Rainfall regimes in many parts of the world have become increasingly dominated by fewer, but more extreme, rainfall events. Understanding how tree growth responds to changes in the frequency and intensity of rain events is critical to predicting how climate change will impact on forests and woodlands in the future. In this study, we used five tree-ring records of the native Australian conifer *Callitris columellaris* that span a large (> 20°) latitudinal and climatic gradient from the mesic (tropical) north to the xeric (semi-arid) south of Australia to investigate how inter-annual and spatial variation in the delivery of rainfall (the intensity and frequency of rain events) influences tree growth. In semi-arid biomes (~300–400 mm rainfall annually), tree growth is most strongly related to the amount of rainfall from heavy (> 75th percentile) rain days or the number of extreme (> 90th percentile) rain days, regardless of differences in the seasonal distribution and average intensity of rainfall among sites. Our findings also indicate that there is likely a minimum threshold amount of daily rainfall (~5 mm) that is required to stimulate tree growth in the semi-arid zone. In contrast, in the tropics (> 800 mm annual rainfall), inter-annual variation in growth is best explained by total growing season rainfall or the number of rain days > ~5 mm (~50th percentile of rain days) rather than extreme rainfall. Our findings indicate that not all rain events are important for driving tree growth, which has important implications for interpreting climatic signals in tree rings. Our findings also indicate that projected increases in the intensity of extreme rain events are likely to have contrasting impacts on tree growth across biomes, with greater and positive impacts on growth in semi-arid biomes and potentially negative impacts on growth in tropical biomes of Australia.

**Keywords:** *Callitris*, dendroclimatology, precipitation, rainfall intensity and frequency, ring width, thresholds, tree growth, tree rings
Introduction

Extremes of rainfall are potentially more important drivers of plant processes than mean conditions (Knapp et al. 2002, 2008, Kulmatiski and Beard 2013, Reyer et al. 2013, Zeppel et al. 2014). Consequently, shifts in the frequency or intensity of extreme rain events are likely to have significant impacts on plant processes, ecosystem productivity and carbon dynamics (Reyer et al. 2013). However, despite pervasive observations and projections of increases in the frequency and intensity of extreme rainfall events in many regions of the world (IPCC 2013, Alexander 2015, Monier and Gao 2015, Donat et al. 2016, Good et al. 2016, Mallakpour and Villarini 2017, Myhre et al. 2019), remarkably little is known of how important extreme rain events are for driving plant processes, particularly the growth of woody plants, and thus how plant growth may respond to changes in the frequency and intensity of extreme rain events.

The importance of extreme rain events for driving ecosystem productivity and woody plant growth likely differs among biomes depending on their typical potential evapotranspiration and rainfall rates (Reynolds et al. 2004, Gerten et al. 2008, Knapp et al. 2008, Kulmatiski and Beard 2013, Guan et al. 2014, Zeppel et al. 2014, Manea and Leishman 2018). Extreme rain events are thought to be particularly important for driving woody plant growth in xeric (i.e. arid and semi-arid) biomes, where rain events are typically small (< 5 mm) and a large fraction of rainfall is lost to evaporation before it can infiltrate the soil profile (i.e. potential evapotranspiration exceeds rainfall by > 2.5 times; Knapp et al. 2008, Raz-Yaseef et al. 2012). Extreme rain events can infiltrate deeper into the soil profile and result in proportionately smaller evaporative losses than smaller rain events in xeric biomes (Kulmatiski and Beard 2013, Tugwell-Wootton et al. 2020) and thus may be important for driving woody plant growth by increasing water availability in the root zone (Knapp et al. 2008, Raz-Yaseef et al. 2012, Kulmatiski and Beard 2013). In contrast, in mesic biomes where potential evapotranspiration only slightly exceeds rainfall and rain events are typically large, extreme rain events are likely to be less important for driving tree growth because much of the rainfall from extreme events may be lost to runoff or deep infiltration below the root zone or exceed the capacity of trees to uptake it (Knapp et al. 2008, Ye et al. 2016). However, there is very little empirical evidence of the role of extreme rain events in driving the growth of plants, particularly the growth of woody plants in shrub- or tree-dominated ecosystems across both mesic and water-limited biomes (Beier et al. 2012; but see Kulmatiski and Beard 2013, Ye et al. 2016).

