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RESEARCH ARTICLE

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Change in fire frequency drives a shift in species composition in native *Eucalyptus regnans* forests: Implications for overstorey forest structure and transpiration

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Abstract

The world's most iconic forests are under threat from climate change. Climate-fire-vegetation feedback mechanisms are altering the usual successional trajectories of forests. Many obligate seeder forests across the globe are experiencing regeneration failures and subsequent alterations to their recovery trajectories. For example, the persistence of *Eucalyptus regnans* F. Muell. forests in southeast Australia is highly vulnerable to the effects of climate-driven increases in wildfire frequency. Shortening of the wildfire return interval from >100 years to < 20 years would inhibit or entirely stop regeneration of *E. regnans*, leading to replacement with understorey species such as *Acacia dealbata* Link. In this study, it is hypothesised that following such replacement, forest overstorey structure and transpiration will diverge. An experiment was designed to test this hypothesis by measuring and comparing overstorey transpiration and structural properties, including sapwood area and leaf area, between *E. regnans* and *A. dealbata* over a chronosequence (10-, 20-, 35- and 75-/80-year-old forests). We found that overstorey structure significantly diverged between the two forest types throughout the life cycle of *A. dealbata* after age 20. The study revealed strikingly different temporal patterns of water use, indicating a highly significant eco-hydrologic change as a result of this species replacement. Overall, the results provide a strong indication that after age 20, overstorey transpiration in *Acacia*-dominated forests is substantially lower than in the *E. regnans* forests they replace. This difference may lead to divergence in water yield from forested catchments where this species replacement is widespread.

KEYWORDS
climate change, fire frequency, forest overstorey, hydrologic impact, species shift, structural divergence, water yield

1 | INTRODUCTION

Changes in forest structure resulting from changing forest age and dominant species may alter evapotranspiration. This would have two significant outcomes: fundamentally changing the ecohydrologic functioning of the affected landscape and the alteration of streamflow and other ecosystem services. While forest harvesting, defoliation from pest attack and drought mortality can impact on forest species mix

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and structure, fire is the most significant disturbance agent in temperate forest ecosystems.

Recent studies in Australia (Brookhouse et al., 2013; Feikema et al., 2013; Gharun et al., 2013; Lane et al., 2006, 2010; Nolan et al., 2014, 2015) have focussed on the hydrologic impact of regeneration of eucalypt forests after single fire events, where regeneration follows predictable recovery trajectories. In fire-sensitive ecosystems, however, the occurrence of high-intensity wildfires at short return intervals has the potential to replace the dominant overstorey species with co-occurring understorey species (Adams, 2013; Brown & Johnstone, 2012; Buma et al., 2013; Fairman et al., 2016). For example, climate-driven increases in wildfire frequency are resulting in replacement of previously dominant serotinous conifer forests such as black spruce forests in the Alaskan region (Johnstone et al., 2010), lodgepole pine in the Greater Yellowstone forests (Turner et al., 2019; Westerling et al., 2011), ponderosa pine in the southwestern United States (Savage & Mast, 2005) with broadleaf species and boreal forests in North America (Coop et al., 2020).

Similar climate-driven increases in fire frequency are resulting in species replacement in Australian native serotinous forests. Since 2002, an increase in the fire return interval from the historic >100 years to < 20 years has severely damaged about 1890 km^2 of obligate seeder, *Eucalyptus* forests across Victoria (Keenan & Nitschke, 2016). This includes important water supply catchments for Australia's second-largest city (Melbourne) and Australia's "food bowl," the Murray-Darling Basin. Increases in wildfire frequency and severity in the past two decades in southeast Australia are largely consistent with climate change projections for this region, suggesting changes to fire regimes are linked with climate change (Clarke et al., 2012; Oldenborgh et al., 2020). High yielding water supply catchments in southeast Australia are dominated by fire-sensitive *Eucalyptus regnans* F. Muell. and *Eucalyptus delegatensis* R.T. Baker forests. A single wildfire in these forests results in partial or complete stand replacement (Ashton, 1976a), causing long-term increases in evapotranspiration (Vertessy et al., 2001) and reductions in streamflow (Kuczera, 1987), but a second wildfire occurring before reproductive maturity at age 20 years (Ashton, 1976a) can result in local extirpation of these two obligate-seeder species (Bowman et al., 2014, 2016), and replacement by common understorey species, often *Acacia dealbata* Link (Fairman et al., 2016; Keeley et al., 1999). This occurred over significant areas following large wildfires in 1926 and 1939.

A change from *E. regnans* to *A. dealbata* represents a dramatic shift in vegetation, perhaps one of the most dramatic globally outside of human-induced deforestation. *E. regnans*, the world's tallest Angiosperm, typically grows up to 70–100 m, which is second only to *Sequoia sempervirens* (California redwood). In contrast, *A. dealbata* is a short-lived species, growing to a maximum height of only 30 m (May, 1999). Replacement of the iconic *E. regnans* forests with *A. dealbata* forests opens a new path of successional trajectories in these forested catchments (Figure 1). The ecological implications are very significant, as are the impacts on carbon sequestration, landscape flammability and management options. Hydrologically, we may see marked divergence in forest structure and overstorey transpiration due to differences in sapwood area, leaf area and canopy conductance. The hydrologic signature of these "states", while important for water resource planning, is crucial to our understanding of landscape responses to increased stressors that are a function of climate change.

E. regnans is a long-lived species (up to 500 years) with a very high growth rate and biomass continuing to increase up to at least 250 years of age (Volkova et al., 2018), whereas *A. dealbata* is a relatively short-lived (< 100 years) pioneer species, with biomass peaking

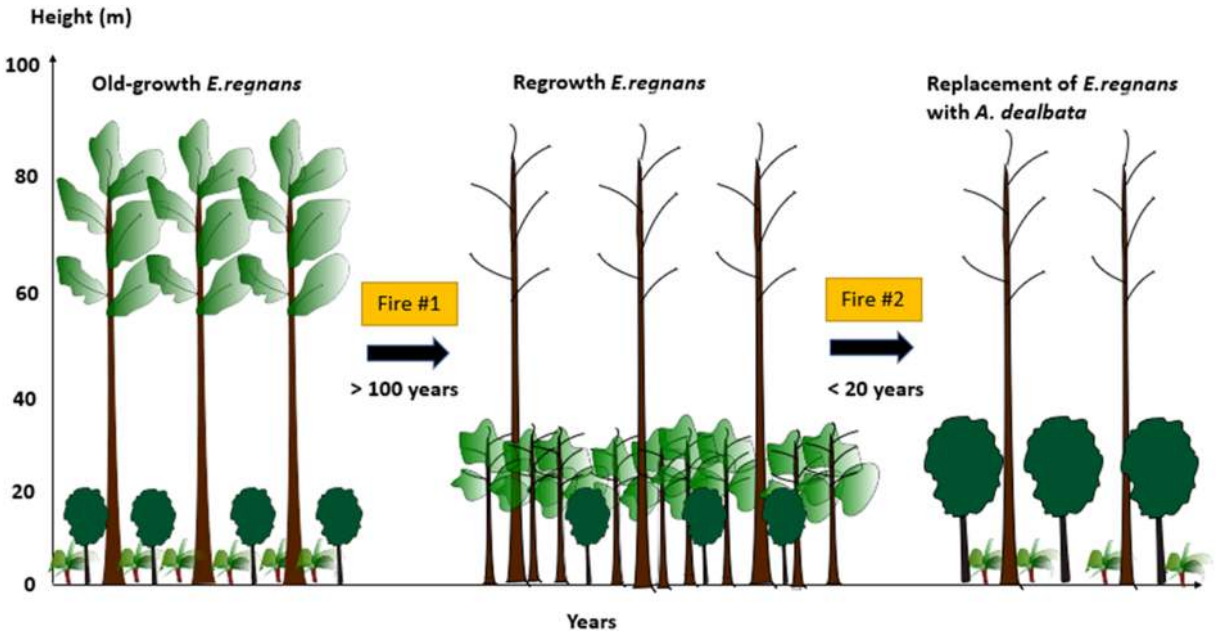


FIGURE 1 Changing successional pathways in *E. regnans* forests as a result of high-frequency fire

20–30 years after regeneration (Trouve et al., 2019). The differences in longevity and growth rates between these two forest types may cause differences in their overstorey transpiration rates throughout their life span. Forest overstorey transpiration is the product of sap velocity and sapwood area of species that are dominant in the overstorey (Dunn & Connor, 1993; Haydon et al., 1996; Kostner, 2001; Vertessy et al., 2001), and thus, stand-scale overstorey transpiration is determined by both mean sap velocity and sapwood area.

Forest sapwood area varies widely with species, age and environmental conditions (Cermak & Nadezhdina, 1998). This may occur due to variation in properties of the hydro-active sapwood among species (Wang et al., 1992). Different species can also show significantly different rates of sap velocity if they possess substantially different water-use strategies (Liu et al., 2017). Even coexisting species sharing similar environmental conditions may transpire differently because of differences in species-specific sensitivities to climate and soil water relations (Link et al., 2014). Sap velocity is driven by short-term variations in meteorological conditions, whereas the sapwood area is determined by stand structural attributes, such as tree diameter, sapwood thickness and stocking density, that change relatively slowly over time, suggesting that climate and forest structure both influence stand transpiration (Cermak & Nadezhdina, 1998; Ewers et al., 2002; Hernandez-Santana et al., 2015; Medhurst & Beadle, 2002). When a shift in overstorey species occurs, divergence in overstorey transpiration is possible because of changes either in climatic and physiological control of sap velocity or structural control of forest sapwood area.

Overstorey dominates the total evapotranspiration of most temperate forests. Wet *E. regnans* forests conform to this, except in their late senescing stage (Vertessy et al., 1998, 2001). Consequently, measurement of overstorey dynamics can illuminate knowledge gaps in the structural, functional, eco-physiological and eco-hydrological effects of replacement of *E. regnans* forests with *A. dealbata*.

Except in young forests, changes in sap velocity were studied well in mature and old-growth *E. regnans* forests. Previous studies based on mature and old-growth stages of *E. regnans* showed that sap velocity does not change significantly with the forest age (Benyon et al., 2017; Dunn & Connor, 1993). While much is known about the ecohydrology of *E. regnans* forests (Benyon et al., 2015, 2017; Kuczera, 1987; Vertessy et al., 1998, 2001), only one study has examined co-dominant stands of *E. regnans* and *A. dealbata*. Hawthorne et al. (2018) showed that mean sap velocity of 20-year-old *E. regnans* during summer (December to March) was 12.8 cm h^{-1} compared with 7.5 cm h^{-1}, in *A. dealbata* of the same age, indicating overstorey sap velocity of *E. regnans* was 71% higher than *A. dealbata* even under the same environmental conditions with similar LAI. This work suggested that there was a marked change in fluxes between the species at this age. However, this study was not designed to enable detailed comparison of water use between these two forest types over their life cycle. On reflection, the knowledge gap for forest hydrological aspects for *A. dealbata* requires further illumination, as no studies examine sap velocity, sapwood area or transpiration throughout the life cycle of *A. dealbata* forests. Given predictions that more frequent burns in *E. regnans* forests will result in their replacement by *A. dealbata*, it is timely to compare ecohydrological parameters between the two forest types throughout their life cycles to determine any significant changes in forest structure and overstorey transpiration.

