. *Eucalyptus regnans* damage also increased with *P. apetala* density, but evidence of this effect was weaker. This suggests that, despite similar differences in P_{50}, competition for water between *E. regnans* and *P. apetala* was less intense than that between *P. apetala* and *E. delegatensis*. We propose that this weaker interaction is a result of differences in rooting depth between *E. regnans* and the other two species. We used predawn water potential as a proxy for rooting depth, in which higher (less negative) values indicate greater water access through deeper roots (Bucci *et al.*, 2009; Scholz *et al.*, 2012). Large intraspecific variation in water potential indicates that access to soil water within the site is highly variable, despite strong similarity in tree size, location and age. Largely due to this variation, we did not find significant differences between the three species in predawn water potentials. However, we did observe greater overlap in predawn water potential values and, presumably, rooting depth between *E. delegatensis* and *P. apetala* compared with either species with *E. regnans*. Because overlapping root systems increase competition for water (Manoli *et al.*, 2014), *E. delegatensis* plants co-occurring with high densities of more water-acquisitive *P. apetala* should experience the greatest level of localised water stress. As *E. regnans* appears to be able to access deeper water sources than the other two species, this suggests that this is a possible explanation for the weaker impact of *P. apetala* on damage in *E. regnans* compared with that in *E. delegatensis*. Similarly, hydraulically vulnerable species in a tropical forest were found to have lower drought mortality rates because deeper rooting depths reduced water-stress exposure (Chitra-Tarak *et al.*, 2021).

Tree size

In line with some previous studies (Peng *et al.*, 2011; Keith *et al.*, 2012; Brun *et al.*, 2020) but in contrast with others (Nepstad *et al.*, 2007; Phillips *et al.*, 2010; Bennett *et al.*, 2015), our results indicated that smaller saplings of both eucalypts were more susceptible to drought damage than larger individuals. All trees in this experiment were the same age during the drought with a consequently narrow size range. Nevertheless, within the small size range, resilience to drought in larger trees may be due to greater access to deep soil water reserves reducing the water deficit severity (Giardina *et al.*, 2018). Access to soil water can also depend on drought duration and severity differentially impacting trees of different sizes. Here, the drought was relatively short (Keith *et al.*, 2012; Nolan *et al.*, 2021) but severe as, over a 40-d relatively warm period, the site received a total of 2.6 mm of rain in four widely separated events. Therefore, unusually warm temperatures exacerbating shallow soil evaporation and the absence of any substantial precipitation probably amplified soil drying in the rooting zone of smaller trees, leading to substantial canopy damage. Alternatively, smaller, shaded and suppressed saplings could have had smaller carbon stores than their larger neighbours. While we did not explore this as a potential mechanism for size-dependent differences in drought damage in this study, it has previously been shown in *Populus nigra* saplings that shading depleted nonstructural carbohydrate stores and increased xylem vulnerability to embolism (Tomasella *et al.*, 2021).

Conclusions

This study found that natural drought damage is collectively explained by vulnerability to cavitation, the density of heterospecific neighbours and individual sapling size. These findings support the emerging view that characteristics of the plant hydraulic system are key to developing predictive models that identify which plants are most at risk to future drought. However, focusing on individual plants in isolation from the communities in which they persist does not fully capture the ecological and hydrological complexity of natural forest systems. This

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

approach ignores fine-scale variation in soil moisture due to neighbouring plants and other factors such as microtopography. Our findings demonstrate that neighbouring plants with more resistant xylem can exacerbate damage compared with physiologically weaker neighbours. We highlight the importance of adopting a whole community view to accurately predict natural drought damage and propose that future research should explore whether naturally occurring plant densities influence drought damage across a range of species and forest types.