Understanding growth responses of woody species to changes in the frequency or intensity of extreme rain events is important for several reasons. First, the frequency and intensity of rainfall events may be more important than the mean amount of rainfall for explaining the spatial distribution and growth of woody vegetation. For example, the encroachment of woody vegetation into African savannas has been attributed to increases in rainfall intensity rather than total rainfall (Good and Caylor 2011, Kulmatiski and Beard 2013). Second, wood is a major long-term carbon sink in terrestrial ecosystems (Pan et al. 2011); hence, understanding how wood production is influenced by variation in the frequency or intensity of rain events is critical to understanding the potential impacts of climate change on terrestrial carbon fluxes. Third, tree stem growth (i.e. ring width) is one of the primary sources of information used to understand past climate variability. Tree rings have been used to reconstruct long records of annual or seasonal rainfall amount for many environments around the world where tree growth is primarily limited by water availability. Such reconstructions have played a critical role in identifying the timescales and magnitudes of hydroclimatic variability as well as the frequency of past extreme climatic periods (Cullen and Grierson 2009, Cook et al. 2010, 2015, 2020, Palmer et al. 2015, Allen et al. 2017). However, few tree-ring studies have considered how variation in the way that rainfall is delivered – namely the frequency and intensity of rain events – influences how much of the total rainfall is available for tree use and thus contributes to growth.

Here, we use five records of annual growth (ring width) of the Australian tree conifer Callitris columellaris (Cupressaceae) and instrumental daily rainfall data to investigate how inter-annual variation in the intensity and frequency of rain events influences tree growth. We selected this species because it is one of the few mainland Australian tree species that produces clear growth rings that typically represent annual growth. Callitris columellaris is also widely distributed throughout mainland Australia. Our five sites span > 20° latitude and a broad climatic gradient from the tropical north of Australia to the semi-arid south of Western Australia, providing a unique opportunity to investigate whether the relationship between tree growth and rainfall varies among biomes while keeping species physiology and morphology relatively constant. Callitris spp. have shallow roots (the majority of roots occur in the top 50 cm; Eberbach 2003) and exhibit anisohydric stomatal control and a highly opportunistic water use strategy. Consequently, their growth is highly responsive to rainfall (Brodribb et al. 2013). Similar hydraulic traits are also observed in other Australian small tree species, including the Acacia aneura species complex, which dominate much of the semi-arid and arid woodlands of Australia (Page et al. 2016, Creek et al. 2018). Consequently, while we expect that C. columellaris can respond to smaller rain events than deep-rooted species, we use it here as an indicator of the likely response of shallow-rooted trees and shrubs to variation in the intensity and frequency of rainfall.

Given projected changes in the frequency and intensity of extreme rain events (Alexander 2015, Monier and Gao 2015, Myhre et al. 2019) and evidence of their importance for driving inter-annual variation in productivity and growth in some ecosystems (Heisler-White et al. 2009, Kulmatiski and Beard 2013, Ye et al. 2016, Post and Knapp 2020), we are particularly interested in determining whether extreme rain events are important for driving inter-annual variation in the growth of Callitris. Rather than arbitrarily defining a
Material and methods

Tree growth and rainfall data

We used five ring-width chronologies of Callitris columellaris: three are published (LTY, Cullen and Grierson 2009; CJD, O’Donnell et al. 2015; KOR, Allen et al. 2019) and two have been recently developed (LDE and CHR). To account for potential age-related decline in ring width, we statistically detrended the raw ring-width measurements to remove age-related (non-climatic) trends and converted them to ring-width indices (RWI) as residuals from the detrending curve (Cook and Peters 1997). The LTY, LDE, CJD and CHR ring-width series were first power-transformed to stabilise variance (Cook and Peters 1997) and detrended using an age-dependent spline. The KOR ring-width chronology was used here as it was published in Allen et al. (2019). The KOR series were also power-transformed prior to detrending with a negative exponential or linear model. All series for all sites were detrended in a signal free environment (Melvin and Briffa 2008) using the RCSigFree program (http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software). Further details on the sample size, detrending methods and statistical quality can be found in O’Donnell et al. (2015) for the CJD chronology and Allen et al. (2019) for the KOR chronology. Details of the previously published LTY chronology (1655–2005 CE) can be found in Cullen and Grierson (2009); however, we have now extended the LTY chronology to 2013 CE. Details of the updated LTY chronology and the new LDE and CHR chronologies can be found in Supporting information.

The five sites encompass three distinct climate zones (Fig. 1). Two of the sites (KOR and CHR) are located in the seasonally dry tropics of northern Australia, with the northernmost site, KOR receiving ~1200 mm of rain per year and CHR receiving ~800 mm per year. Despite differences in the average amount of annual rainfall at KOR and CHR, the two sites have very similar daily rainfall distributions (Fig. 2) and seasonal rainfall distribution (Supporting information). The other three sites are all located in semi-arid biomes, but experience different seasonal distributions of rainfall; CJD is located in the sub-tropical semi-arid zone where rainfall is summer dominant, while LDE and LTY are located in the Mediterranean semi-arid zone where rainfall is winter dominant (Supporting information). All three semi-arid sites receive similar mean annual rainfall (~300–400 mm annual rainfall), but rain intensity (daily rainfall) at the sub-tropical CJD site is typically greater than at the Mediterranean sites (Fig. 2). For example, the median (50th percentile) and 90th percentile of daily rainfall at CJD (2 mm and 13 mm) are approximately twice that of LDE and LTY (1 mm and ~7 mm; Fig. 2, Table 2).