In this study, it is hypothesised that if *E. regnans* is replaced with *A. dealbata* due to climate-induced increases in wildfire frequency, forest overstorey structure and transpiration will be altered. The main objectives of this study are, therefore, to (i) determine the divergence in overstorey transpiration between *E. regnans* and *A. dealbata* forests over an age sequence and (ii) identify the major drivers of this divergence process. These objectives were achieved by measuring overstorey sap velocity, sapwood area, and forest structural variables at the plot-scale in 10-, 20-, 35- and 75-/80-year-old stands of *E. regnans* and *A. dealbata*. Structural control and climate control of transpiration were evaluated for understanding the major drivers of forest transpiration after this climate-induced species replacement. It should be noted that although *E. regnans* water use and streamflow has been measured in a number of studies (e.g., Benyon et al., 2015, 2017; Dunn & Connor, 1993; Kuczera, 1987; Vertessy et al., 1998, 2001), stocking densities and structural attributes vary considerably for a given age class. It may be argued that to some extent the work of Kuczera (1987), which produced a curve of streamflow as a function of age, has led to a conceptually attractive understanding of *E. regnans* hydrology, which may be far more variable in reality. Therefore, further measurements of evapotranspiration in these forests are very useful. The significance is that water supply planning, and forest management policy and operations are heavily influenced by the age-streamflow dynamics.

2 | MATERIALS AND METHODS

Our primary research hypothesis, that if *E. regnans* is replaced with *A. dealbata*, forest overstorey structure and transpiration will diverge, was examined by testing five sub-hypotheses as shown in Table 1. While Dunn and Connor (1993) and Benyon et al. (2017) worked in mature and old-growth forests, we undertook measurements in *E. regnans* stands for two reasons: to ensure we were measuring the two species under the same environmental conditions and to fill in data gaps for young stands. Given the expense and time commitment of sapflux work across multiple stand ages, we restricted our sapflow measurements to one to two plots per species per age to test sub-hypotheses 1, 3, and 4. As stand structural attributes that determine sapwood area are much more variable both spatially and with forest age (Benyon et al., 2017; Haydon et al., 1996; Vertessy et al., 2001), a larger number of inventory plots were used (Table S1) to test sub-hypotheses 2 and 5.

2.1 | Site description, sap velocity plots

Sap velocity measurements were taken from 10-, 20-, 35- and 75-/80-year-old *E. regnans* and *A. dealbata* forests (Figure 2). During site selection, preference was given to forests which were regenerated purely with *A. dealbata* or *E. regnans* after stand-replacing

TABLE 1 Summary of sub-hypotheses tested

Sub-hypothesis (H)	Test	Test hypothesis	
		Null hypothesis	Alternative hypothesis
1.0	Stand mean sap velocity varies significantly with species and age	H_0: Stand mean sap velocity does not significantly vary with species and age	H_1: Stand mean sap velocity varies significantly with species and age
2.0	Sapwood area varies significantly with species and age	H_0: Stand sapwood area does not significantly vary with species and age	H_1: Stand sapwood area varies significantly with species and age
3.0	Stand mean transpiration varies significantly with species and age	H_0: Stand mean transpiration does not significantly vary with species and age	H_1: Stand mean transpiration varies significantly with species and age
4.0	Stand mean transpiration is controlled more by stand sapwood area than by stand mean sap velocity	H_0: Stand mean transpiration is not controlled more by stand sapwood area than by stand mean sap velocity	H_1: Stand mean transpiration is controlled more by stand sapwood area than by stand mean sap velocity
5.0	Stand sapwood area is controlled by stand structure	H_0: Stand sapwood area is not controlled by stand structure	H_1: Stand sapwood area is controlled by stand structure (stocking density, mean dbh and mean sapwood thickness, stand basal area)

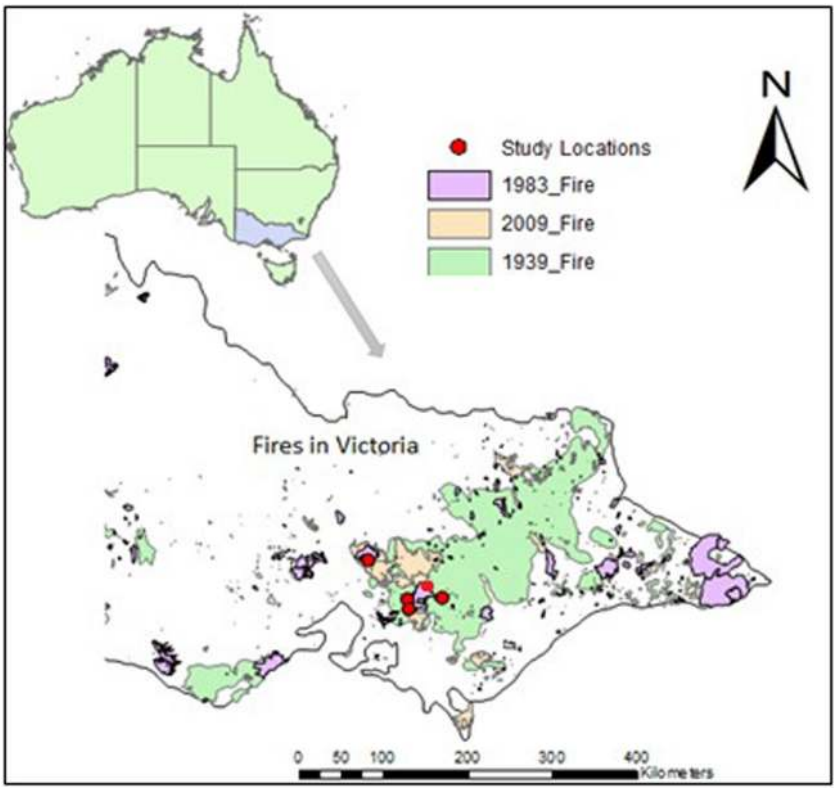


FIGURE 2 Locations of the measurement plots

fires. Both *E. regnans* and *A. dealbata* are evergreen forests. *E. regnans* is broad-leaved, whereas *A. dealbata* is a compound leaved species. After high severity fires, these two forests regenerate from seeds as even-aged forests. To accurately account for differences in species-specific sap velocity responses to climate, adjacent forests of the two species were selected from each age class where possible. The selected sites were located in areas typical of the wetter forests of southeast Australia.

2.1.1 | 10-year-old forests

Plots at Bunyip Road (BR) and Wallaby Creek (WC) were selected to represent pure patches of 10-year-old forests of both species (Table 2).

The plots at Bunyip Road (Lat: −37.919872°, Long: 145.764781°) were located within the Bunyip State Forest, in the southern part of Victoria's central highlands. Bunyip Forest has a mean annual rainfall

TABLE 2 Measurements of water use plots

Age	Species	Site/plot ID	Stand density (trees/ha)	DBH (cm)	SWT (cm)	SA (m^2 ha^{-1})
10	*A. dealbata*	WCA_1	2999 (8)	9.7 ± 1.1	2.50	14.0
10	*A. dealbata*	BRA_1	3791 (6)	10.3 ± 0.7	2.72	21.1
10	*E. regnans*	WCE_1	3791 (8)	9.7 ± 0.9	1.64	13.0
10	*E. regnans*	BRE_1	3112 (7)	9.9 ± 1.0	2.68	17.6
20	*A. dealbata*[a]		695 (5)	18.0 ± 2.4	2.0	6.7
20	*E. regnans*[a]		702 (5)	26.2 ± 3.5	2.3	11.7
35	*A. dealbata*	BCA_4	477 (8)	22.8 ± 2.9	1.40	4.40
35	*E. regnans*	BCE_4	605 (8)	34.1 ± 7.8	2.13	11.6
80	*A. dealbata*	TR_3	212 (5)	35.1 ± 2.7	1.38	3.0
80	*A. dealbata*	TR_4	332 (8)	30.6 ± 3.0	1.23	3.6
80	*E. regnans*[a]		128	83.5 ± 7.6	2.6	7.5

Note: Stand density (number of sap flow sample trees shown in brackets), mean sapwood thickness (SWT), mean stem diameter at breast height, DBH (with confidence interval) and stand sapwood area (SA) in each experimental plot. WC indicates Wallaby Creek, BR is Bunyip Road, BC is Britannia Creek, TR is Toorongo Road; A indicates *Acacia dealbata* and E is *Eucalyptus regnans*. The numbers 1, 3 and 4 indicate the plot number out of the larger number of inventory plots of each species in each location (Table S1). Sap velocities were measured in WCA_1 and WCE_1 from 12/01/2017 to 01/05/2018, BRA_1 and BRE_1 from 16/10/2017 to 30/04/2018, BCA_4 and BCE_4 from 20/09/2018 to 12/02/2019, and TR_3 and TR_4 from 04/10/2017 to 14/01/2019. Structural data for 20-year-old forests of both species and 75-year-old *E. regnans* forests were adopted from Hawthorne et al. (2018) and Benyon et al. (2017), respectively (indicate in [a] in the table).

of ~1400 mm, which is adequate for the growth of tall *E. regnans* forests. The monthly mean maximum temperature in January and July are 24.5°C and 10.3°C, respectively. *E. regnans* forest is the dominant vegetation on south-facing aspects. Many parts of Bunyip Forest were severely burnt in the 2009 wildfire and regenerated with *E. regnans*, but some patches regenerated with pure *A. dealbata*. The soils in *E. regnans* forest is commonly Krasnozem type, rich in organic matter, deep (>5 m) and well drained (Ashton, 1976b). Sap velocity of both forest types at Bunyip (Table 2, plots BRA_1 and BRE_1) was measured from 16/10/2017 until equipment was stolen on 30/04/2018.

The second 10-year-old site (Lat: −37.455117°, Long:145.194413°) was located at Wallaby Creek on the southern part of the Hume Plateau, approximately 45 km northeast of Melbourne. The dominant vegetation in this catchment is also *E. regnans* forests, regenerated in 2009 after severe wildfire killed large areas of iconic old-growth *E. regnans*. As with Bunyip Forest, some patches in Wallaby Creek regenerated with pure *A. dealbata*. Mean annual rainfall at Wallaby Creek of ~1200 mm is lower than at Bunyip and is at the lower end of the rainfall range that can sustain *E. regnans*. Monthly mean maximum temperature is 28.5°C in January (summer) and 10.7°C in July (winter). Sap velocity in *A. dealbata* and *E. regnans* at Wallaby Creek (Table 2, plots WCA_1 and WCE_1) was measured from 12/01/2017 to 01/05/2018.

