Variation in stem hydraulic capacitance in two *Eucalyptus pauciflora* subspecies across an elevation gradient

Mei Davey*[1], Pia Cunningham[1], James Davies[1]

* Corresponding author: u7121419@anu.edu.au
[1] Research School of Biology, ANU, Canberra, ACT, Australia

Abstract

Vegetation dieback is a concerning environmental phenomenon whose frequency appears to be increasing globally. The rate of dieback has recently intensified throughout subalpine snow gum woodlands in Kosciuszko National Park for reasons that are not well understood. There is a lack of research focused on the changes in stand hydraulics across elevation and how this may influence snow-gum susceptibility to woodborer-associated dieback. This study examined the relationship between stem hydraulic capacitance and elevation in two subspecies of *Eucalyptus pauciflora* (Sieber ex Spreng.) which appear to be differentially affected by dieback: *Eucalyptus pauciflora* subspecies *niphophila* (Maiden and Blakely) and *Eucalyptus pauciflora* subspecies *pauciflora* (Sieber ex Spreng.). Stem hydraulic capacitance and saturated water content was measured in 100 trees, ten from each of ten sites evenly spaced across a 1,000m elevation gradient. Across subspecies, we observed a significant decrease in stem hydraulic capacitance with elevation. The response of stem hydraulic capacitance to elevational change was species-specific. Further research should focus on other drought traits across snow gum subspecies and elevation to create a broader understanding of stand hydraulics and other physiological traits influencing woodborer-associated dieback susceptibility.

Running Title: Stem hydraulic capacitance and elevation in *Eucalyptus pauciflora*

Key Words: dieback, woodborer, water stress, hydraulics, *Eucalyptus pauciflora* subspecies *niphophila*, *Eucalyptus pauciflora* subspecies *pauciflora*, *Phoracantha*

Introduction

Climate change presents a significant and imminent threat to the diversity and persistence of delicate alpine systems, which are vulnerable due to their reliance on long-lasting snow cover, low temperatures and exacerbated temperature change at higher elevations (Gilbert & Vincent 2013; Mountain Research Initiative EDW Working Group 2015). Current climate change predictions suggest that more frequent and severe drought events will pose severe problems for forest persistence (Allen *et al*. 2010; Nolan *et al*. 2021). Forest-scale dieback is an abnormal regression of the tree canopy, leading to the eventual death of the entire stand. Climate change – more specifically, the predicted increase in heatwave and drought events – will potentially cause this phenomenon to become more widespread globally (Allen 2009; Ward-Jones 2020). Although vegetation dieback has a complex aetiology, chronic or acute climate-induced drought appears to be a significant driver, increasing plant stress and

vulnerability to insect predation; in fact, research has repeatedly shown that droughts are associated with an increase in vegetation dieback (van Mantgem & Stephenson 2007; Allen *et al*. 2010; Jactel *et al*. 2012).

In Kosciuszko National Park (KNP), of the Snowy Mountains region of southern NSW, Australia, a large-scale dieback event is in progress across the snow gum woodlands that dominate the sub-alpine region (NSW National Parks and Wildlife Service 2003; Ward-Jones 2021). *Eucalyptus pauciflora* is a species of snow gum that occupies a wide geographical range. *Eucalyptus pauciflora* subsp. *pauciflora* occurs from sea level to ~1,600m in Victoria, NSW, South Australia, Tasmania and Queensland (Doherty *et al*. 2015). *Eucalyptus pauciflora* subsp. *niphophila* is largely restricted to above 1,600m in parts of ACT, NSW and Victoria (Doherty *et al*. 2015). Recent data on snow gum dieback in KNP found that the likelihood of exhibiting dieback symptoms was associated with elevation; specifically, the likelihood of showing symptoms of dieback was greatest towards 1,500–1,600m above sea level (ASL) (Ward-Jones 2020). Anecdotally, this is the elevation at which subsp. *pauciflora* begins to transition into subsp. *niphophila*. Preliminary observations by Ward-Jones (2020) link the snow gum dieback to eucalypt wood borer beetles of the *Phoracantha* genus whose larvae feed on the phloem and cambium tissues of living stands, causing ringbarking and, ultimately, death (Hanks *et al*. 1991, 1993).