We obtained instrumental rainfall data from the Australian Bureau of Meteorology, (http://www.bom.gov.au/climate/data/). Owing to the remote locations of our sites, there were few long, high-quality instrumental records of rainfall within 50 km of the sites. Consequently, we searched for stations within a 2° × 2° area centred on each site to find between 3 and 8 stations with long (> 60 years) daily rainfall data near each site and then calculated the mean of daily rainfall across these stations to generate a regional daily rainfall dataset. Further details of the rainfall data used here can be found in Supporting information.

Rainfall variables and regression models

We used the monthly_response() function in the DendroTools package (Jevšenak and Levanič 2018) in R 3.6.1 (https://www.r-project.org) to calculate Pearson correlations between RWI and total rainfall for each month as well as for all periods between 3 and 12 consecutive months out of a possible 24-month window (previous calendar year and current calendar year). We determined that the growth (as RWI) of C. columellaris was most strongly related to total annual (12 month) rainfall at CJD and CHR and to rainfall during a shorter (< 12 month) ‘growing season’ at KOR, LDE and LTY (Supporting information). Consequently, we use the following seasons to define ‘growing season’ rainfall variables: total annual rainfall for CJD (Dec–Nov; 12 months) and CHR (Jun–May; 12 months) and autumn-winter rainfall for LDE (Feb–Aug; 7 months) and LTY (Jan–Sep; 9 months). For the wet-tropical KOR site, we included rainfall in the transitional seasons both before (Sep–Nov) and after (Mar–Jun) the main wet season in the ‘growing season’ (7 months total) as rainfall in both seasons is strongly related to tree growth while rainfall during the wet season months (Dec–Feb) is not (Supporting information).

We conducted several analyses to determine whether all rainfall events or only part of the daily rainfall size distribution – particularly the extreme upper tail – is responsible for driving most of the inter-annual variation in growth of C. columellaris. We used a flexible approach to test the hypothesis that only rain events above some threshold value drive inter-annual variation in growth. We defined thresh to be the minimum amount of daily rainfall required to drive growth and then considered a range of values for thresh between 0.1 and 30 mm. A threshold of 0.1 mm means that all rain days are counted, while a threshold of 30 mm means that only rain days with at least 30 mm rainfall are counted. We varied the
value of $thresh$ from 0.1 mm to 30 mm in 0.1 mm increments (i.e. 300 possible $thresh$ values). For each of the 300 possible $thresh$ values, we then calculated two predictor variables for each year; the number of days in the growing season when rainfall exceeded the threshold, $Days_{>thresh}$, and the sum of rainfall from those days, $Rain_{>thresh}$. For each of the 300 possible $thresh$ values, we then fitted a simple linear model with RWI as the response variable and $Days_{>thresh}$ as the predictor, using the `lm()` function in the base package of R (<www.r-project.org>). For each of the 300 possible $thresh$ values, we also fitted a linear model with RWI as the response variable and $Rain_{>thresh}$ as the predictor; however, given that the relationships between $C.\ columellaris$ growth and rainfall amount is non-linear (concave down) in the tropics (O’Donnell et al. 2021), we also tested whether quadratic polynomial models explained the relationship between RWI and $Rain_{>thresh}$ better than simple linear models at the tropical sites using F-tests (the `anova()` function in R). Quadratic polynomials showed a significantly better fit to the RWI data at the tropical sites than simple linear models for all $Rain_{>thresh}$ values we tested (i.e. between 0.1 and 30 mm). Hence for the two tropical sites, all relationships between rainfall amount ($Rain_{>thresh}$) and growth were modelled with quadratic polynomials. For the semi-arid sites, these relationships were best described by linear models.

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Figure 1. Location of the five $Callitris\ columellaris$ sites in relation to annual rainfall and rainfall seasonality zones of Australia. Coloured shading indicates the 1961–1990 mean annual (January–December) rainfall amount (data sourced from the Australian Bureau of Meteorology: <http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp>). Dashed lines indicate boundaries between areas with summer-dominated, uniform (both summer and winter) or winter-dominated rainfall distributions (data sourced from the Australian Bureau of Meteorology: <http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp?maptype=seasb#maps>). Solid black lines indicate state and territory boundaries; white dots indicate the location of some state capital cities.