2.1.2 | 20-year-old forests

Sap velocity data representing small pure patches of each species located in a 60 m × 60 m, mixed 20-year-old stand of *E. regnans* and *A. dealbata* stands at ~550 m elevation on the northern edge of the Maroondah water supply catchment about 80 km north-east of Melbourne were obtained from Hawthorne et al. (2018). They measured sap velocity in three small circular plots (mean plot diameter 12 m) of each species located within the 60 m × 60 m area from mid-October 2015 to early April 2016. The mean sapwood area and LAI for each species was determined for the stand using nine larger inventory plots. As with the other sites used in the present study, the climate is temperate, with monthly mean maximum temperatures of 23°C in January and 9°C in July and mean annual rainfall of ~1800 mm. The soil is deep, well-drained loam with high water holding capacity (Hawthorne et al., 2018).

2.1.3 | 35-year-old forests

The 35-year-old sites (Table 2) were located at Britaniana Creek (BC), approximately 80 km east of Melbourne (Lat: −37.806765°, Long:145.665704°). The climate in this region is also temperate, with a mean annual rainfall of ~1500 mm, and monthly mean maximum temperatures of 25.4°C in January and 9.4°C in July. As with the other sites, soils in this region are deep, rich in organic matter and have high water holding capacity. *E. regnans* and *A. dealbata* forests regenerated after a wildfire in February 1983 were selected to represent 35-year-old forests. Sap velocity of both forest types was measured from 20/09/2018 to 12/02/2019.

2.1.4 | 75-/80-year-old forests

Two plots on Toorongo Road (TR) in Upper Yarra catchment (part of Yarra Ranges National Park), in Victoria's central highlands, 110 km east of Melbourne, last burnt in January 1939, were selected to

represent 80-year-old *A. dealbata* (Lat: −37.769263°, Long: 146.149871°). The climate is cool temperate with a mean annual rainfall of ~1800 mm and monthly mean maximum temperature of 20.8°C in January and 7.2°C in July. Sap velocity was measured from 04/10/2017 to 14/01/2019 (Table 2).

Two years of sap velocity data for two *E. regnans* plots aged ~75 years located in Maroondah catchment ~80 km northeast of Melbourne were obtained from Benyon et al. (2017). The climate and soils are similar to the other sites, with mean annual rainfall of ~1800 m.

2.2 | Forest overstorey transpiration

Forest overstorey transpiration is the product of sap velocity and sapwood area of species that are dominated in the overstorey (Kostner, 2001) and thus, stand scale overstorey transpiration is strongly linked with both sap velocity and sapwood area of the forest (Equation 1).

$$\text{Overstorey T} = \text{Mean SV_os} \times \text{SA_os} \quad (1)$$

where Overstorey T = Transpiration from the forest overstorey, Mean SV_os = Mean sap velocity of a representative sample of trees in the overstorey, SA_os = Stand sapwood area (total sapwood cross-sectional area of the forest overstorey per unit of ground area).

Sub-hypothesis 3, which stand mean transpiration varies significantly with species and age, was evaluated by comparing stand mean overstorey transpiration across species-age combinations. To do this, SA_OS in Equation (1) was estimated for each species/age as the mean of all inventory plots in which SA was determined (plots in Table S1), whereas SV_OS was the mean of the one or two sap velocity measurement plots in each species/age class (plots in Table 2).

2.3 | Selection of sample trees for sap velocity measurements

Sap velocity was measured concurrently in between five and eight sample trees per plot in each species/age class combination (Table 2). Sample trees were randomly selected from circular plots that were 15 m in diameter in the 10-year-old and 35-year-old stands and 24 m in diameter in the 80-year-old *A. dealbata* plots. These selected sample trees represented the entire size class distribution of each plot.

Sap velocity was also measured in a large, 80-year-old *E. regnans* tree near plot TR_4 (age 80) using four sap flow meters from April 2018 to January 2019 for comparison with the 75-year-old *E. regnans* sap velocity data from Benyon et al. (2017).

2.4 | Measurement and estimation of sap velocity

This study used the heat ratio method (ICT International, Armidale, NSW) to measure sap velocity in all species/age classes, consistent with the studies of Hawthorne et al. (2018) and Benyon et al. (2017). Each HRM (heat ratio method) sap flow meter (SFM) includes a heater probe located between two sensor probes positioned 5 mm above and below the heater. Each sensor probe contains sensors located 7.5 and 22.5 mm from the probe tip. Sap velocity near to the heartwood was recorded by the inner sensor and sap velocity near the cambium was recorded by the outer sensor. The middle needle generated a 25-J heat pulse every 30 min. Following each heat pulse, the ratio of temperature increase in the downstream (upper) sensor compared with the upstream (lower) sensor was measured by the logger. Heat pulse velocity (*Vh*) was then estimated by the logger using this ratio, as shown in Equation (2) (Marshall, 1958).

$$\text{Vh} = \frac{\text{K}}{\text{x}} \ln\left(\frac{\text{V1}}{\text{V2}}\right) 3600 \quad (2)$$

where k is the thermal diffusivity ($cm^2\ s^{-1}$), x is the distance (cm) between the heater and the two temperature sensors, and v_1 and v_2 are temperature increases from initial temperature (°C) in the downstream and upstream sensors, respectively.

Thermal diffusivity (*k*) (Marshall, 1958), thermal conductivity (*Kw*) of dry wood (Swanson & Whitfield, 1981), moisture content (*mc*), green density (ρ), basic density (ρb) and wound correction factors (Burgess et al., 2001) were estimated to correct the sap flow velocity in each sample tree. Sap velocity in the xylem tissues can be determined using corrected heat pulse velocity and other estimated and available factors in the literature (Equation 3).

$$\text{SV} = \frac{\text{Vc}\,\rho\text{b}\,(\text{Cw} + \text{mcCs})}{\rho\text{sCs}} \quad (3)$$

where *SV* is the corrected sap flow velocity, *Vc* is the heat pulse velocity corrected for the wound effect, ρb is the basic density of wood ($kg\ m^{-3}$), *Cw* is the specific heat capacity of the wood (1200 $J\ kg^{-1}{}^{\circ}C^{-1}$ at 20°C; Becker & Edwards, 1999; Bleby et al., 2004), *Cs* is the specific heat capacity of sap (4182 $J\ kg^{-1}{}^{\circ}C^{-1}$ at 20°C; Bleby et al., 2004), *mc* is moisture content of wood and ρs is the density of sap.

When the downstream and upstream probe holes are drilled exactly the same distance above and below the heater, Equations (2) and (3) will give *SV* of zero at times when there is no sap movement. Bias caused by small inaccuracies in drilling the probe holes can be corrected for using the calculated *SV* at times when sap is not flowing, known as the zero baseline. Some of the plots were in national parks and so rather than damaging the trees by cutting the xylem with a chain saw below the sensors as is the most accurate method, the zero baseline was estimated by assuming the minimum flow calculated during each measurement period represented true zero flow. Then, the zero-baseline correction for sap velocity in each sensor was calculated as the difference between sap velocity of each sensor and the predetermined baseline of the respective sensor. Finally, weights were assigned to inner and outer sensors

of each logger depending on the position of the inner sensor relative to the location of the sapwood/heartwood boundary.

2.5 | Meteorological measurements

Meteorological variables were measured in both *E. regnans* and *A. dealbata* forests to account for seasonal variations in climate at each site. Temperature and relative humidity sensors were set up at the centre of each water use plot, and data were logged using CR1000 data loggers (Campbell Scientific Inc, Logan, UT, USA). Vapour pressure deficit (VPD) was calculated using the temperature and humidity measurements. Automatic weather stations were set up in clearings approximately 5 km away from each experimental site to measure weather conditions and precipitation in the open. These automatic weather stations measured rainfall (mm), solar radiation (W/m^2), air temperature (°C), relative humidity (%) and wind speed (m/s) every 4 min. Data from weather stations in the open were cross-validated with data from Bureau of Meteorology (BOM) weather station numbers 88060, 86094, and 85079. Weather data were also obtained from the SILO database (Scientific Information for Landowners; https://www.longpaddock.qld.gov.au/silo) for the last 116 years (1900–2016) to identify anomalies of rainfall during the data collection period and also to verify the proper functioning of weather stations at the study sites.

2.6 | External drivers of sap velocity

Climate drivers of transpiration were examined by modelling sap velocity versus meteorological variables. Sap flux per unit of VPD was used as a proxy for canopy conductance (Buckley et al., 2012) to test the influence of soil water on sap velocity. Practical difficulties in measuring root zone soil moisture in remote locations that were hard to access meant we were unable to measure changes in soil water for this study. Instead, daily root zone soil moisture in the study plots was modelled using the grid-based Australian Landscape Water Balance Model (AWRA-Lv6, Frost et al., 2018). The main purpose of this was to determine whether there may have been periods when transpiration was limited by low root zone soil moisture. Linear regression of sap flux density: VPD ratio against modelled root zone soil moisture indicated that the regression coefficient for root zone soil moisture was not significant for both *E. regnans* and *A. dealbata* stands ($P > 0.05$; R^2: 0.002 for *E. regnans* and R^2: 0.0007 for *A. dealbata*). Therefore, root zone soil moisture did not appear to be a controlling factor of sap velocity in both *E. regnans* and *A. dealbata* in this study.

2.7 | Overstorey forest structural measurements in *E. regnans* and *A. dealbata* forests

For measurement of forest structure, additional pure patches of *E. regnans* and *A. dealbata* were identified using knowledge from academic and professional experts, Google explorer and Near maps. Including the eight water use plots, 35 inventory plots were selected from 10-year-old stands at Wallaby Creek and Bunyip, from 35-year-old stands at Portus Road and Britannia Creek and from 80-year-old *A. dealbata* stands at Toorongo Road, Link Road and Mount Toorongo Road (Table S1). In addition, the 75-year-old *E. regnans* plots that were measured by Benyon et al. (2017) were incorporated in the analysis to enable structural comparison between the two forests at age 75/80. Stocking density, stand basal area, stand sapwood area, stand mean sapwood thickness, stand mean dbh, tree dbh and tree sapwood area were measured in five to eight inventory plots in each species-age combination. Data representing pure stands of *E. regnans* and *A. dealbata* from Hawthorne et al. (2018) were used to compare overstorey structure at age 20.

2.7.1 | Forest sapwood area

Sapwood thickness was measured in a random sample of trees in each plot, representing all diameter classes. On average, 83% of trees in each plot were selected to measure both sapwood thickness and bark thickness. Two to four sapwood cores were taken from around each stem at breast height using a 5-mm-diameter increment corer. Sapwood thickness was measured in each sample core after staining with 1% Methyl-Orange solution (to detect the sapwood-heart-wood boundary) and tree sapwood area at breast height was estimated using the mean sapwood thickness and under-bark stem diameter measurements. For trees in which sapwood thickness was not measured, a linear regression relationship between tree basal area and tree sapwood area was used to predict sapwood area (number of trees ranged from 17 to 63, with R^2 ranging from 0.59 to 0.98). Stand sapwood area was estimated for each inventory plot as the sum of the sapwood areas of the individual trees, expressed in $m^2\ ha^{-1}$.