Acknowledgements

We acknowledge the Lairmairrener people, the traditional custodians of the land on which this research was undertaken. TGB is supported by an Australian Government Research Training Programme (RTP) scholarship and acknowledges the provision of scholarship support from the Gottstein Trust. TGB and MJH acknowledge funding by the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation and the Ecological Society of Australia. TJB acknowledges funding from the ARC Centre of Excellence for Plant Success in Nature and Agriculture CE200100015. We thank Sustainable Timbers Tasmania for providing access to the study site and Elizabeth Bell for assistance with data collection.

Author contributions

TGB, MJH and TJB conceived and designed the field data collection; TGB, CR and MJH collected the field data, and TGB performed the laboratory experiments with contributions from TJB; TGB, SAR and MJH analysed the data; TGB wrote the manuscript with contributions from all authors.

ORCID

Travis G. Britton https://orcid.org/0000-0003-1202-116X
Timothy J. Brodribb https://orcid.org/0000-0002-4964-6107
Mark J. Hovenden https://orcid.org/0000-0001-7208-9700
Shane A. Richards https://orcid.org/0000-0002-9638-5827

Data availability

All data used in this study are available through the Dryad Digital Repository at https://doi.org/10.5061/dryad.931zcrjk8.

References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD *et al.* 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution* **1**: 1285–1291.

Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, Meiners JM, Tredennick AT, Veblen KE. 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters* **21**: 1319–1329.

Ambrose AR, Baxter WL, Martin RE, Francis E, Asner GP, Nydick KR, Dawson TE. 2018. Leaf-and crown-level adjustments help giant sequoias maintain favorable water status during severe drought. *Forest Ecology and Management* **419**: 257–267.

Anderegg WR, Flint A, Huang C, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* **8**: 367–371.

Anderegg WR, Klein T, Bartlett M, Sack L, Pellegrini AF, Choat B, Jansen S. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences, USA* **113**: 5024–5029.

Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM. 2016. The mechanisms and consequences of interspecific competition among plants. *Annual Review of Ecology, Evolution, and Systematics* **47**: 263–281.

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting linear mixed-effects models using LME4. *Journal of Statistical Software* **67**: 1–48.

Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**: 15139.

Blackman CJ, Li X, Choat B, Rymer PD, De Kauwe MG, Duursma RA, Tissue DT, Medlyn BE. 2019. Desiccation time during drought is highly predictable across species of *Eucalyptus* from contrasting climates. *New Phytologist* **224**: 632–643.

Bourbia I, Carins-Murphy MR, Gracie A, Brodribb TJ. 2020. Xylem cavitation isolates leaky flowers during water stress in pyrethrum. *New Phytologist* **227**: 146–155.

Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* **7**: 185–189.

Brodribb T, Brodersen CR, Carriqui M, Tonet V, Rodriguez Dominguez C, McAdam S. 2021. Linking xylem network failure with leaf tissue death. *New Phytologist* **232**: 68–79.

Brodribb TJ, Carriqui M, Delzon S, Lucani C. 2017. Optical measurement of stem xylem vulnerability. *Plant Physiology* **174**: 2054–2061.

Brodribb TJ, Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* **149**: 575–584.

Brodribb TJ, Holbrook NM. 2004. Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist* **162**: 663–670.

Brodribb TJ, Powers J, Cochard H, Choat B. 2020. Hanging by a thread? Forests and drought. *Science* **368**: 261–266.

Brodribb TJ, Skelton RP, McAdam SA, Bienaimé D, Lucani CJ, Marmottant P. 2016. Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New Phytologist* **209**: 1403–1409.

Brun P, Psomas A, Ginzler C, Thuiller W, Zappa M, Zimmermann NE. 2020. Large-scale early-wilting response of Central European forests to the 2018 extreme drought. *Global Change Biology* **26**: 7021–7035.

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Arce ME. 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia* **160**: 631–641.

Buckley TN. 2019. How do stomata respond to water status? *New Phytologist* **224**: 21–36.

Bureau of Meteorology. 2020. *Special climate statement 70 update – drought conditions in Australia and impact on water resources in the Murray-Darling Basin: Commonwealth of Australia.* [WWW document] URL http://www.bom.gov.au/climate/current/statements/scs70.pdf.