Figure 2. Empirical cumulative probability distribution of daily rainfall for each of the five study sites. Probability distributions are based on ~110 years (1908–2018 CE) of daily rainfall data. Note: The x-axis has been truncated at 30 mm; the maximum daily rainfall amount was 290 mm at CHR.
We plotted the resulting model \( R^2 \) for each of the 300 possible values of \( \text{thresh} \) for each of the two predictors (\( \text{Rain}_{\text{thresh}} \) and \( \text{Days}_{\text{thresh}} \); Fig. 3). For each site, we observed a peak in \( R^2 \) and defined the threshold value where \( R^2 \) was maximised as the ‘optimal’ threshold. We then called the value of \( \text{Days}_{\text{thresh}} \) at this optimal threshold (the number of days when rainfall exceeded this optimal threshold), \( \text{Days}_{\text{optimal thresh}} \). Similarly, we called the value of \( \text{Rain}_{\text{thresh}} \) at the optimal threshold, \( \text{Rain}_{\text{optimal thresh}} \) (Table 1). For each site and each of the two predictor variables, we then determined if the model using the optimal threshold explained ‘significantly’ more variance in RWI than the model without a threshold, using a conservative criterion of \( \Delta R^2 > 0.02 \). We compared differences in AIC and \( R^2 \) among models and also p-values from F-tests and found that for these data, our criterion for ‘significance’ of \( \Delta R^2 > 0.02 \) is more conservative than the generally accepted criterion of AIC > 2 or \( p < 0.05 \) from an F-test.

We also determined whether the number of extreme rain days (\( \text{Days}_{\text{extremethresh}} \)) or the amount of rainfall from extreme rain days (extreme rainfall, \( \text{Rain}_{\text{extremethresh}} \)) was a better predictor of RWI than all rain days or total rainfall (i.e. no threshold) using the same \( \Delta R^2 > 0.02 \) criterion. For this purpose, we defined the extreme threshold as the 90th percentile (i.e. heaviest 10%) of daily rainfall across all rain days of the entire rainfall record for each site (i.e. ~1908–2016 CE).

We note that the optimal rainfall threshold for \( \text{Days}_{\text{optimal thresh}} \) is not necessarily the same as the optimal threshold for \( \text{Rain}_{\text{optimal thresh}} \). For each site, and for both vary among sites. On the other hand, the value of the threshold used for calculating both \( \text{Days}_{\text{extremethresh}} \) and \( \text{Rain}_{\text{extremethresh}} \) is the same (the 90th percentile) within a site, but varies among sites.

**Results**

**Rainfall amount**

For the three semi-arid sites, we found stronger relationships between growth (as RWI) and rainfall amount if the smallest daily rain events were excluded from rainfall totals. For each site, a range of threshold values resulted in rainfall amount variables that were better predictors (\( \Delta R^2 > 0.02 \)) than total rainfall (i.e. no threshold; Fig. 3). For example, at CJD, rainfall from rain days that exceed a range of thresholds between 3.0 and 12.2 mm explained > 2% more variance in RWI than total rainfall (blue shading; Fig. 3c). For each of the semi-arid sites, the optimal rainfall thresholds (maximum \( R^2 \)) were between 4.7 and 6.8 mm and equivalent to the 74th to 90th percentile of daily rainfall (Table 2, Fig. 3c–e). Relationships between RWI and \( \text{Rain}_{\text{optimal thresh}} \) at the semi-arid sites were linear (Fig. 4a) and strong (\( R^2 = 0.45–0.75 \); Table 2) and showed similar slopes (Fig. 4a; Supporting information).

The optimal rainfall threshold and extreme rainfall threshold (90th percentile) at LTY were almost identical (6.8 and 6.6 mm) indicating that the extreme upper tail (> 90th percentile) of the daily rainfall distribution best explains inter-annual variation in RWI (Table 2, Fig. 3e). \( \text{Rain}_{\text{extremethresh}} \) (> 7.8 mm) was also a significant and strong predictor of RWI at LDE, explaining as much variance as total rainfall (\( R^2 = 0.59 \) for both; Table 2) and showing a similar slope (Supporting information). However, \( \text{Rain}_{\text{optimal thresh}} \) (> 4.7 mm), which represents the 81st percentile of daily rainfall was a better predictor (\( R^2 = 0.61 \)) of RWI than extreme rainfall (\( \text{Rain}_{\text{extremethresh}} \); Table 2, Fig. 3d). At the sub-tropical semi-arid CJD site, the extreme rainfall threshold (12.9 mm) was more than twice the size of the optimal threshold (5.5 mm) and greater than the extreme threshold for both of the Mediterranean semi-arid sites (6.6 mm at LTY and 7.8 mm at LDE; Table 2). Despite this large difference, \( \text{Rain}_{\text{extremethresh}} \) at CJD was a better predictor of RWI (\( R^2 = 0.73 \)) than total rainfall (\( R^2 = 0.70 \)), although a weaker predictor of RWI than \( \text{Rain}_{\text{optimal thresh}} \) (\( R^2 = 0.75 \); Table 2, Fig. 3c). In contrast to the two winter-rainfall dominated semi-arid sites (LDE and LTY), the proportion of variance in RWI explained by rainfall amount did not decline steeply with increasing threshold size at the summer-rainfall dominated semi-arid CJD site (Fig. 3). In fact, rainfall from > 95th percentile rain days (i.e. > 21.5 mm) at CJD was nearly as good as a predictor of RWI (i.e. \( \Delta R^2 < 0.02 \)) as total rainfall. In addition, rainfall from the highest threshold we tested (i.e. > 30 mm), which is equivalent to the 97th percentile of daily rainfall at CJD still explained more than 62% of the variance in RWI (Fig. 3c).