2.7.2 | LAI measurement

Leaf area index (LAI) in each of the water use plots was estimated using hemispherical canopy images taken with a Nikon Coolpix 8400 digital camera equipped with an FC 8 mm fisheye lens. From each plot, 20–25 images were collected during different seasons to calculate average LAI for each species age class. Image acquisition was made before sunrise or under overcast conditions to avoid direct sunlight, which may cause errors in LAI estimation (Welles & Norman, 1991). The exposure of the camera was calibrated at each LAI measurement plot as described by Macfarlane et al. (2007). All hemispherical images were analysed using the Hemi view 2.1 (Delta-T devices, Ltd., Cambridge, UK) image processing software package.

2.8 | Statistical analysis

Sub-hypothesis 1 that stand mean sap velocity varies significantly with species and age was tested using two-sample *t* tests (Dunn &

Connor, 1993) and Mann–Whitney test (Becker, 1996). Samples comprised of long-term average sap velocity of individual trees in each species-age class. The effects of species and age on sap velocity were tested using data from all sites at long term and daily time resolutions. To avoid any bias due to the seasonal effects on sap velocity and transpiration, statistical analysis was confined to the 151 days of the year (October–February), when sap velocity data were available for all species/age class combinations measured in 2017–2018 (Bunyip Road, Wallaby Creek, Toorongo Road) and 2018–2019 (Britannia Creek). We made an assumption that the extra data from the Hawthorne et al. (2018) and Benyon et al. (2017) for the same 151-day period of the year (but in different years) could be used in these analyses. While environmental conditions were clearly not identical, they were not out of the "ordinary" (i.e., no drought/heat waves or extreme wet periods).

As well as comparing plot mean sap velocities directly, to remove the effects of site and year to year differences in climatic conditions, tree and stand mean sap velocities were adjusted to a common set of climatic conditions. When sap velocity is not water limited, as was the case in this study, VPD is the main external driver of transpiration via its effect on sap velocity. We compared current and previously measured mean sap velocity data from all species and age class combinations after normalising mean sap velocities to account for differences in VPD. This was done by fitting a regression of daily mean sap velocity of each sample tree against daily mean VPD at each site. These fitted relationships were then used to estimate daily mean sap velocity for each tree using the daily VPD averaged across all sites: for each of the 151 days of the year common to all sites, the average VPD across all sites was calculated and then the tree-specific relationship between sap velocity and VPD was used to estimate the daily sap velocity for each tree. This enabled a direct comparison of plot mean sap velocity for the 151-day period as if all sites had experienced exactly the same sequence of daily VPDs.

Age-related structural divergence was tested using a two-way analysis of variance (ANOVA) and Tukey's post hoc analysis (for multiple pairwise comparisons). Then, the statistical significance of species and age effects on stand mean dbh, stand basal area and stand density was evaluated.

Differences in daily transpiration between the two forest types across the age classes were tested with a two-factor repeated measure ANOVA. Multiple comparisons across species and ages were undertaken with Tukey's HSD post hoc test (H_3).

2.9 | Examining structural control of transpiration

To evaluate which variable (sap velocity or stand sapwood area) is more important in determining stand transpiration in the two forest types, sub-hypothesis 4 was tested by comparing the strength of regression relationships between stand mean daily transpiration and stand sapwood area and between stand mean daily transpiration and stand mean sap velocity. Further, multiple linear regression was used to determine the statistical significance and relative importance of sap velocity (SV) and sapwood area (SA) in driving stand mean daily transpiration (T).

Sub-hypothesis 5 that stand sapwood area is controlled by stand structural properties was tested using regression relationships between stand sapwood area, and stand basal area in all water use plots. Further, the variations in stand density, stand basal area and stand sapwood thickness between species along the age sequence were evaluated.

3 | RESULTS

3.1 | Species and age effect on sap velocity

Sub-hypothesis 1.0, which mean sap velocity (unadjusted for VPD) varies significantly with species and age, was supported but with a low degree of confidence. Over the October to February period,

TABLE 3 Mean sap velocity (cm h^{-1}) for the two species by age for the October to February period

	Age			
Species	**10**	**20**	**35**	**75/80**
Sap velocities unadjusted for VPD				
A. dealbata	10.3 ± 1.6	8.6 ± 1.4	8.2 ± 2.3	10.5 ± 2.6
E. regnans	9.7 ± 1.4	14.7 ± 1.6	9.6 ± 2.9	12.4 ± 1.9
P value (*t* test) at 5% significance	0.580	0.000	0.457	0.198
P value (Mann–Whitney) at 5% significance	0.505	0.000	0.494	0.194
Sap velocities adjusted for VPD				
A. dealbata	11.6 ± 2.0	8.6 ± 1.9	7.5 ± 2.0	11.7 ± 2.8
E. regnans	11.8 ± 2.0	13.4 ± 0.6	8.6 ± 3.0	11.9 ± 1.7
P value (*t* test) at 5% significance	0.920	0.031	0.592	0.857

Note: Directly measured sap velocity is denoted as sap velocity unadjusted for VPD and sap velocities adjusted for VPD is normalised sap velocities for differences in VPD. The age 20 data are from Hawthorne et al. (2018) and the age 75 *E. regnans* data are from Benyon et al. (2017) (± indicates the 95% confidence interval for mean sap velocity).

mean sap velocity (SV) averaged for the 20-, 35- and 75-/80-year-age classes was about 34% higher in *E. regnans*, but the difference was only statistically significant at age 20 (Table 3). At age 10, mean SV was slightly lower in *E. regnans*, but was not significantly different compared with *A. dealbata* ($P > 0.05$). Further, mean sap velocity did not differ significantly between Benyon et al. (2017) data and the 80-year-old large single *E. regnans* tree near plot TR_4, that allowed us to use Benyon et al. (2017) data in the analysis.

The Hawthorne et al. (2018) data for age 20 showed that SV in *A. dealbata* was significantly lower ($P < 0.05$) compared with *E. regnans*. Mean SV was also lower at ages 35 and 80 in *A. dealbata*, but those differences were less and not statistically significant ($P > 0.05$).

After adjustment of the plot mean sap velocity data to remove the effect of differences in VPD, the results were similar (Table 3) but the statistical significance of differences was lower. The VPD-adjusted mean SV of both the youngest and oldest age classes, for which the most data were collected, were very similar in both species. At all ages, adjusted mean SV was higher in *E. regnans*, but the difference was only significant at the Hawthorne et al. (2018) 20-year-old site. Across all ages the adjusted mean SV was 9.9 cm $hour^{-1}$ for *A. dealbata* and 11.4 cm $hour^{-1}$ for *E. regnans*. Without the 20-year-old site the difference between species was less (10.3 vs 10.8 cm $hour^{-1}$).

Although the species-specific difference in sap velocity was relatively small at longer-term time steps, species-specific differences in sap velocity were evident at daily time steps. Analysis of relationships between meteorological variables and daily mean sap velocity at each site indicated that VPD is the major climatic driver of sap velocity in both forest types (Figure 3). Differences in quantified relationships between mean daily sap velocities and mean daily VPD suggest that species and age contributed to variability in sap velocity (Figure 4). However, these two factors were not strong enough to cause distinctively different sap velocity responses between the two forest types.

3.2 | Species and age effects on sapwood area

Sub-hypothesis 2 was supported with a high degree of confidence. Based on the larger sample of inventory plots (Table S1), *A. dealbata* exhibited a four-fold decline in overstorey sapwood area (SA) over time, from a mean of 16.3 m^2 ha^{-1} at age 10 to 3.8 m^2 ha^{-1} at age 80, whereas the SA of *E. regnans* declined by only half between age 10 and 75 (15.5 m^2 ha^{-1} at age 10 to 7.5 m^2 ha^{-1} at age 75; Figure 5). At age 10, the difference in mean SA between species was not statistically significant ($P > 0.05$), but it was at ages 20, 35, and 75/80 ($P < 0.05$).

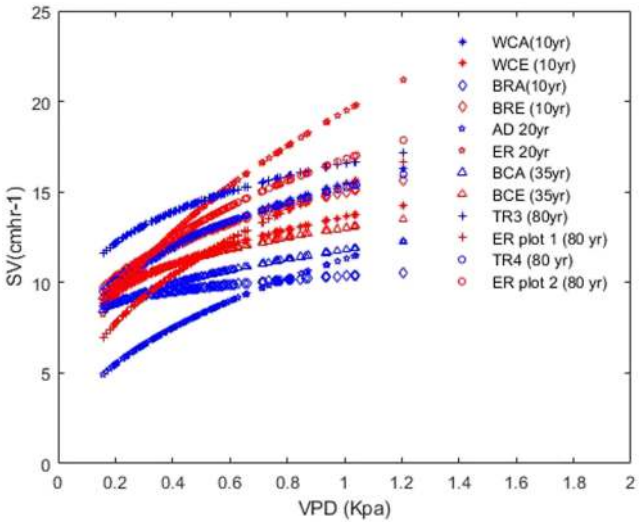


FIGURE 4 Sap velocity response prediction for the two species in different sites when considering the average VPD across the sites (Quantified relationships: WCA – $15.43 \times VPD^{0.2843}$, WCE – $13.61 \times VPD^{0.2327}$, BRA $-10.35 \times VPD^{0.0914}$, BRE – $14.98 \times VPD^{0.2344}$, AD 20 yr – $11.292 \times VPD^{0.4481}$, ER 20 yr – $19.436 \times VPD^{0.4625}$, BCA – $7.307 \times VPD^{0.3237} + 4.491$, BCE – $13.01 \times VPD^{0.185}$, TR_3 – $16.56 \times VPD^{0.1916}$, ER plot 1 – $15.37 \times VPD^{0.4251}$, TR_4 – $15.23 \times VPD^{0.254}$, ER plot 2 – $16.8 \times VPD^{0.3289}$)

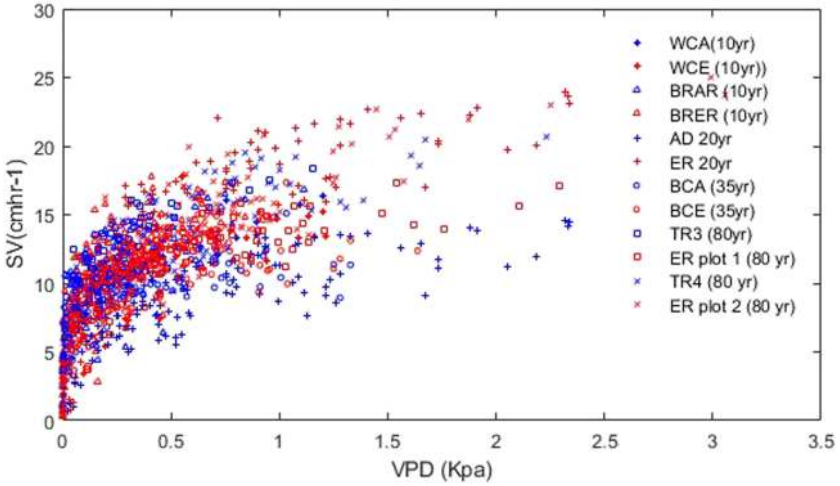


FIGURE 3 Daily mean sap velocity in relation to daily mean VPD for *A. dealbata* and *E. regnans* in different sites (WCA – Wallaby Creek *A. dealbata*, WCE – Wallaby Creek *E. regnans*, BRAR – Bunyip *A. dealbata*, BRER – Bunyip *E. regnans*, AD 20 yr and ER 20 yr – data from Hawthorne et al., 2018, for 20 year old *A. dealbata* and *E. regnans*, BCA – Britaniana Creek *A. dealbata*, BCE – Britaniana Creek *E. regnans*, TR_3 and TR_4 – Torongo road *A. dealbata*, ER plot 1 and 2 – data from Benyon et al., 2017, for 75 year old *E. regnans*)