There is a paucity of research focused on changes in stand hydraulics with elevation and how hydraulics may influence the vulnerability of stands to woodborer-induced dieback, particularly regarding the current snow gum dieback in KNP. Consequently, there is an urgent need to understand physiological traits that may influence the vulnerability of snow gum subspecies to dieback, particularly because the two subspecies appear to be differentially affected.

Hydraulic capacitance (from here on capacitance) is a function of a plant's tissue (organ-specific) and describes the ability of plant tissue to both store and release water into the xylem (Scholz *et al*. 2011, p. 343). Put simply, capacitance is the change in water content for a given change in water potential (Bryant *et al*. 2021). In response to changes in xylem pressure, capacitance can buffer daily fluctuations in xylem potential, thereby reducing the risk of embolism, and inferring elasticity to the plant's water transport system (Meinzer *et al*. 2009; Scholz *et al*. 2011, p. 343). Since capacitance plays a role in stabilising xylem potential and avoiding hydraulic failure, it is an important trait to consider when assessing how a plant copes with drought stress (Meinzer *et al*. 2009). However, there may be a trade-off between having a high capacitance and maintaining tissue water content. Stands with high capacitance have greater fluctuations in their diurnal tissue water content, leaving them with low water content more frequently throughout the day (Bryant *et al*. 2021). Therefore, it is reasonable to hypothesise that stands with high capacitance are more vulnerable to woodborer attacks as they spend a larger proportion of the day with low tissue water content. Accordingly, it would be valuable to test for differences in hydraulic stem capacitance (from here on stem capacitance) in subspecies of *E. pauciflora* – one that appears to be affected by dieback: subsp. *niphophila*, and one that is unaffected: subsp. *pauciflora*.

Plants transport water through a negative tension gradient from the soil to the leaves, which is generated through transpiration (Kim *et al*. 2014). However, this tension renders the xylem vulnerable to embolism formation within the xylem vessels, leading to the rupture of xylem conduits by cavitation (Brodersen *et al*. 2014). Water stress can lead to tree mortality by inducing hydraulic failure (Allen 2009; Meinzer *et al*. 2009). Plants subjected to drought experience a decline in water content and in water potential (Ψ), resulting in loss of cell turgor and protoplasm collapse (Bryant *et al*. 2021). A drop in Ψ increases xylem tension and, subsequently, the risk of cavitation (Bryant *et al*. 2021). Water stress in trees may be associated with a greater vulnerability to wood borers following drought. Previous research

has shown that *Phoracantha* larvae cannot survive in well-watered bark and instead show greater survivability in water-stressed stands (Nahrung *et al.* 2014).

Aims and hypotheses

In this study we aimed to explore the relationship between stem capacitance and elevation in subsp. *niphophila* and subsp. *pauciflora* in KNP. While the two subspecies are closely related, subsp. *niphophila* appears to be more susceptible to dieback than subsp. *pauciflora*; hence, we aimed to develop understanding of how capacitance varies between the subspecies and over elevation.

We hypothesised that as the higher-elevation subspecies, subsp. *niphophila* would have a higher stem capacitance than the lower-elevation subspecies, subsp. *pauciflora*. Hence, stem capacitance would increase with elevation.

Higher elevations in KNP have wetter soils (Körner & Cochrane 1985). Therefore, these trees can afford to lose more water from the tissues given a change in water potential, as it will likely be rehydrated rapidly. In addition, because high capacitance trees experience wider fluctuations in their daily water cycles, they will reach a lower water saturation deficit than those with low hydraulic capacitance (Körner & Cochrane 1985). Körner and Cochrane (1985) showed that higher elevation trees in KNP reach higher daily water saturation deficit values than lower trees; hence, they may have high hydraulic capacitance.

Methods

Sample species

The two snow gum subspecies of interest were *Eucalyptus pauciflora* subsp. *niphophila* and *Eucalyptus pauciflora* subsp*. pauciflora*. Subspecies *pauciflora* is distributed on slopes below around 1,600m, while subsp. *niphophila* dominates above 1,600m. To distinguish the subspecies before sampling, leaf samples from *E. pauciflora* subspecies were collected, and differences in leaf and bud characteristics were observed based on the descriptions provided by Green (1969).