In contrast to the semi-arid sites, we found that excluding the smallest events from rainfall totals (i.e. using a threshold) at the tropical sites did not substantially improve the relationship between RWI and rainfall amount (i.e. \( \Delta R^2 < 0.02 \); Fig. 3a–b). While optimal rainfall thresholds (highest \( R^2 \)) were found, these were not better predictors of RWI than total rainfall (i.e. \( \Delta R^2 < 0.02 \); Table 2). However, excluding the smallest events (< 5.9 mm at CHR or < 7.3 mm at KOR) from rainfall totals did not result in a substantial loss of explanatory power compared to using total rainfall as a predictor (i.e. \( \Delta R^2 < 0.02 \)); Fig. 3a–b). Extreme rainfall thresholds were much greater at the tropical sites than at the semi-arid sites (i.e. > 22 mm for CHR and > 25.3 mm for KOR) and \( \text{Rain}_{\text{extremethresh}} \) at the tropical sites was a weaker predictor of RWI than total rainfall, explaining approximately 13% less of the variance in RWI (Table 2). In the case of KOR, \( \text{Rain}_{\text{extremethresh}} \) also showed a more concave relationship with growth than total rainfall or \( \text{Rain}_{\text{optimal thresh}} \) (Supporting information).

**Number of rain days**

Across both semi-arid and tropical climate zones, relationships between RWI and the number of all rain days (> 0 mm) were typically quite weak (\( R^2 < 0.23 \); Table 3). However, applying thresholds of 0.4 mm or more (up to ~22 mm for LTY, CHR and KOR, > 30 mm for LDE and CJD) to define the number of rain days improved the variance in RWI explained (i.e. \( \Delta R^2 > 0.02 \); Fig. 3). At the semi-arid sites, the optimal rain day thresholds (i.e. 7.8–20.1
Figure 3. Proportion of variance in ring-width index (RWI) of *Callitris columellaris* explained ($R^2$) by the amount of rainfall (blue) or the number of rain days (red) during the growing season that exceed a threshold between 0 mm (all rainfall/all rain days) and 30 mm. Vertical dotted lines indicate the optimal thresholds (highest $R^2$) for rainfall amount ($Rain_{optimal\_thresh}$; blue) and the number of rain days ($Days_{optimal\_thresh}$; red) during the growing season. Shaded blue vertical bands indicate the range of threshold values for rainfall amount that are considered better predictors ($\Delta R^2 > 0.02$) of RWI than total rainfall (0 mm threshold). Shaded red vertical bands indicate the range of threshold values for the number of rain days that produce $R^2$ values within 0.02 of the optimal threshold. Vertical dashed black lines indicate the 90th percentile of daily rainfall at each site.
mm) represented extreme rain days (i.e. 90–95th percentile, Table 3). Both Days_{optimal.thresh} and Days_{extreme.thresh} were better predictors of RWI than the number of all rain days at the semi-arid sites, improving the variance explained by 25–60% (Table 3, Fig. 3c–e; Supporting information). While Days_{optimal.thresh} or Days_{extreme.thresh} were strong predictors of RWI at the semi-arid arid sites, they were less important than any measure of rainfall amount (total, Rain_{optimal.thresh} or Rain_{extreme.thresh}; Table 2, 3, Fig. 3c–e).

The optimal thresholds for the number of rain days at the tropical sites represented only the 55–60th percentile of daily rainfall (Table 3). Days_{optimal.thresh} at the tropical sites was a better predictor of RWI than the number of all rain days or Days_{extreme.thresh} explaining ~20% more variance in RWI (Table 3). In contrast to the semi-arid sites, the number of Days_{extreme.thresh} was either as good or a better predictor of RWI than any measure of rainfall amount (Fig. 3a–b, Table 2, 3).

### Discussion

Extreme rain events are particularly important for driving tree growth in semi-arid Australia, where we found that the heaviest 10–25% of rain days explain the most inter-annual variation in growth of *Callitris columellaris*. This finding is consistent with other studies in water-limited biomes, which show that variation in the intensity and frequency of extreme rain events is more important than total rainfall for driving tree growth (Kulmatiski and Beard 2013) or ecosystem productivity (Heisler-White et al. 2008, 2009, Ye et al. 2016).