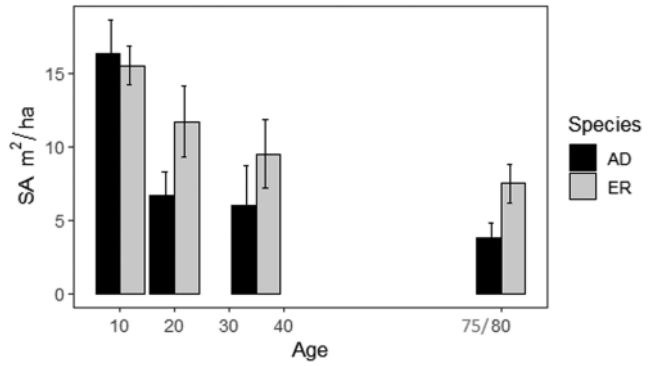


FIGURE 5 Variation of overstorey sapwood area between the two forest types with age (vertical bars represent the upper and lower 95% confidence intervals of stand sapwood area for each species-age class)

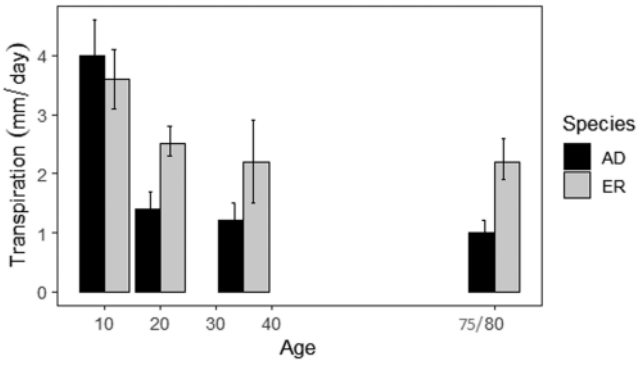


FIGURE 6 Comparison of overstorey transpiration for the October to February period between *A. dealbata* (AD) and *E. regnans* (ER) forests with stand age (vertical bars show upper and lower 95% confidence intervals of daily transpiration for each species-age group). Transpiration for 20-year-old forests was estimated using data from Hawthorne et al. (2018) and for the 75-year old *E. regnans* from Benyon et al. (2017)

3.3 | Comparison of overstorey transpiration between *E. regnans* and *A. dealbata* forests

Sub-hypothesis 3.0, which stand mean overstorey transpiration (T) varies significantly with species and age, was supported with a high degree of confidence. Over the period of the year when sap velocity data were available from all water use plots (October–February), mean daily T differed significantly among species and age classes after age 10 ($P < 0.001$). Further, there was a four-fold variation in daily T across the eight species/age combinations (Figure 6).

At age 10, overstorey T was slightly higher in *A. dealbata* (4.0 mm day^{-1} and 3.6 mm day^{-1} for *A. dealbata* and *E. regnans*, respectively), although the difference was not statistically significant. However, overstorey T of the two forest types began to diverge from 20 years onwards (lower in Acacia, Figure 6). This divergence continued to increase up to age 75/80 (1.0 mm day^{-1} in *A. dealbata* vs. 2.2 mm day^{-1} in *E. regnans*) and was statistically significant ($P < 0.005$) in all age classes from 20 years onwards. The results suggest that SA area exerts a strong control on stand T and reduces with stand age, but at a faster rate in *A. dealbata*.

3.4 | Drivers of differences in overstorey transpiration between *E. regnans* and *A. dealbata* forests

Sub-hypothesis 4.0, which stand mean T is controlled more by stand SA than by mean SV, was supported with a high degree of confidence. Large differences in mean overstorey T between species and age classes evident in Figure 6 were mainly correlated with the overstorey SA. The relationship between stand mean T and SA was far stronger than between T and SV: variation in stand sapwood area explained 95% of the variation in stand mean T, whereas the T versus SV relationship was weak ($R^2 = 0.04$). Further, multiple linear regression analysis suggests that SA was the only statistically significant determinant of stand mean T ($P < 0.05$). SA alone explained 95% of the variability in T between plots, while sap velocity explained additional variability of only 0.002%, confirming that stand SA is the main driver of stand mean T.

3.5 | The link between the divergence in forest structure and overstorey sapwood area in the two forest types

A strong relationship between tree SA and tree basal area strongly supports acceptance of sub-hypothesis 5.0: stand structure controls stand sapwood area (Figure 7) in the two forest types.

SA in *E. regnans* forests diverges dramatically from that of *A. dealbata* forests over time because *E. regnans* forests have significantly higher stand basal area from age 20 onwards (Figure 8). Average stand density in *A. dealbata* forests declined from 3940 trees ha^{-1} at age 10 to 308 trees ha^{-1} by age 80. In *E. regnans*, the rate of self-thinning was proportionally greater: stocking declined from only slightly (4%) less than *A. dealbata* at 10 years (3763 trees ha^{-1}) to 57% less than *A. dealbata* (131 trees ha^{-1}) by age 75. However, the dominant *A. dealbata* overstorey begins to die off rapidly at around 75 to 80 years of age, suggesting *A. dealbata* stands significantly reduce stand density after age 75 compared with *E. regnans* forest. This stand density comparison suggests that *A. dealbata* should have a higher stand sapwood area than *E. regnans* because up to age 80 the acacias always have higher stand density. However, in fact, after age 10, the opposite is true: *E. regnans* has a higher stand sapwood area after age 10. This is mainly because a significantly higher stand basal area exerts a stronger influence in the opposite direction to reduce the rate of reduction in stand sapwood area in *E. regnans* compared with in *A. dealbata* after age 10 (Figure 8).

Stand mean dbh and basal area both diverge markedly between species but in the opposite direction to stocking density (Figure 8).

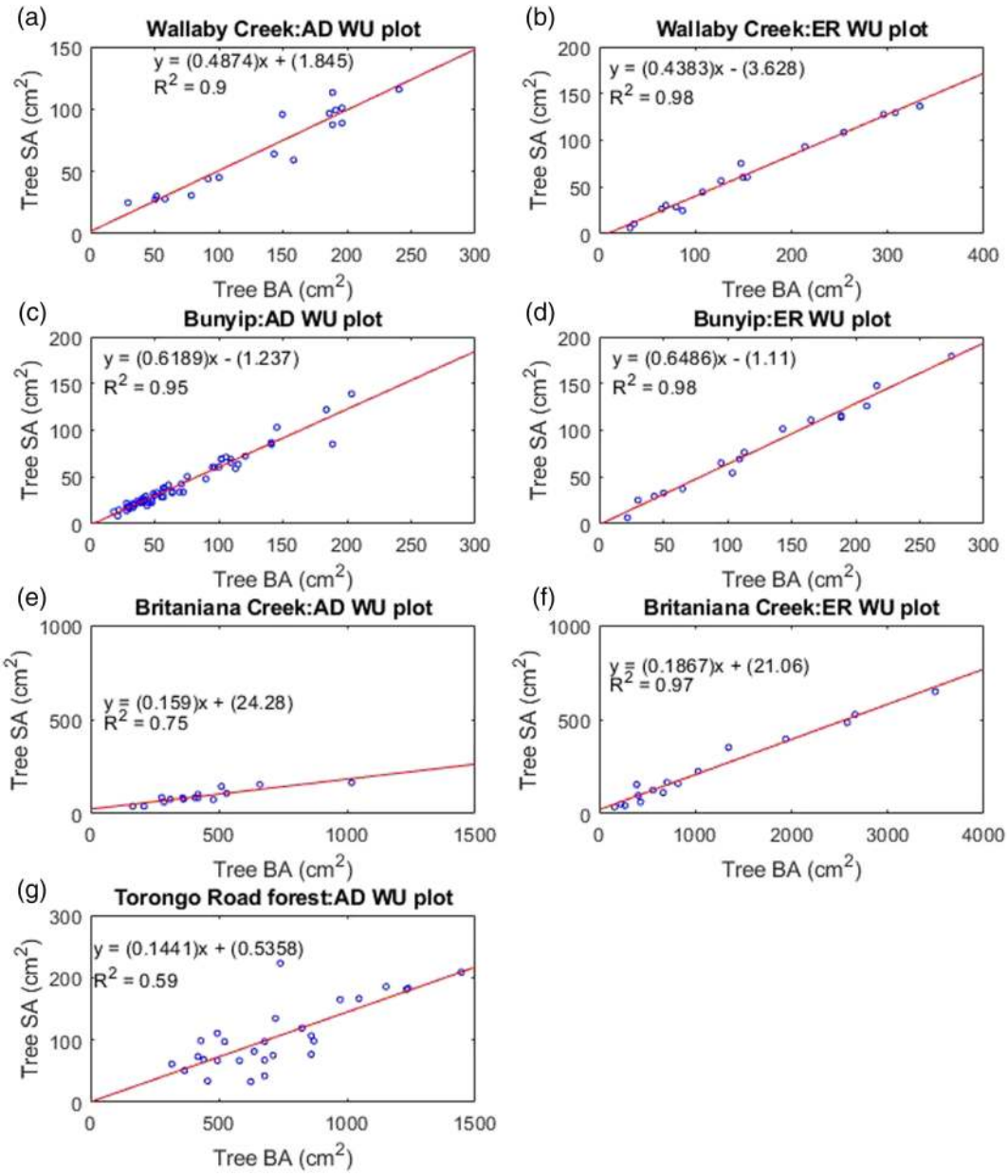


FIGURE 7 Linear regression fits between tree sapwood area and tree basal area for all water use (WU) plots of *A. dealbata* and *E. regnans* forests. (a) Wallaby Creek *A. dealbata* water use plot; (b) Wallaby Creek *E. regnans* water use plot; (c) Bunyip *A. dealbata* water use plot; (d) Bunyip *E. regnans* water use plot; (e) Britaniana Creek *A. dealbata* water use plot; (f) Britaniana Creek *E. regnans* water use plot; (g) Toorongo Road TR_3 and TR_4 *A. dealbata* water use plots

From age 20 onwards there is a statistically very large difference in both mean dbh and stand basal area between the two species. This divergence increases up to age 75/80, by when median dbh and stand basal area are both almost three times larger in *E. regnans* (Figure 8). At age 10, both stands had similar distributions of individual tree basal area (Figure 9a). At age 35, there is still some overlap in these frequency distributions of tree basal area, but higher positive skewness in tree basal area distribution in *E. regnans* forests (Figure 9b) resulted in higher stand basal area compared with *A. dealbata* forests (Figure 8). By age 75/80 this positive skewness in *E. regnans* basal areas is no longer evident, but there is very little overlap between the basal area distributions of the two species (Figure 9c).