Site selection

Data collection was completed in early December 2021 during a La Niña weather cycle. Sampling was conducted at ten sites adjacent to Kosciuszko Road along a high-resolution elevational gradient that continued from Charlotte Pass lookout (highest elevation) to Creel Bay, Lake Jindabyne (lowest elevation). The elevation and GPS coordinates for each site are shown in Table 1. The 1,600m–1,500m transition zone from subsp*. niphophila* to subsp*. pauciflora* woodlands was excluded from the study due to the extensive hybridisation that occurs and the associated difficulty of distinguishing subspecies.

Each subspecies was measured at five sites varying in elevation; subsp*. niphophila* sites were an average of 74m apart in elevation while the subsp. *pauciflora* sites were an average of 91m apart in elevation (Table 1). Sites were randomly chosen based on their elevation, their accessibility and the representation of the relevant species. All trees sampled had a diameter at breast height (DBH) greater than 10cm and did not display later symptoms of woodborer dieback based on guidelines established previously by Fenner School of Environment and Society, that is, bark intact with no signs of borer galleries nor frass holes (Ward-Jones 2020).

Ten trees were sampled at each site, and one terminal branch of approximately 1m was sampled from each tree. From the branch, five leaf-stem cuttings were sectioned off (approximately 15cm in length), each consisting of at least one healthy petiole and leaf.

Stem-leaf cuttings were placed into separate sealable bags labelled by site letter and tree number; these bags were breathed into to ensure high humidity within them and, once sealed, were stored in large black bags to block light from reaching the samples and cease photosynthetic reactions.

Table 1: Overview of sites, ID, elevation and GPS coordinates.

| Subspecies | Elevation (m) | GPS | |
		Latitude	Longitude
niphophila	1946	-36.43664S	148.3248E
	1830	-36.435624S	148.3332E
	1790	-36.429949S	148.3621E
	1710	-36.393548S	148.4313E
	1660	-36.38524S	148.4511E
pauciflora	1430	-36.349747S	148.5649E
	1340	-36.349654S	148.5481E
	1250	-36.344476S	148.5373E
	1070	-36.351293S	148.5196E
	967	-36.363342S	148.4804E

Measuring hydraulic capacitance

Sample analysis was undertaken on the days immediately following sampling. To obtain stem capacitance (C) (gg^{-1} MPa^{-1}) for each tree, relative stem water content (WC) (gg^{-1}) and leaf water potential (Ψ_{leaf}) (MPa) were measured to construct pressure-volume (p-v) curves from which the slope (stem capacitance) could be generated (Figure 1).
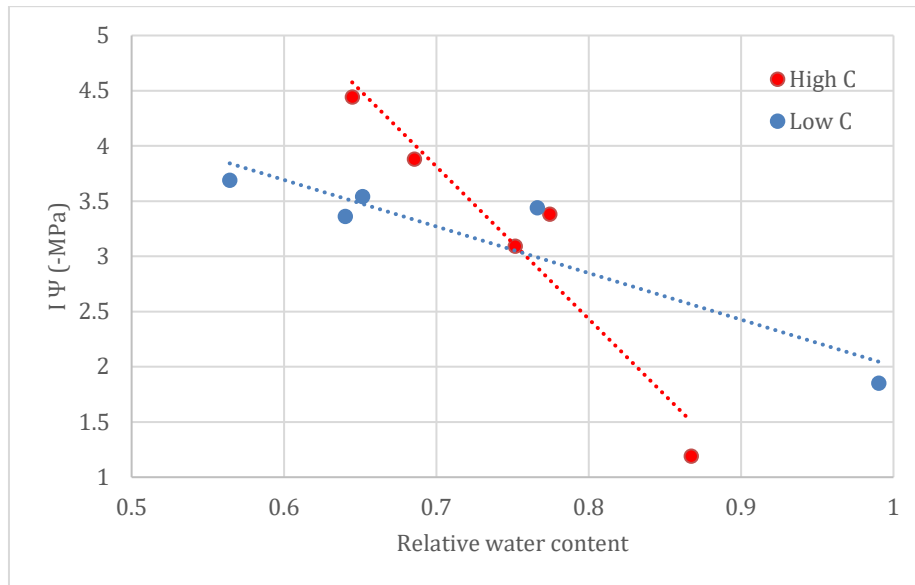
Figure 1: *An illustrative pressure-volume curve showing two different allometric relationships between stem pressure (Ψ) and stem water volume (relative water content). Different levels of slope will result in either high or low capacitance strategies. The data points for each line represent one tree. The absolute value for capacitance is the slope of the line.*