Our finding that smaller rain events (< ~5 mm; Table 2) contribute proportionately less or perhaps not at all to growth than larger events in semi-arid Australia is also consistent with the concept of ‘effective’ or ‘biologically important’ rainfall in semi-arid and arid systems, where a minimum threshold of rainfall is required to stimulate plant productivity and growth (Noy-Meir 1973, Ogle and Reynolds 2004, Schwinning and Sala 2004). Small rain events, particularly temporally isolated events, are unlikely to penetrate far into the soil profile in water-limited environments because much of the rainfall is either intercepted (by the canopy and litter) or lost to evaporation. Instead, larger events are generally required to infiltrate soil to a depth where it becomes plant-available and can trigger assimilation processes (Huxman et al. 2004, Reynolds et al. 2004, Knapp et al. 2008, Raz-Yaseef et al. 2012, Kulmatiski and Beard 2013).

Several empirical studies support the concept of ‘effective’ rain events in semi-arid and arid environments, reporting measurable physiological responses (i.e. increases in water use and/or gas exchange) of shallow-rooted shrubs or trees (Burgess 2006, Zeppel et al. 2008, Zhao and Liu 2010, Eamus et al. 2013) or increases in ecosystem productivity (Li et al. 2015, Fan et al. 2016) typically only following larger rain events. For example, Burgess (2006) found that rain events < 4 mm in semi-arid southwest Australia (i.e. the same climate zone as our LTY and LDE sites) did not generate a sap flow response in a suite of shrubs and trees, including another *Callitris* species (*C. arenaria*, previously known as...
Actinostrobus arenarius). Our findings provide evidence that the concept of 'effective' rain events also applies to the growth of shallow rooted trees in water-limited ecosystems and suggest that the threshold-responses that have been widely documented in immediate physiological processes (water use and gas exchange) of woody plants are carried over into the process of wood production.

Extreme rainfall was not as important for driving tree growth in the tropical north of Australia, where total rainfall (from all rain events) explained much more (> 13%) of the variance in growth than extreme rainfall. However, rainfall from the smallest (< ~50th percentile) events was also not particularly important for explaining variation in growth of Callitris in the tropics (i.e. excluding events < 5.9 mm for CHR or < 7.3 mm for KOR) did not substantially reduce the explained variance; i.e. ΔR² < 0.02, Fig. 3a–b). In contrast, the relationship between RWI and the number of rain days (Days > thresh) in the tropics was greatly improved (by > 20%) if the smallest rain events were excluded (Fig. 3, Table 3). While we found optimal thresholds for Days > thresh (of 5.2 mm for CHR and 7.2 mm for KOR) that explained the most variance in RWI at each tropical site, a range of thresholds between ~4.5 and 6 mm at both sites (specifically between 2.1 and 6 mm for CHR and between 4.5 and 7.4 mm for KOR) were considered as good predictors of RWI as the optimal threshold (i.e. R² within 0.02 of the optimal threshold; Fig. 3). Previously, Cook and Heerdegen (2001) noted that the mean daily potential evaporation during the wet season in the Australian tropics was > ~5 mm and they consequently defined 'rain days' for this region as days when rainfall exceeded 5 mm (i.e. rainfall exceeded potential evaporation). Our findings are consistent with the definition of 'rain days' used by Cook and Heerdegen (2001) and provide further support for the use of a threshold of ~5 mm to define rain days that are important for tree growth in tropical northern Australia.

Our results suggest that the relative importance (ΔR²) of the number of rain days > optimal threshold (Days > optimal.thresh) during the 'growing season'.

Figure 4. Relationships between ring-width index (RWI) of Callitris columellaris and (a) amount of rainfall from days with rainfall > optimal threshold (Rain > optimal.thresh) and (b) the number of rain days > optimal threshold (Days > optimal.thresh) during the growing season at tropical (blue) and semi-arid (yellow-red) sites. Lines represent fitted models. In (a) CJD, LDE and LTY are fitted with simple linear models, KOR and CHR are fitted with quadratic polynomial models. In (b) all sites are fitted with simple linear models. See Table 2 and 3 for optimal threshold values and Supporting information for the model parameter estimates and standard errors for each model.

| Site | All rain days | Days > optimal.thresh | Days > extreme.thresh |
|------|---------------|-----------------------|----------------------|
|      | R²            | Threshold (mm) | PCTL | R² | Threshold (mm) | R² | Season (no. months) |
| Tropical | 0.124 | 7.2 | 59.7 | 0.424 | 25.3 | 0.214 | Sep–Nov + Mar–Jun (7) |
| KOR | 0.234 | 5.2 | 55.6 | 0.439 | 22.0 | 0.246 | Jun–May (12) |
| CHR | 0.092 | 20.1 | 94.6 | 0.690 | 12.9 | 0.640 | Dec–Nov (12) |
| Semi-arid | | | | | | | |
| CJD | 0.119 | 7.8 | 90.0 | 0.515 | 7.8 | 0.515 | Feb–Aug (7) |
| LDE | 0.083 | 9.6 | 94.3 | 0.431 | 6.6 | 0.375 | Jan–Sep (9) |
| LTY | | | | | | | |

Bold values indicate the variable(s) that showed the greatest predictive skill (i.e. R² > 0.02 greater than other models) within each site (i.e. within rows). All models were simple linear regression models. PCTL = percentile; the percentage of rain days with rainfall less than the optimal threshold in the full time series of rain data for each site.