Chitra-Tarak R, Xu C, Aguilar S, Anderson-Teixeira KJ, Chambers J, Detto M, Faybishenko B, Fisher RA, Knox RG, Koven CD *et al.* 2021. Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* **231**: 1798–1813.

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, Lopez R, Medlyn BE. 2018. Triggers of tree mortality under drought. *Nature* **558**: 531.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752.

Clark JS, Iverson L, Woodall CW, Allen CD, Bell DM, Bragg DC, D'Amato AW, Davis FW, Hersh MH, Ibanez I *et al.* 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology* **22**: 2329–2352.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

Craine JM, Dybzinski R. 2013. Mechanisms of plant competition for nutrients, water and light. *Functional Ecology* **27**: 833–840.

Cunningham SC, Read J. 2006. Foliar temperature tolerance of temperate and tropical evergreen rain forest trees of Australia. *Tree Physiology* **26**: 1435–1443.

Domec J-C, Gartner BL. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees* **15**: 204–214.

Dwyer JM, Fensham RJ, Fairfax RJ, Buckley YM. 2010. Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. *Journal of Vegetation Science* **21**: 573–585.

Fajardo A, McIntire EJ, Olson ME. 2018. When short stature is an asset in trees. *Trends in Ecology & Evolution* **34**: 193–199.

Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. *Forest Ecology and Management* **432**: 164–178.

Fichtner A, Schnabel F, Bruelheide H, Kunz M, Mausolf K, Schuldt A, Härdtle W, von Oheimb G. 2020. Neighbourhood diversity mitigates drought impacts on tree growth. *Journal of Ecology* **108**: 865–875.

Gause GF. 1934. *The struggle for existence*. Baltimore, MD, USA: The Williams & Wilkins Company.

Gauthey A, Peters JMR, Carins-Murphy MR, Rodriguez-Dominguez CM, Li X, Delzon S, King A, López R, Medlyn BE, Tissue DT *et al.* 2020. Visual and hydraulic techniques produce similar estimates of cavitation resistance in woody species. *New Phytologist* **228**: 884–897.

Gerwin MR, Brinkhoff R, Britton T, Porter M, Mallett RK, Hovenden MJ. 2020. Testing the impact of community composition on the productivity of a cool temperate eucalypt forest: the Australian Forest Evenness Experiment (AFEX). *Australian Journal of Botany* **68**: 310–319.

Giardina F, Konings AG, Kennedy D, Alemohammad SH, Oliveira RS, Uriarte M, Gentine P. 2018. Tall Amazonian forests are less sensitive to precipitation variability. *Nature Geoscience* **11**: 405–409.

Goldberg DE, Barton AM. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**: 771–801.

Gurevitch J, Morrow LL, Wallace A, Walsh JS. 1992. A meta-analysis of competition in field experiments. *American Naturalist* **140**: 539–572.

Hickey J, Kostoglou P, Sargison G. 2000. Tasmania's tallest trees. *Tasforests* **12**: 105–122.

Hochberg U, Windt CW, Ponomarenko A, Zhang Y-J, Gersony J, Rockwell FE, Holbrook NM. 2017. Stomatal closure, basal leaf embolism, and shedding protect the hydraulic integrity of grape stems. *Plant Physiology* **174**: 764–775.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences* **50**: 346–363.

Johnson DJ, Condit R, Hubbell SP, Comita LS. 2017. Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. *Proceedings of the Royal Society B: Biological Sciences* **284**. doi: 10.1098/rspb.2017.2210.

Johnson DM, Wortemann R, McCulloh KA, Jordan-Meille L, Ward E, Warren JM, Palmroth S, Domec J-C. 2016. A test of the hydraulic vulnerability segmentation hypothesis in angiosperm and conifer tree species. *Tree Physiology* **36**: 983–993.