Water potential

The stem-leaf cuttings were left to equilibrate for 30 minutes in the sealed bags, and then Ψ_{leaf} was obtained using a Scholander pressure chamber (1050, PMS Instruments Albany). Pressure-volume curves were created from five data point measurements (one measure for each leaf-stem cutting, for each tree) using a progressive bench drying method, as follows.

The first cutting was measured straight out of the humid bag after the 30-minute equilibrium time. The other four cuttings were bench dried for around 15 minutes. Then, the second cutting was measured for water content and water potential while the three remaining cuttings went back in the humid bags and black-out bag for storage. the three remaining cuttings were dried for another 15 minutes, then the third cutting was measured while the other two went back in the bags for storage, and so on. Ideally, each successive cutting would have been dried for 15 minutes longer than the previous cutting (0 minutes, 15 minutes, 30 minutes, 45 minutes, 60 minutes); however, the bench drying time was allowed to vary to permit sufficient time for the Ψ_{leaf} to decline by 0.3-0.5 MPa between measurements, given that humidity in the field laboratory could not be controlled.

Water content

To obtain water potential for each leaf, a 1cm section of its stem was cut and weighed to obtain fresh mass (g). Each stem section was then dehydrated for 72 hours at 75°C (the time required to reach a stable mass) and then re-weighed to obtain dry mass (g). Relative water content was calculated as follows:

$$WC = \frac{fresh\ mass - dry\ mass}{dry\ mass}$$

Davey *et al.*: Variation in stem hydraulic capacitance with elevation in *Eucalyptus pauciflora*

C was calculated for each tree using the following formula:

$$C = \frac{\Delta WC}{\Delta \Psi}$$

Where ΔWC is the change in water content, and $\Delta \Psi$ is the change in leaf water potential.

Measuring stem saturated water content

Saturated stem water content was calculated as the y-intercept (WC axis) of the linear fit of WC (gg-1) versus Ψ (MPa) used to obtain capacitance, that is, the WC when Ψ = 0 MPa.

Statistical analysis

All data analysis was conducted using the R programming environment under the RStudio operating environment using the linear mixed effects modelling package *lme4* (Bates *et al.* 2015). Analysis was done in R and RStudio 3.6.1 (R Development Core Team 2019). Differences in mean stem capacitance between subspecies, sites, elevation and interaction terms were tested using analysis of variance (ANOVA). A generalised linear model was used to assess how capacitance varied with elevation and between subspecies, and how capacitance varied over elevation for each subspecies separately. Stem capacitance was the response variable; elevation and subspecies were the predictor variables. A significance level of α = <0.05 was used for all statistical analysis.