Table 3. Proportion of variance in RWI of Callitris columellaris explained by the number of rain days (all, Days > optimal.thresh, or Days > extreme.thresh) during the 'growing season'.
and rainfall amount is commonly used in the Australian tropics (> 1500 mm) was more strongly related to the number of rain days > 5 mm than the relative amount of rainfall. However, at the tropical site with lower rainfall (CHR; ~800 mm annual rainfall), the number of Days_{optimal,thresh} (> 5.2 mm) and total rainfall during the growing season explained similar proportions of variance in growth. There are a few possible explanations for the stronger relationship between *Callitris columellaris* growth and Days_{optimal,thresh} than rainfall amount at the higher rainfall end of the Australian tropics. First, much of the rainfall in the tropics occurs as part of extreme rain events (i.e. > 41% of annual rainfall is from > 25 mm rain days at KOR; Table 2). It is likely that much of the rainfall from extreme rain events is not used by shallow rooted trees, either because it exceeds the capacity of the trees to uptake and use it (as growth may become more limited by light or nutrient availability), or because much of it is lost to runoff or deeper into the soil profile below rooting depth (Mott 1974, Cook and Heerdegen 2001). Drew et al. (2014) observed that the size of stem increments of *Callitris columellaris* in tropical northern Australia (> 1700 mm) was not consistently related to the size of rain events. In particular, Drew et al. (2014) concluded that larger rain events did not consistently lead to larger stem increments. Hence, while a large proportion of rainfall is delivered in extreme events in the wet tropics, extreme rain events likely contribute proportionately less to growth than they do to rainfall totals, resulting in weaker relationships between rainfall amount and growth. Second, the number of Days_{optimal,thresh} may provide a better indication of the relative opportunity for growth (i.e. the occurrence of favourable conditions for growth) than rainfall amount. Even in years with high rainfall, tree growth may be limited by water-availability at times if rainfall is distributed into fewer, but higher-intensity rainfall events resulting in more frequent or longer dry intervals between rain events (Knapp et al. 2008, Ye et al. 2016).

### Potential impacts of intensification of rainfall regimes on growth

Climate models predict an increase in the intensity of extreme rain events across both the tropical zone of northern Australia and the semi-arid zone of western Australia (CSIRO 2015). Our results from tropical Australia are consistent with empirical studies of productivity in other mesic ecosystems (Fay et al. 2008, Manea and Leishman 2018, Padilla et al. 2019, Felton et al. 2020) and suggest that an increase in the intensity of rain events in the Australian tropics could potentially have a negative impact on tree growth if the redistribution of rainfall into fewer, larger events results in longer dry periods in between rain events and/or a greater proportional loss of rainfall to runoff or infiltration deep into the soil profile (Knapp et al. 2008, Ye et al. 2016). Our findings for semi-arid biomes of Australia are consistent with empirical studies in other water-limited ecosystems, which show increased tree growth (Kulmatiski and Beard 2013) or ecosystem productivity (Heisler-White et al. 2008, 2009) in response to an increase in the relative contribution of rainfall from extreme events. Thus, in contrast to mesic biomes, an increase in the intensity of extreme rainfall events in water-limited biomes (e.g. semi-arid Australia) is likely to have significant and positive impacts on tree growth, by increasing soil water availability and infiltration to the rooting zone. Such an effect has been observed in Kruger National Park, South Africa, where an artificial shift to fewer, more intense rain events resulted in deeper infiltration and favoured the growth of woody plants over grasses (Kulmatiski and Beard 2013). However, in the semi-arid southwest of Australia, where the LTY and LDE sites are located, in addition to an increase in the intensity of rainfall events, climate models predict a decline in winter (growing season) rainfall amount in the future (CSIRO 2015). While the degree to which the intensity of rain events in semi-arid southwest Australia will change versus the amount of growing season rainfall remains uncertain (CSIRO 2015), our findings suggest that the positive effect of an increase in the intensity of rain events on the growth of shallow-rooted trees and shrubs may at least partially counteract the negative effect of an overall reduction in growing season rainfall.