Kavanagh KL, Pangle R, Schotzko AD. 2007. Nocturnal transpiration causing disequilibrium between soil and stem predawn water potential in mixed conifer forests of Idaho. *Tree Physiology* **27**: 621–629.

Keith H, Van Gorsel E, Jacobsen KL, Cleugh HA. 2012. Dynamics of carbon exchange in a *Eucalyptus* forest in response to interacting disturbance factors. *Agricultural and Forest Meteorology* **153**: 67–81.

Klein T. 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Functional Ecology* **28**: 1313–1320.

Kursar TA, Engelbrecht BM, Burke A, Tyree MT, EI Omari B, Giraldo JP. 2009. Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology* **23**: 93–102.

Li X, Blackman CJ, Choat B, Duursma RA, Rymer PD, Medlyn BE, Tissue DT. 2018. Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant, Cell & Environment* **41**: 646–660.

Losso A, Bär A, Dämon B, Dullin C, Ganthaler A, Petruzzellis F, Savi T, Tromba G, Nardini A, Mayr S. 2019. Insights from *in vivo* micro-CT analysis: testing the hydraulic vulnerability segmentation in *Acer pseudoplatanus* and *Fagus sylvatica* seedlings. *New Phytologist* **221**: 1831–1842.

MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**: 377–385.

Manoli G, Bonetti S, Domec J-C, Putti M, Katul G, Marani M. 2014. Tree root systems competing for soil moisture in a 3D soil–plant model. *Advances in Water Resources* **66**: 32–42.

Martin-StPaul N, Delzon S, Cochard H. 2017. Plant resistance to drought depends on timely stomatal closure. *Ecology Letters* **20**: 1437–1447.

Maslin B. 2001. Acacia dealbata. In: Orchard AE, Wilson AJG, eds. *Flora of Australia*. Melbourne, Australia: ABRS/CSIRO, 234.

McDowell NG, Ryan MG, Zeppel MJB, Tissue DT. 2013. Feature: improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. *New Phytologist* **200**: 289–293.

Meakem V, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Muller-Landau HC, Wright SJ, Hubbell SP, Condit R, Anderson-Teixeira KJ. 2018. Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytologist* **219**: 947–958.

Millar CI, Stephenson NL. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* **349**: 823–826.

Mitchell PJ, O'Grady AP, Hayes KR, Pinkard EA. 2014. Exposure of trees to drought-induced die-off is defined by a common climatic threshold across different vegetation types. *Ecology and Evolution* **4**: 1088–1101.

Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* **88**: 2259–2269.

Nolan RH, Gauthey A, Losso A, Medlyn BE, Smith R, Chhajed SS, Fuller K, Song M, Li X, Beaumont LJ *et al.* 2021. Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought. *New Phytologist* **230**: 1354–1365.

Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* **1**: 467–471.

Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, López-González G, Malhi Y, Monteagudo A, Peacock J, Quesada CA *et al.* 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**: 1344–1347.

Phillips OL, van der Heijden G, Lewis SL, López-González G, Aragão LEOC, Lloyd J, Malhi Y, Monteagudo A, Almeida S, Dávila EA *et al.* 2010. Drought–mortality relationships for tropical forests. *New Phytologist* **187**: 631–646.

Piao T, Comita LS, Jin G, Kim JH. 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* **172**: 207–217.

Pillet M, Joetzjer E, Belmin C, Chave J, Ciais P, Dourdain A, Evans M, Hérault B, Luyssaert S, Poulter B. 2018. Disentangling competitive vs. climatic drivers of tropical forest mortality. *Journal of Ecology* **106**: 1165–1179.

Powers JS, Vargas-G G, Brodribb TJ, Schwartz NB, Pérez-Aviles D, Smith-Martin CM, Becknell JM, Aureli F, Blanco R, Calderón-Morales E *et al.* 2020. A catastrophic tropical drought kills hydraulically vulnerable tree species. *Global Change Biology* **26**: 3122–3133.