Results

Subspecies *niphophila* had lower hydraulic capacitance than subsp*. pauciflora.* Across all sites, *C* declined with increasing elevation. However, there was a subspecies–elevation interaction, suggesting that capacitance in each subspecies varies differently with changes in elevation. For subsp*. pauciflora*, there was no variation in stem capacitance in response to changing elevation (Figure 2; Table 2); however, in subsp*. niphophila*, stem capacitance was lower with increasing elevation (Figure 2; Table 2). Hence, stem capacitance in subsp. *niphophila* was highest towards the lower elevations of its range (1,600m ASL). Furthermore, there was a strong positive correlation between stem saturated water content and stem capacitance (Figure 3), suggesting a possible mechanistic association between the two variables.
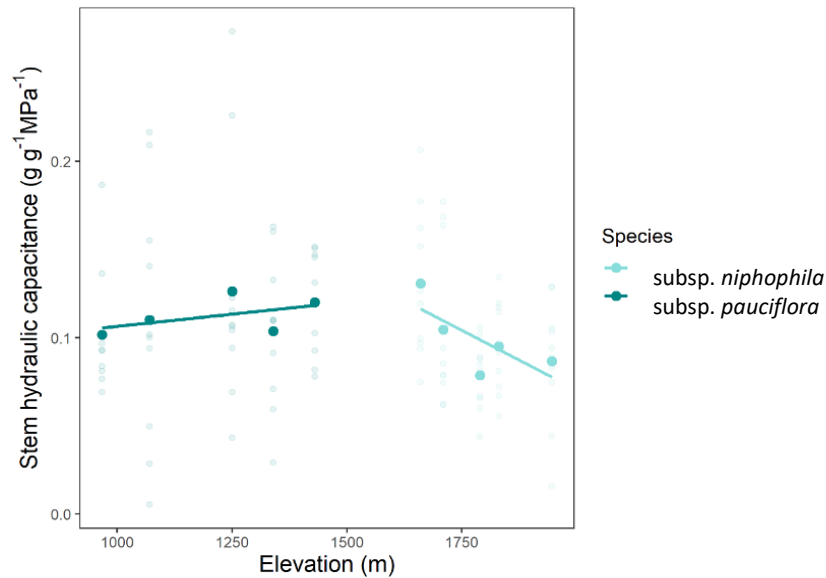
Figure 2: Relationship between stem hydraulic capacitance, elevation, and subspecies in Eucalyptus pauciflora subsp. pauciflora and subsp. niphophila. Generalised linear model (GLM) analysis yielded: a difference in capacitance between subspecies (p<0.05); an overall decline in capacitance with increasing elevation (p<0.01); a subspecies–elevation interaction on capacitance (p<0.05). Within each subspecies, GLM analysis yielded: a decrease in capacitance with increasing elevation in subsp. niphophila (p<0.05); no effect of elevation on capacitance in subsp. pauciflora (p=0.52).

Table 2: Statistical outputs for a multiple linear model analysing the variation in capacitance of two *Eucalyptus* subspecies with elevation.

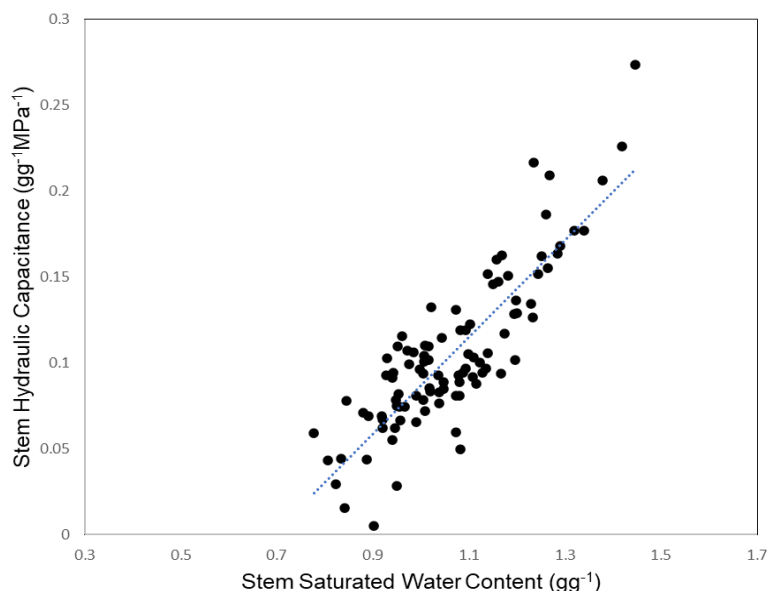| Coefficients	Estimate	SE	t-value	Pr(>t)
Subsp. *niphophila*				
Intercept	0.34	0.11	2.98	0.0036
Elevation	-0.00014	0. 000052	-2.6	0.0112
Subsp. *pauciflora*				
Intercept	0.08	0.052	1.5	0.14
Elevation	0.000028	0. 000043	0.65	0.52

Figure 3: *Relationship between saturated stem water content (gg^{-1}) and capacitance (gg^{-1} MPa^{-1}).*

Discussion

The aim of the present study was to examine the relationship between stem capacitance and elevation in two subspecies of *E. pauciflora*. Subspecies *niphophila* appears to be disproportionately susceptible to woodborer-associated dieback, compared to subsp. *pauciflora*. In performing this study, we wished to contribute to a broader understanding of the emerging snow gum dieback phenomenon in KNP, specifically to a deeper understanding of water relations in trees distributed in higher and lower elevations, and the ways in which plant hydraulics may be influencing subspecies-specific vulnerability to woodborer dieback.