### Implications for dendroclimatology and its application

Our target species, *Callitris columellaris*, is commonly used in Australian dendroclimatological research (Cullen and Grierson 2007, 2009, Baker et al. 2008, D’Arrigo et al. 2008, Sgherza et al. 2010, O’Donnell et al. 2015, 2018, Allen et al. 2019). Hence, understanding how the intrannual distribution of rainfall, not just total amount, influences their growth is important for interpreting past climatic variability from their growth rings. Our findings here and previously (O’Donnell et al. 2021) show that the relationship between growth of *C. columellaris* and rainfall amount in the tropics is of a non-linear concave down form, where reductions in growth in dry years are greater than increases in growth in wet years (Dannenberg et al. 2019, Gherardi and Sala 2019). Thus, ring widths of *C. columellaris* in the tropics exhibit asymmetry in the recording of extreme years – they record extreme dry years more accurately than extreme wet years. Consequently, tree-ring records from the Australian tropics may be useful as indicators of particularly dry years, but are less useful for distinguishing between years of average or high rainfall (Drew et al. 2014). Similarly, Wise and Dannenberg (2019) found that asymmetric capture of extreme events was common in tree-ring records from the western United States, where a third of tree-ring records captured dry but not wet extremes.
Interestingly, our findings suggest that tropical C. columellaris tree-ring records are more suited to reconstructing the occurrence of rain days > ~5 mm (optimal threshold) than rainfall amount. While the number of rain days is not a common target for reconstruction (but see Woodhouse and Meko 1997), a reconstruction of the number of > ~5 mm rain days may be more meaningful than total rainfall for interpreting past variability in hydroclimate that is important to plant productivity and growth in the tropics and is worth further investigation.

Tree growth at the semi-arid sites exhibit strong and linear relationships with total rainfall amount; relationships that have already been used to interpret past variability of rainfall in northwest and southwest Australia (Cullen and Grierson 2009, O’Donnell et al. 2015). Our findings suggest that these records are more suited to reconstructing ‘biologically important’ (i.e. > optimal threshold) rainfall than total rainfall and can therefore help to better understand the timescales and magnitudes of variation in the portion of rainfall that is important for plant productivity and growth. Our findings also indicate that tree-ring width records from semi-arid Australia, where relationships with extreme rainfall and the number of extreme rain days were strong and where extreme rainfall contributes a large proportion of annual and growing season rainfall (Table 2; Lavender and Abbs 2013), could be used to understand past variability of extreme rainfall or the frequency of extreme rain events. Such potential for using tree-ring records to reconstruct extreme rainfall events has been demonstrated in the southwestern United States (Steinschneider et al. 2018). There is particularly strong potential for developing a reconstruction of extreme rainfall events in the sub-tropical, semi-arid biomes of northwest Australia, where the relationship between C. columellaris growth and the amount of extreme rainfall or the number of extreme rain events is very strong. Even if we had used a more conservative definition of ‘extreme’, these relationships remain strong; for example, using a definition of > 97th percentile (> 30 mm) for extreme rain days, extreme rainfall explains more than 60% of the variance in growth (Fig. 3). The potential to use tree-ring records from semi-arid Australia to better understand past variability of the occurrence of extreme events is particularly important given the high level of uncertainty surrounding extreme climate risk.

Conclusions

The ecological impacts of changes in the frequency and intensity of rainfall have been of increasing interest in the last decade (Knapp et al. 2008, Kulmatiski and Beard 2013, Manea and Leishman 2018, Padilla et al. 2019, Felton et al. 2020), but are still poorly resolved compared to some other aspects of global change. Our study provides important empirical evidence of the role of rain intensity and frequency in driving tree growth and provides new insights into how projected changes in rainfall regimes may impact tree growth across different biomes. Our findings indicate that projected intensification of rainfall regimes is likely to drive contrasting growth responses in mesic and water-limited biomes of Australia; potentially leading to declines in growth in mesic tropical biomes and increases in growth in water-limited semi-arid biomes. However, our findings are based on a single, shallow-rooted tree species, which we use as an indicator species. The growth response of our target species, C. columellaris, is likely representative of some other widespread small Australian tree species that exhibit similar hydraulic traits such as the Acacia aneura complex of species. However, further research is needed to determine whether the growth responses we observed for C. columellaris can be used to predict the growth responses of other shallow-rooted woody species, and in particular, whether the growth responses of deep-rooted woody species are likely to differ from those of shallow-rooted species. Our findings also indicate that growth rings of C. columellaris in water-limited biomes may provide a new avenue to reconstruct and better understand past variability of extreme rain events over multi-centennial timescales. This information is critical for placing recent and projected future changes in the frequency and intensity of extreme rain events in a long-term context and for better predicting the ecosystem impacts of such changes.

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Author contributions

Alison O’Donnell: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). Michael Renton: Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). Kathryn Allen: Data curation (equal); Methodology (equal); Writing – review and editing (equal). Pauline Grierson: Data curation (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

The three unpublished ring width chronologies (LTY, LDE and CHR) have been uploaded to Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kkwh70s4d> O’Donnell et al. 2021. The CJD and KOR ring width chronologies are available from the International Tree Ring Data Bank: AUSL037 (https://www.ncdc.noaa.gov/paleo/study/18957) and AUSL054 (https://www.ncdc.noaa.gov/paleo/study/27375).

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