R Development Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rice KJ, Matzner SL, Byer W, Brown JR. 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* **139**: 190–198.

Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS *et al.* 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* **528**: 119.

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B *et al.* 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* **9**: 676–682.

Scholander PF, Bradstreet ED, Hemmingsen E, Hammel H. 1965. Sap pressure in vascular plants: negative hydrostatic pressure can be measured in plants. *Science* **148**: 339–346.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation

Scholz FG, Bucci SJ, Arias N, Meinzer FC, Goldstein G. 2012. Osmotic and elastic adjustments in cold desert shrubs differing in rooting depth: coping with drought and subzero temperatures. *Oecologia* **170**: 885–897.

Simonin K, Kolb TE, Montes-Helu M, Koch GW. 2006. Restoration thinning and influence of tree size and leaf area to sapwood area ratio on water relations of *Pinus ponderosa*. *Tree Physiology* **26**: 493–503.

Skelton RP, West AG, Dawson TE. 2015. Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences, USA* **112**: 5744–5749.

Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL. 2019. Which trees die during drought? The key role of insect host-tree selection. *Journal of Ecology* **107**: 2383–2401.

Tardieu F, Simonneau T. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany* **49**: 419–432.

Tomasella M, Casolo V, Natale S, Petruzzellis F, Kofler W, Beikircher B, Mayr S, Nardini A. 2021. Shade-induced reduction of stem non-structural carbohydrates increases xylem vulnerability to embolism and impedes hydraulic recovery in *Populus nigra*. *New Phytologist* **231**: 108–121.

Trenberth KE, Dai A, Van Der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J. 2014. Global warming and changes in drought. *Nature Climate Change* **4**: 17–22.

Trinder CJ, Brooker RW, Robinson D. 2013. Plant ecology's guilty little secret: understanding the dynamics of plant competition. *Functional Ecology* **27**: 918–929.

Tyree MT, Sperry JS. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Biology* **40**: 19–36.

Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672–683.

Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate* **23**: 1696–1718.

Walsh N, Entwisle T. 1999. *Flora of Victoria: dicotyledons Cornaceae to Asteraceae*. Melbourne, Australia: Inkata Press.

Ward D, Shrestha MK, Musli I. 2006. Are invasive mistletoes killing *Ziziphus spina-christi*? *Israel Journal of Plant Sciences* **54**: 113–117.

Waring RH, Cleary BD. 1967. Plant moisture stress: evaluation by pressure bomb. *Science* **155**: 1248–1254.

Williams K, Potts B. 1996. The natural distribution of *Eucalyptus* species in Tasmania. *Tasforests* **8**: 39–165.

Wyse SV, Macinnis-Ng CM, Burns BR, Clearwater MJ, Schwendenmann L. 2013. Species assemblage patterns around a dominant emergent tree are associated with drought resistance. *Tree Physiology* **33**: 1269–1283.

Young DJN, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* **20**: 78–86.

Zhu Y, Queenborough S, Condit R, Hubbell S, Ma K, Comita L. 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecology Letters* **21**: 506–515.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Size-frequency distributions of *Eucalyptus delegatensis* and *Eucalyptus regnans* in AFEX treatments.

Fig. S2 Size-frequency distributions of *Pomaderris apetala* and *Acacia dealbata* in AFEX treatments.

Fig. S3 Summed basal area of each species in transects.

Fig. S4 Species transect density and summed basal are correlation.

Fig. S5 Scatterplots of eucalypt damage and individual tree basal area.

Fig. S6 Scatterplots of *Eucalyptus delegatensis* damage and species transect densities.

Fig. S7 Scatterplots of *Eucalyptus regnans* damage and species transect densities.

Fig. S8 Unnormalized stomatal conductance (g_s) in response to declining leaf water potential.

Table S1 Summary of the AFEX evenness treatments.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

© 2021 The Authors
New Phytologist © 2021 New Phytologist Foundation