We hypothesised that stem capacitance would increase with elevation; however, this hypothesis was not supported by the results (Figure 2). Across all sites, stem capacitance decreased with elevation (Table 2). We also hypothesised that subsp. *niphophila* would have a higher stem capacitance than subsp. *pauciflora*. This hypothesis was not supported by the data (Figure 3; Table 2).

Tree stands with the highest stem capacitance were those around elevations of 1,400-1,600m. Ward-Jones (2020) associated these elevations with more severe and frequent incidences of dieback. This was true for both of the subspecies that we studied (Figure 2). Within each subspecies' respective distribution, we observed declines in stem capacitance with increasing elevation in subsp*. niphophila*, but no variation in response to elevation in subsp*. pauciflora* (Table 2).

We found a difference in stem capacitance between the two subspecies overall, when not controlling for elevation (Figure 2). One of the aims of this study was to understand phenotypic differences due to genotype from phenotypic differences due to environment. This effort is complicated by the fact that our two study areas did not overlap. While there is an area of the Perisher Valley where the two subspecies coexist (approx. 1,400–1,600m ASL), *E. pauciflora* is known to readily hybridise with other species (Whiffin 1981), and identification of its subspecies is difficult and contentious (Green 1969). Therefore, this

Davey *et al.*: Variation in stem hydraulic capacitance with elevation in *Eucalyptus pauciflora*

overlapping area (the transition zone) was excluded to ensure that we were working with distinct subspecies. Difference in stem capacitance between the subspecies may be explicable by reference to their different ecologies. We can consider soil moisture at high versus low elevations. The range of subsp. *niphophila* is smaller than that of subsp. *pauciflora*: subsp. *niphophila* is restricted to cold, high elevation zones. With rising yearly temperatures, the snow line is receding upslope, increasing evaporative demand and generating water stress (Stephenson *et al.* 2018). At lower elevations (e.g., 1,400m–1,600m ASL) at the base of the snowline, stands may have adapted a higher-capacitance strategy to mitigate severe hydraulic damage. In these environments, snow cover would be less constant and thus we could assume that high capacitance would be more valuable to enable quick responses to rapid snowmelt. Furthermore, Korner and Cochrane, in their study of *E. pauciflora* trees in Perisher Valley (1985), showed that water potential increased with elevation. High capacitance is understood to buffer the demands of transpiration and maintain steady water potential (Scholz *et al.* 2011; Bryant *et al.* 2021). Hence, we retain our assumption that high capacitance is more likely to be exhibited in more variable environments.

Another possible explanation of the decreasing stem capacitance with elevation in subsp. *niphophila* may be due to the relationship between elevation and tissue density. While we did not measure wood density for this study, increasing elevation is associated with increases in wood density. Lower temperatures decrease the rate of mitotic division, thus limiting the rate of tissue formation and xylogenesis (Rossi *et al.* 2007). Furthermore, the duration of the growing season decreases with elevation, resulting in denser tissue growth at higher elevations (Körner 2021, p. 161). Figure 3 displays the relationship between stem saturated water content (WC) and stem hydraulic capacitance. Saturated WC is considered a reliable measure of the maximum water storage capacity of stem tissue. We observed a strong positive correlation between stem capacitance and stem saturated WC (Figure 3). Tissue density influences the maximum water storage capacity. As denser tissues have a lower water storage capacity, the high-elevation tree stands would be expected to have lower hydraulic capacitance (Iqbal *et al.* 2013; Körner 2008). Because of the tissue density–water storage relationship, it may be inferred that stands with the lowest capacitance have denser tissues, because capacitance is partly a function of water storage. The trees in this study with the lowest capacitance are the high-elevation stands of subsp. *niphophila.* In the context of woodborer-associated dieback, a potential explanation for the differential susceptibility of low-elevation stands of subsp. *niphophila* to dieback may be that larvae are better able to penetrate and survive in tissues of lower density (and lower water content), which would explain why dieback is most severe in lower-elevation stands; however, this proposal remains speculative until it can be tested by additional research.