Results suggest that stand dbh and stand basal area start to diverge from age 20 onwards (lower in *A. dealbata* forests, Figure 8). This stand structural divergence continues to increase up to age 75/80. Thus, the maximum divergence was observed at age 75/80. This suggests that the two species started their life as structurally similar stands, but by age 20 they have started to develop into structurally different forests.

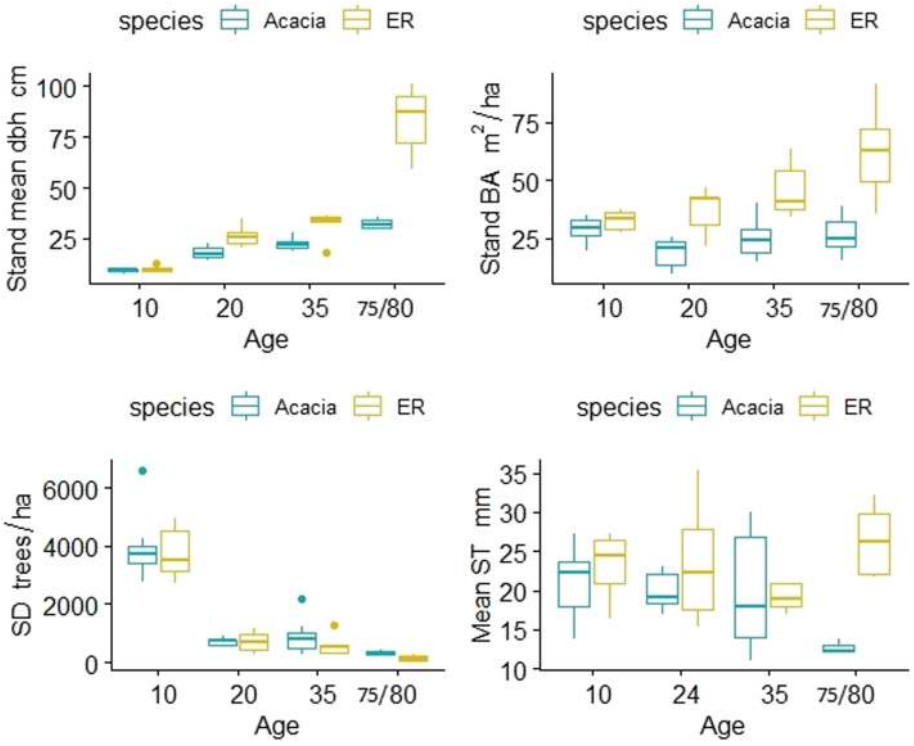


FIGURE 8 The variation of stand mean dbh, stand basal area, stand density and mean sapwood thickness (ST) between species and age. Each box plot represents first quartile, third quartile, and median of the data set (line in the middle of each box). Whisker plots represent the minimum and the maximum from first and third quartile, respectively. Individual points are extreme observations in each species-age group

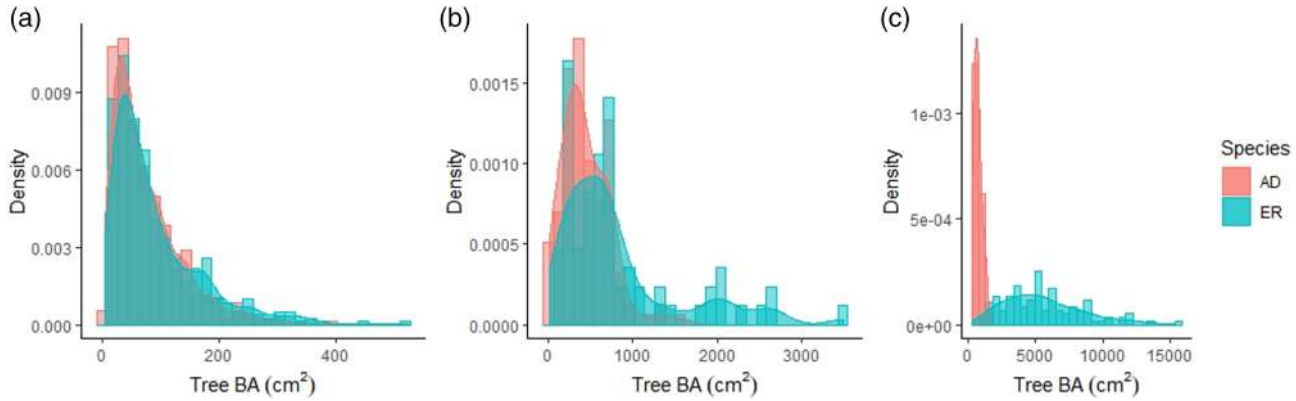


FIGURE 9 Kernel density estimations for tree basal area (BA) between *A. dealbata* and *E. regnans* forests across the age sequence. (a) 10-year old forests, (b) 35-year old forests, and (c) 75-/80-year old forests

3.6 | The relationship between LAI and overstorey transpiration

LAI, usually considered to be a primary determinant of mean T, varied only slightly among species and age classes. On average, overstorey LAI of 10-year-old *A. dealbata* forests was 8% higher than that of same-aged *E. regnans* forests. However, at age 35 and 75/80, overstorey LAI in *E. regnans* was slightly higher than that of *A. dealbata* (Figure 10). Transpiration per LAI was significantly higher in *E. regnans* after age 20 (Table 4). This was due to higher sapwood area per LAI in *E. regnans* for a given age (Table 4). Therefore, differences in LAI between the two species alone cannot explain the proportionally much larger differences in stand mean transpiration evident in the present study.

4 | DISCUSSION

Climate change is likely to drive a variety of ecohydrological consequences in forests. Included in these changed forcings is increased wildfire frequency with potential for broadscale changes in dominant species that may in turn alter evapotranspiration and streamflow. This study is one of the very few to have quantified the hydrologic effect of this ecological shift via the long-term effect on transpiration. The results from this study imply that in the long-term, replacement of *E. regnans* forests with *A. dealbata* will substantially reduce overstorey transpiration. The analysis shows that the structure of the two forests plays a key role in determining overstorey transpiration. While age-related forest structural changes and forest water use in *E. regnans* forests have been well studied in the literature, as have the impacts

on water yield following a single wildfire, the long-term effect on overstorey transpiration of a species shift from *E. regnans* forests to *A. dealbata* has not previously been investigated. Our results suggest that divergence in stand structure between *E. regnans* and *A. dealbata* forests after age 10 is a strong driver of the observed differences in overstorey transpiration over a chronosequence.

4.1 | Changes in sap velocity, forest sapwood area and overstorey transpiration

Previous studies in *E. regnans* showing that mean sap velocity does not change significantly with forest age and that changes in overstorey transpiration with age are largely driven by changes in sapwood area. Vertessy et al. (1995, 2001), Benyon et al. (2017) and Dunn and Connor (1993) are largely in concert with our findings. However, a limitation of these previous studies was their focus almost exclusively on the hydrological behaviour of mature and old-growth forests. Prior to Hawthorne et al. (2018), the only measurement of transpiration in *E. regnans* < 50 years old was in a single 15-year-old stand measured for only a short period from September to November by Vertessy et al. (1995). Their reported mean sap velocity of 11.9 cm h^{-1} compares to our mean at age 10 of 9.7 cm h^{-1}, albeit for a different period of the year. When adjusted to a common set of mean daily VPD data, our mean SV for 10 year old *E. regnans* was similar to that of *A. dealbata* (11.8 vs. 11.6 cm h^{-1}) and to the mean SV of 75-year-old *E. regnans* (11.9 cm h^{-1}). Our measurements are more representative of young stands of *E. regnans* as we included forests in different ecological conditions and for longer measurement periods. The transpiration rate per unit of leaf area was highest in young stands of both species (Table 4) due to very high sapwood area in young stands (Figure 5). The transpiration estimated from this study (including the Benyon et al., 2017, and Hawthorne et al., 2018, data) is largely a function of sapwood area.

To our knowledge, this is the first study to investigate hydrological parameters in pure *A. dealbata* forests over a chronosequence. Since the long-term average daily mean sap velocity in *A. dealbata* is relatively constant with forest age (Table 3), annual overstorey transpiration of *A. dealbata* forests can be predicted solely as a function of stand sapwood area. SA to LAI ratio (or Huber value) decreased with stand age in *A. dealbata* forests which is consistent with previous findings in a range of species (Kostner et al., 2002; Mokany et al., 2003; Watson et al., 1999). In general, age-related reductions in overstorey transpiration and overstorey sapwood area in *A. dealbata* forests follow a similar trend to that of *E. regnans* forests but compressed into a much shorter time scale.

The data show the forest structure and overstory hydrologic functioning of *E. regnans* and *A. dealbata* forests are closely matched during the first 10 years of their life but then begin to diverge. Overstorey transpiration and overstorey sapwood area in *A. dealbata* forests peak around age 10–20 and then rapidly decline over the next 60 years. However, both of those variables decline only gradually between age 10 and 75 in *E. regnans* forests, resulting in a significant contrast in forest structure and water use between the two forest types after age 20. This is possibly because *A. dealbata* forests have a regeneration-oriented life cycle, so that *A. dealbata* forests put more effort into reproduction and accumulation of a large seed store in the soil to ensure persistence over the long run (May, 1999). In contrast, *E. regnans* forests have a growth-oriented life cycle. *E. regnans* forests put more effort into biomass production (Volkova et al., 2018) and as a consequence, age-related reduction in overstorey sapwood area after the peak is more gradual within the first 80 years of their life cycle.

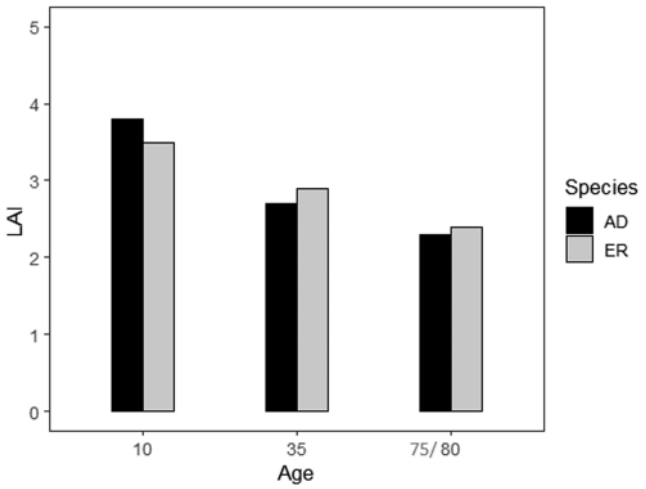


FIGURE 10 Comparison of overstorey LAI between *E. regnans* and *A. dealbata* aged 10, 35 and 75/80 years

TABLE 4 Changes in T/LAI and SA/LAI with forest age for *E. regnans* and *A. dealbata*

Transpiration per LAI (T/LAI) (mm day^{-1})			Sapwood area per LAI (SA/LAI) (m^2ha^{-1})	
Age	*A. dealbata*	*E. regnans*	*A. dealbata*	*E. regnans*
10	1.05	1.03	4.3	4.4
20	0.60	0.93	2.7	4.2
35	0.44	0.76	2.2	3.3
75/80	0.43	0.92	1.7	3.0

Note: LAI was measured at each water use plot of 10, 35- and 80-year-old forests. LAI for 20-year-old forests of both species and 75-year-old *E. regnans* forests were adopted from Hawthorne et al. (2018) and Watson et al. (1999), respectively.