Understanding the drivers of snow gum dieback is a multifactorial and complex process. In this study, we focused on stem hydraulic capacitance, but there are undoubtedly other environmental and physiological factors influencing the susceptibility of *E. pauciflora* subspecies to woodborer-linked dieback. For instance, both bark moisture content and tree diameter at breast height (DBH) have been associated with snow gum vulnerability to insect invasion (Hanks *et al.* 1991, 1993; Nahrung *et al.* 2014). Tree size and height may also influence hydraulic capacitance and be deserving of investigation in relation to woodborer dieback (Scholz *et al.* 2011, p. 345).

This study represents only a snapshot of the tree stands at one instance in time, and, therefore, we cannot comment on any temporal trends with this data alone. However, there is the potential to create a longitudinal study by geotagging trees and re-examining traits within stands to analyse changes over time. Above, we explained that we excluded trees in the transition zone from 1,400 to 1,600m because of the extensive hybridisation that occurs in this zone and the associated difficulty of distinguishing subspecies. However, it would be

beneficial to sample from this zone in future studies, because dieback appears to be most severe in this zone (Ward-Jones 2020).

Future studies exploring a broader collection of drought-related traits such as leaf hydraulic capacitance, minimum leaf/stem cuticular vapour conductance, and characteristics of xylem vessels (diameter/distribution) could yield further insight into variation in whole-tree hydraulics between *E. pauciflora* subspecies and in response to elevation. An immediate extension of this study would be to look at wood density changes with elevation – specifically in subsp. *niphophila*. A difference in wood density between subspecies is currently the most plausible explanation of why there was a decline in stem capacitance with elevation in subsp. *niphophila*. We presume that there will be a negative correlation between stem saturated WC (and stem capacitance) and tissue density in *E. pauciflora*. Finally, it may be valuable to examine changes in wood compositional structure with elevation in subsp. *niphophila*, as this may also affect stand hydraulics and thus possibly have implications for woodborer susceptibility. For example, Fisher *et al.* (2007) looked at changes in xylem vessel diameter with elevation in *Myrtaceae*, and showed that vessel diameter was reduced at high elevations (>2,000m ASL), which the authors interpreted as part of a strategy to reduce the risk of freeze-induced cavitation.

Conclusions

Our study found a significant decline in stem capacitance with elevation, which contradicted our hypothesis. However, we did demonstrate that there is a significant difference in stem capacitance between subspecies. While there was an overall decline in stem capacitance with elevation, capacitance appeared to be highest for both subspecies in the elevation range where preliminary observations suggest woodborer dieback is most severe. It is beyond the scope of this study to suggest why *Phoracantha* have not progressed into lower-elevation stands, or why subsp. *niphophila* appears to be more severely affected by woodborer-associated dieback. An immediate extension of this study would be to revisit the sampled stands and look at changes in wood density across elevation in the subspecies.

Acknowledgements

References

Allen CD (2009) Climate-induced forest dieback: an escalating global phenomenon? *Unasylva* **60**, 43–49.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**, 660–684.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.

Davey *et al.*: Variation in stem hydraulic capacitance with elevation in *Eucalyptus pauciflora*

Brodersen C, Jansen S, Choat B, Rico C, Pitterman J (2014) Cavitation resistance in seedless vascular plants: The structure and function of interconduit pit membranes. *Plant Physiology* **165**, 895–904.

Bryant C, Fuenzalida TI, Brothers N, Mencuccini M, Sack L, Binks O, Ball MC (2021) Shifting access to pools of shoot water sustains gas exchange and increases stem hydraulic safety during seasonal atmospheric drought. *Plant, Cell & Environment* **44**, 2898–2911.

Doherty MD, McDougall KL, Wright GT (2015) The flora of Kosciuszko National Park, New South Wales: summary and overview. *Cunninghamia* **15**, 13–68.