4.2 | Shift in species composition due to climate change impacts

Regeneration success is one of the factors that determine species distribution at the landscape and regional scale (Mok et al., 2012). Climate warming is likely to affect seed production (Redmond et al., 2012), seedling recruitment (Boucher et al., 2020; Johnstone et al., 2010), abundance and distribution of species (Mok et al., 2012) and tree survival (Mitchell et al., 2014) and in many fire-prone forest systems the stress of increased fire frequency may produce tipping points.

These compound disturbances of drought and fire have the potential to drive widespread disruption to eco-hydrologic functioning (Mirus et al., 2017), resulting in a shift in eco-hydrologic regime (Blount et al., 2020). There are growing numbers of studies focused on ecological aspects of species replacements such as changes in climate-fire-vegetation interactions, succession pathways, carbon stocks and ecological resilience in response to perturbations. Quantification of change in evaporative fluxes as a consequence of vegetation change is still very limited, despite the importance of understanding how these systems respond to repeated disturbance, and how vegetation-water feedbacks may be affected. Pfautsch et al. (2010) reported that *E. regnans* forests containing mid and understory strata had higher water use in comparison to single storey stands. This indicates that water use tends to be changed with the compositional changes in these forests. During the present study, we found distinct water use signals from pure patches of *E. regnans* and *A. dealbata*.

The finding in this study that VPD is the principal climatic driver of transpiration is germane (though not surprising) not only to the current transpirative regime, but for future climate where higher average VPD is predicted for southeast Australia (DELWP, 2019) and many other environments (e.g., SW USA). We note that rainfall via soil moisture availability was for the most part not a limiting factor in our study. Clearly, high soil moisture deficits will also limit transpiration. The combination of high atmospheric demand and low water supply is most likely to exacerbate water stress. This link between rising temperatures, decreasing rainfall and lower humidity is of course the climatic combination that drives wildfire, with four "mega fire" events in southeast Australia since 2003, including the unprecedented "Black Summer" fires of 2019–2020 that burnt almost 5 million ha over four states. It is this apparent change in fire regime that results in the species change studied in this paper.

Extensive wildfires could change watershed outputs across the globe (Robinne et al., 2018). In the context of climate-induced vegetation change in southeast Australia, the present study provides a strong indication of lower overstorey transpiration in *Acacia* dominated forests. At the senescing stage of *A. dealbata*, understorey may off-set the loss of overstorey transpiration and eventually shift the evapotranspiration regime towards shrubby forests. These alterations may lead to divergence in catchment water yield. This study clearly demonstrates a link between differences in overstorey transpiration and differences in forest structure between the two forest types over the chronosequence, suggesting that time since forest replacement can be used as a proxy for detecting water use change and streamflow change over time in response to climate change and multiple burns.

5 | CONCLUSIONS

Increases in wildfire frequency due to climate change may induce changes in dominant species. Our research has shown that this could have important long-term consequences for water supplies. Replacement of *E. regnans* with *A. dealbata* in water supply catchments in southeast Australia would result in a reduction in overstorey transpiration after about 20 years, due mainly to divergence in sapwood area. In both forest types, sapwood area reduced with stand age after age 20, but at a faster rate in *A. dealbata*. In *E. regnans* forests, reduction in stand sapwood area from age 10 to age 75 was relatively low compared with that of *A. dealbata*. Therefore, overstorey transpiration in *A. dealbata* declined markedly between age 10 and age 80, whereas overstorey transpiration in *E. regnans* declined much less between the same ages.

This study also reveals that mean sap velocity was always higher in *E. regnans* compared with *A. dealbata* from age 20 onwards, but only statistically significantly so at age 20. Species has a significant effect on sap velocity at three different time resolutions, namely, long-term (seasonal), monthly and daily time resolutions. Although the species-specific difference in sap velocity was relatively small at longer-term time steps such as seasonal and mean annual scale, species-specific differences in sap velocity were evident at daily and sometimes monthly time steps. VPD is the main driver of sap velocity in both *A. dealbata* and *E. regnans* forests. Increases in mean VPD in future may increase mean transpiration rates, off-setting the effects of species change from *E. regnans* to *A. dealbata*.

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CONFLICT OF INTEREST

The authors declare they have no conflicts of interest to disclose.

AUTHOR CONTRIBUTIONS

Shyanika Lakmali: Methodology; conceptualization; data curation; formal analysis; writing – original draft; visualization. **Richard G. Benyon**:

Methodology; conceptualization; data curation; formal analysis; writing – review and editing; supervision; project administration; funding acquisition; resources. **Gary J. Sheridan**: Methodology; conceptualization; writing – review and editing; supervision; project administration; funding acquisition; resources. **Patrick N. J. Lane**: Methodology; conceptualization; data curation; formal analysis; writing – review and editing; supervision; project administration; funding acquisition; resources.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Adams, M. A. (2013). Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecology and Management*, *294*, 250–261. https://doi.org/10.1016/j.foreco.2012.11.039

Ashton, D. H. (1976a). The development of even-aged stands of *Eucalyptus regnans* F. Muell. In Central Victoria. *Australian Journal of Botany*, *24*(3), 397–414. https://doi.org/10.1071/BT9760397

Ashton, D. H. (1976b). Phosphorus in Forest ecosystems at Beenak, Victoria. *The Journal of Ecology*, *64*(1), 171. https://doi.org/10.2307/2258689

Becker, P. (1996). Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. *Tree Physiology*, *16*(1–2), 295–299. https://doi.org/10.1093/treephys/16.1-2.295

Becker, P., & Edwards, W. R. N. (1999). Corrected heat capacity of wood for sap flow calculations. *Tree Physiology*, *19*(11), 767–768. https://doi.org/10.1093/treephys/19.11.767

Benyon, R. G., Lane, P. N. J., Jaskierniak, D., Kuczera, G., & Haydon, S. R. (2015). Use of a forest sapwood area index to explain long-term variability in mean annual evapotranspiration and streamflow in moist eucalypt forests. *Water Resources Research*, *51*(7), 5318–5331. https://doi.org/10.1002/2015wr017321

Benyon, R. G., Nolan, R. H., Hawthorn, S. N. D., & Lane, P. N. J. (2017). Stand-level variation in evapotranspiration in non-water-limited eucalypt forests. *Journal of Hydrology*, *551*, 233–244. https://doi.org/10.1016/j.jhydrol.2017.06.002

Bleby, T. M., Burgess, S. S. O., & Adams, M. A. (2004). A validation, comparison and error analysis of two heat-pulse methods for measuring sap flow in *Eucalyptus marginata* saplings. *Functional Plant Biology*, *31*(6), 645–658. https://doi.org/10.1071/FP04013

Blount, K., Ruybal, C. J., Franz, K. J., & Hogue, T. S. (2020). Increased water yield and altered water partitioning follow wildfire in a forested catchment in the western United States. *Ecohydrology*, *13*(1), e2170. https://doi.org/10.1002/eco.2170

Boucher, D., Gauthier, S., Thiffault, N., Marchand, W., Girardin, M., & Urli, M. (2020). How climate change might affect tree regeneration following fire at northern latitudes: A review. *New Forests*, *51*(4), 543–571. https://doi.org/10.1007/s11056-019-09745-6

Bowman, D. M. J. S., Murphy, B. P., Neyland, D. L. J., Williamson, G. J., & Prior, L. D. (2014). Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology*, *20*(3), 1008–1015. https://doi.org/10.1111/gcb.12433

Bowman, D. M. J. S., Williamson, G. J., Prior, L. D., & Murphy, B. P. (2016). The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Ecology and Biogeography*, *25*(10), 1166–1172. https://doi.org/10.1111/geb.12484

Brookhouse, M. T., Farquhar, G. D., & Roderick, M. L. (2013). The impact of bushfires on water yield from south East Australia's ash forests. *Water Resources Research*, *49*(7), 4493–4505. https://doi.org/10.1002/wrcr.20351

Brown, C. D., & Johnstone, J. F. (2012). Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, *266*, 34–41. https://doi.org/10.1016/j.foreco.2011.11.006

Buckley, T. N., Turnbull, T. L., Pfautsch, S., Gharun, M., & Adams, M. A. (2012). Differences in water use between mature and post-fire regrowth stands of subalpine *Eucalyptus delegatensis* R. Baker. *Forest Ecology and Management*, *270*, 1–10. https://doi.org/10.1016/j.foreco.2012.01.008

Buma, B., Brown, C. D., Donato, D. C., Fontaine, J. B., & Johnstone, J. F. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *Bioscience*, *63*(11), 866–876. https://doi.org/10.1525/bio.2013.63.11.5

Burgess, S. S. O., Adams, M. A., Turner, N. C., Beverly, C. R., Ong, C. K., Ahmed, A. H. K., & Bleby, T. M. (2001). An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology*, *21*, 589–598. https://doi.org/10.1093/treephys/21.9.589

Cermak, J., & Nadezhdina, N. (1998). Sapwood as the scaling parameter-defining according to xylem water content or radial pattern of sap flow? *Annales des Sciences Forestières*, *55*(5), 509–521. https://doi.org/10.1051/forest:19980501

Clarke, H., Lucas, C., & Smith, P. (2012). Changes in Australian fire weather between 1973 and 2010. *International Journal of Climatology*, *33*(4), 931–944. https://doi.org/10.1002/joc.3480

Coop, J. D., Parks, S. A., Stevens-Rumann, C. S., Crausbay, S. D., Higuera, P. E., Hurteau, M. D., … Rodman, K. C. (2020). Wildfire-driven Forest conversion in Western North American landscapes. *Bioscience*, *70*(8), 659–673. https://doi.org/10.1093/biosci/biaa061

Department of Environment, Land, Water and Planning. (2019). Victoria's Climate Science Report 2019, 39 p. ISBN 978-1-76077-852-1.

Dunn, G. M., & Connor, D. J. (1993). An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiology*, *13*(4), 321–336. https://doi.org/10.1093/treephys/13.4.321

Ewers, B. E., Mackay, D. S., Gower, S. T., Ahl, D. E., Burrows, S. N., & Samanta, S. S. (2002). Tree species effects on stand transpiration in northern Wisconsin. *Water Resources Research*, *38*(7), 8-1–8-11. https://doi.org/10.1029/2001wr000830

Fairman, T. A., Nitschke, C. R., & Bennett, L. T. (2016). Too much, too soon? A review of the impacts of increasing wildfire frequency on tree demography and structure in temperate forests. *International Journal of Wildland Fire*, *25*(8), 831–848. https://doi.org/10.1071/WF15010

Feikema, P. M., Sherwin, C. B., & Lane, P. N. J. (2013). Simulating the combined effects of climate and wildfire on streamflow. Proceedings - 20th International Congress on Modelling and Simulation, MODSIM, 2848–2854. https://doi.org/10.36334/modsim.2013.l13.feikema

Frost, A. J., Ramchurn, A., & Smith, A. (2018). The Australian landscape water balance model (AWRA-L v6). Technical description of the Australian water resources assessment landscape model version 6, technical report, Bureau of Meteorology.