Fisher JB, Goldstein G, Jones TJ, Cordell S (2007) Wood vessel diameter is related to elevation and genotype in the Hawaiian tree *Metrosideros polymorpha* (Myrtaceae). *American Journal of Botany* **94**, 709–715.

Gilbert A, Vincent C (2013) Atmospheric temperature changes over the 20th century at very high elevations in the European Alps from englacial temperatures. *Geophysical Research Letters* **40**, 2102–2108.

Green JW (1969) Taxonomic problems associated with continuous variation in *Eucalyptus pauciflora* (snow gum) (Myrtaceae). *Taxon* **18**, 296–276.

Hanks LM, Paine TD, Millar JG, Campbell CD, Schuch UK (1991) Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *Oecologia* **119**, 400–407.

Hanks LM, Paine TD, Millar JG (1993) Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. *Oecologia* **95**, 22–29.

Heritage Office and Department of Urban Affairs and Planning (1996) 'Regional histories: regional histories of New South Wales'. (Heritage Office and Department of Urban Affairs and Planning: Sydney, Australia)

Iqbal A, Beasugrand J, Garnier P, Recous S (2013) Tissue density determines the water storage characteristics of crop residues. *Plant and Soil* **367**, 285–299.

Jactel H, Petit J, Desprez-Loustau M, Delzon S, Piou D, Battisti A, Koricheva J (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* **18**, 267–276.

Kim HK, Park J, Hwang I (2014) Investigating water transport through the xylem network in vascular plants. *Journal of Experimental Botany* **65**, 1895–1904.

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologica* **115**, 445–459.

Körner C (2008) Winter crop growth at low temperature may hold the answer for alpine treeline formation. *Plant Ecology and Diversity* **1**, 3–11.

Körner C (2021) 'Alpine plant life: functional plant ecology of high mountain ecosystems', third edition. (Springer: Cham, Switzerland)

Körner C, Cochrane PM (1985) Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. *Oecologia* **66,** 443–455.

Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* **23**, 922–930.

Mountain Research Initiative EDW Working Group (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change* **5**, 424–430.

Nahrung HF, Smith TE, Wiegand AN, Lawson SA, Debuse VJ (2014) Host tree influences on longicorn beetle (Coleoptera: Cerambycidae) attack in subtropical *Corymbia* (Myrtales: Myrtaceae). *Environmental Entomology* **43**, 37–46.

New South Wales National Parks and Wildlife Service (2003) 'The bioregions of New South Wales: their biodiversity, conservation and history.' (NSW National Parks and Wildlife Service: Hurtsville, Australia)

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

Rossi S, Deslauriers A, Anfodillo T, Carraro V (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologica* **152**, 1–12.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

RStudio Team (2020). RStudio: integrated development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/. (Version 1.3.1093).

Scholz FG, Phillips NG, Bucci SJ, Meinzer FC, Goldstein G. (2011) Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In 'Size- and age-related changes in tree structure and function.' (Eds F Meinzer, B Lachenbruch, T Dawson) *Tree Physiology* **4**. (Springer: Dordrecht, Netherlands)

Stephenson NL, Das JA, Ampersee, NJ, Cahill KG, Caprio AC, Sanders JE, Williams AP (2018) Patterns and correlates of giant sequoia foliage dieback during California's 2012–2016 hotter drought. *Forest Ecology and Management* **419–420**, 268–278.

van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* **10**, 909–916.

Ward-Jones J (2020) Dieback of subalpine snow gums, *Eucalyptus pauciflora* ssp. *niphophila* in Perisher Valley, Kosciuszko National Park: A description of symptoms and landscape drivers. Master's thesis, The Australian National University, Canberra, ACT, Australia.

Ward-Jones J (2021) 'Spotting snow-gum dieback: guide for recording incidental observations of snow-gums exhibiting dieback symptoms using the ArcGIS *Survey123* application.' Fenner School of Environment and Society, The Australian National University, Canberra, Australia.

Whiffin T (1981) Analysis of hybridization between *Eucalyptus pauciflora* Sieber ex Spreng. and *E. radiata* Sieber ex DC. (Myrtaceae). *Botanical Journal of the Linnean Society* **83**, 237–250.