Gharun, M., Turnbull, T. L., & Adams, M. A. (2013). Stand water use status in relation to fire in a mixed species eucalypt forest. *Forest Ecology and Management*, *304*, 162–170. https://doi.org/10.1016/j.foreco.2013.05.002

Hawthorne, S. N. D., Benyon, R. G., & Lane, P. N. J. (2018). Changes in evapotranspiration components following replacement of *Eucalyptus regnans* with *Acacia* species. *Hydrological Processes*, *32*(2), 241–252. https://doi.org/10.1002/hyp.11410

Haydon, S. R., Benyon, R. G., & Lewis, R. (1996). Variation in sapwood area and throughfall with forest age in mountain ash (*Eucalyptus regnans* F. Muell.). *Journal of Hydrology*, *187*(3–4), 351–366. https://doi.org/10.1016/S0022-1694(96)03016-8

Hernandez-Santana, V., Hernandez-Hernandez, A., Vadeboncoeur, M. A., & Asbjornsen, H. (2015). Scaling from single-point sap velocity measurements to stand transpiration in a multispecies deciduous forest: Uncertainty sources, stand structure effect, and future scenarios. *Canadian Journal of Forest Research*, *45*(11), 1489–1497. https://doi.org/10.1139/cjfr-2015-0009

Johnstone, J. F., Chapin, F. S., Hollingsworth, T. N., Mack, M. C., Romanovsky, V., & Turetsky, M. (2010). Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research*, *40*(7), 1302–1312. https://doi.org/10.1139/X10-061

Keeley, J. E., Ne'eman, G., & Fotheringham, C. J. (1999). Immaturity risk in a fire dependent pine. *Journal of Mediterranean Ecology*, *1*, 41–48.

Keenan, R. J., & Nitschke, C. (2016). Forest management options for adaptation to climate change: A case study of tall, wet eucalypt forests in Victoria's central highlands region. *Australian Forestry*, *79*(2), 96–107. https://doi.org/10.1080/00049158.2015.1130095

Kostner, B. (2001). Evaporation and transpiration from forests in Central Europe—Relevance of patch-level studies for spatial scaling. *Meteorology and Atmospheric Physics*, *76*(1–2), 69–82. https://doi.org/10.1007/s007030170040

Kostner, B., Falge, E., & Tenhunen, J. D. (2002). Age-related effects on leaf area/sapwood area relationships canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiology*, *22*, 567–574. https://doi.org/10.1093/treephys/22.8.567

Kuczera, G. (1987). Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *Journal of Hydrology*, *94*(3–4), 215–236. https://doi.org/10.1016/0022-1694(87)90054-0

Lane, P. N. J., Feikema, P. M., Sherwin, C. B., Peel, M. C., & Freebairn, A. C. (2010). Modelling the long-term water yield impact of wildfire and other forest disturbance in eucalypt forests. *Environmental Modelling and Software*, *25*(4), 467–478. https://doi.org/10.1016/j.envsoft.2009.11.001

Lane, P. N. J., Sheridan, G. J., & Noske, P. J. (2006). Changes in sediment loads and discharge from small mountain catchments following wildfire in south eastern Australia. *Journal of Hydrology*, *331*, 495–510. https://doi.org/10.1016/j.jhydrol.2006.05.035

Link, P., Simonin, K., Maness, H., Oshun, J., Dawson, T., & Fung, I. (2014). Species differences in the seasonality of evergreen tree transpiration in a Mediterranean climate: Analysis of multiyear, half-hourly sap flow observations. *Water Resources Research*, *50*, 1869–1894. https://doi.org/10.1002/2013wr014023

Liu, X., Zhang, B., Zhuang, J. Y., Han, C., Zhai, L., Zhao, W. R., & Zhang, J. C. (2017). The relationship between sap flow density and environmental factors in the Yangtze River Delta region of China. *Forests*, *8*(3), 74. https://doi.org/10.3390/f8030074

Macfarlane, C., Arndt, S. K., Livesley, S. J., Edgar, A. C., White, D. A., Adams, M. A., & Eamus, D. (2007). Estimation of leaf area index in eucalypt forest with vertical foliage, using cover and full-frame fisheye photography. *Forest Ecology and Management*, *242*(2–3), 756–763. https://doi.org/10.1016/j.foreco.2007.02.021

Marshall, D. C. (1958). Measurements of sap flow in conifers. *Plant Physiology*, *33*(6), 385–396. https://doi.org/10.1104/pp.33.6.385

May, B. (1999). Silver wattle (*Acacia dealbata*): Its role in the ecology of the mountain ash forest and the effect of alternative silvicultural systems on its regeneration[PhD Thesis]. Department of Botany, The University of Melbourne.

Medhurst, J. L., & Beadle, C. L. (2002). Sapwood hydraulic conductivity and leaf area—Sapwood area relationships following thinning of a *Eucalyptus nitens* plantation. *Plant, Cell and Environment*, *25*(8), 1011–1019. https://doi.org/10.1046/j.1365-3040.2002.00880.x

Mirus, B. B., Ebel, B. A., Mohr, C. H., & Zegre, N. (2017). Disturbance hydrology: Preparing for an increasingly disturbed future. *Water Resources Research*, *53*(12), 10007–10016. https://doi.org/10.1002/2017wr021084

Mitchell, P. J., O'Grady, A. P., Hayes, K. R., & Pinkard, E. A. (2014). Exposure of trees to drought-induced die-off is defined by a common climatic threshold across different vegetation types. *Ecology and Evolution*, *4*(7), 1088–1101. https://doi.org/10.1002/ece3.1008

Mok, H. F., Arndt, S. K., & Nitschke, C. R. (2012). Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of south-eastern Australia. *Global Change Biology*, *18*(3), 1053–1072. https://doi.org/10.1111/j.1365-2486.2011.02591.x

Mokany, K., McMurtrie, R. E., Atwell, B. J., & Keith, H. (2003). Interaction between sapwood and foliage area in alpine ash (*Eucalyptus delegatensis*) trees of different heights. *Tree Physiology*, *23*(14), 949–958. https://doi.org/10.1093/treephys/23.14.949

Nolan, R. H., Lane, P. N. J., Benyon, R. G., Bradstock, R. A., & Mitchell, P. J. (2014). Changes in evapotranspiration following wildfire in resprouting eucalypt forests. *Ecohydrology*, *7*, 1363–1377. https://doi.org/10.1002/eco.1463

Nolan, R. H., Lane, P. N. J., Benyon, R. G., Bradstock, R. A., & Mitchell, P. J. (2015). Trends in evapotranspiration and streamflow following wildfire in resprouting eucalypt forests. *Journal of Hydrology*, *524*, 614–624. https://doi.org/10.1016/j.jhydrol.2015.02.045

Oldenborgh, G. J., Krikken, F., Lewis, S., Leach, N. J., Lehner, F., Saunders, K. R., van Weele, M., Haustein, K., Li, S., Wallom, D., Sparrow, S., Arrighi, J., Singh, R. P., van Aalst, M. K., Philip, S. Y., Vautard, R., & Otto, F. E. L. (2020). Attribution of the Australian bushfire risk to anthropogenic climate change. *Natural Hazards and Earth System Sciences (EGU)*, *21*, 941–960. https://doi.org/10.5194/nhess-2020-69

Pfautsch, S., Bleby, T. M., Rennenberg, H., & Adams, M. A. (2010). Sap flow measurements reveal the influence of temperature and stand structure on water use of *Eucalyptus regnans* forests. *Forest Ecology and Management*, *259*(6), 1190–1199. https://doi.org/10.1016/j.foreco.2010.01.006

Redmond, M. D., Forcella, F., & Barger, N. N. (2012). Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, *3*(12), art120. https://doi.org/10.1890/es12-00306.1

Robinne, F. N., Bladon, K. D., Miller, C., Parisien, M. A., Mathieu, J., & Flannigan, M. D. (2018). A spatial evaluation of global wildfire-water risks to human and natural systems. *Science of the Total Environment*, *610–611*, 1193–1206. https://doi.org/10.1016/j.scitotenv.2017.08.112

Savage, M., & Mast, J. N. (2005). How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research*, *35*(4), 967–977. https://doi.org/10.1139/x05-028

Swanson, R. H., & Whitfield, D. W. A. (1981). Numerical analysis of heat pulse velocity and theory. *Journal of Experimental Botany*, *32*(1), 221–239. https://doi.org/10.1093/jxb/32.1.221

Trouve, R., Nitschke, C. R., Andrieux, L., Willersdorf, T., Robinson, A. P., & Baker, P. J. (2019). Competition drives the decline of a dominant midstorey tree species. Habitat implications for an endangered marsupial. *Forest Ecology and Management*, *447*, 26–34. https://doi.org/10.1016/j.foreco.2019.05.055

Turner, M. G., Braziunas, K. H., Hansen, W. D., & Harvey, B. J. (2019). Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences of the United States of America*, *166*(23), 11319–11328. https://doi.org/10.1073/pnas.1902841116

Vertessy, R. A., Benyon, R. G., O'Sullivan, S. K., & Gribben, P. R. (1995). Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, *15*(9), 559–567. https://doi.org/10.1093/treephys/15.9.559

Vertessy, R. A., Watson, F. G. R., & O'Sullivan, S. K. (2001). Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology and Management*, *143*(1–3), 13–26. https://doi.org/10.1016/S0378-1127(00)00501-6

Vertessy, R. A., Watson, F. G. R., O'Sullivan, S. K., Davis, S. H., Campbell, R., Benyon, R. J., & Haydon, S. R. (1998). Predicting water yield from mountain ash forest catchments. Industry report no. 98/4, cooperative research Centre for Catchment Hydrology.

Volkova, L., Roxburgh, S. H., Weston, C. J., Benyon, R. G., Sullivan, A. L., & Polglase, P. J. (2018). Importance of disturbance history on net primary productivity in the world's most productive forests and implications for the global carbon cycle. *Global Change Biology*, *24*(9), 4293–4303. https://doi.org/10.1111/gcb.14309

Wang, J., Ives, N., & Lechowicz, M. (1992). The relation of foliar phenology to xylem embolism in trees. *Functional Ecology*, *6*(4), 469–475. https://doi.org/10.2307/2389285

Watson, F. G. R., Vertessy, R. A., & Grayson, R. B. (1999). Large-scale modelling of forest hydrological processes and their long-term effect on water yield. *Hydrological Processes*, *13*(5), 689–700. https://doi.org/10.1002/(sici)1099-1085(19990415)13:5<689::aid-hyp773>3.0.co;2-d

Welles, J. M., & Norman, J. M. (1991). Instrument for indirect measurement of canopy architecture. *Agronomy Journal*, *83*(5), 818–825. https://doi.org/10.2134/agronj1991.00021962008300050009x

Westerling, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H., & Ryan, M. G. (2011). Continued warming could transform greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(32), 13165–13170. https://doi.org/10.1073/pnas.1110199108

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