Received: 22 May 2023 | Accepted: 1 October 2023

DOI: 10.1111/1365-2745.14214

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

The competitive effect of neighbouring plants on the growth of two eucalypts is stronger in dry conditions

Travis G. Britton[1,2] | Shane A. Richards[1] | Melissa R. Gerwin[1] | Rose E. Brinkhoff[1,2] | Mark J. Hovenden[1,2]

[1]School of Natural Sciences, University of Tasmania, Hobart, Tasmania, Australia

[2]ARC Training Centre for Forest Value, School of Natural Sciences, University of Tasmania, Hobart, Tasmania, Australia

Correspondence
Travis G. Britton
Email: t.britton@westernsydney.edu.au

Present address
Travis G. Britton, Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, New South Wales, Australia.

Funding information
Holsworth Wildlife Research Endowment

Handling Editor: Chengjin Chu

Abstract

1. Plant growth is influenced by interactions with neighbouring plants. The strength and direction of the cumulative neighbourhood effect on growth can depend on neighbour properties, such as their abundance, size and proximity, as well as the degree of similarity between interacting plants and their traits, which can be captured by the species identity of neighbours. Such interactions are also influenced by the local environmental conditions that are largely determined by climate. Because neighbour and climatic effects are typically explored in isolation, particularly in long-lived species such as trees, it is unclear how the impacts of neighbours on plant growth shift in response to temporal variation in climatic conditions.
2. Here, we explored how neighbouring plants impact the annual growth of two eucalypts, *Eucalyptus delegatensis* and *Eucalyptus regnans*, over three growing seasons in an experimental forest in south-east Tasmania, Australia. We assessed whether eucalypt growth rates could be described by the number, size, proximity, and species identity of neighbours, and how the strength of this effect was influenced by the growing season climatic conditions.
3. We found that climate and neighbouring plants had an interactive impact on eucalypt growth. Neighbours had a consistent, competitive effect on the growth of both eucalypts in all three growing seasons which was strongly related to the cumulative neighbourhood biomass. The identity of neighbours was important in determining *E. regnans* growth only, whereby distinguishing neighbours according to functional group best described growth. Over all three growing seasons, we predicted that, on average, neighbours reduced *E. delegatensis* and *E. regnans* mean annual growth by 60.5% and 48.4%, respectively. However, the strength of the competitive effect of neighbours on eucalypt growth was related to growing season climate, being strongest when conditions were hot and dry and weakest in cool, wet conditions.
4. *Synthesis*: Given the consistent results observed in two co-occurring eucalypts, our findings suggest that drier and hotter climatic conditions increase the strength of competitive effects on tree growth. This has implications for future

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

forest productivity given projected increased temperatures and variation in rainfall patterns globally.

KEYWORDS
climate change, competition, drought, facilitation, neighbour, plant–plant interaction, stress-gradient hypothesis, tree growth

1 | INTRODUCTION

Interactions among co-occurring plants are key determinants of individual plant growth (Connell, 1983). Neighbouring plants interact for the essential resources required for growth and moderate microclimate conditions by buffering against extreme temperature and wind exposure (Le Roux & McGeoch, 2010; Montgomery et al., 2010), all of which can influence potential growth rates (Criddle et al., 1997). Thus, interactions among neighbouring plants take a variety of forms and the cumulative effect of all neighbours contributes to the observed growth rate of a given plant (Trinder et al., 2013). Importantly, interactions among neighbouring plants are increasingly recognised as a dynamic process which can vary in strength and direction, such as in response to altered environmental conditions (Bimler et al., 2018; Britton et al., 2021; Del Río et al., 2014). A greater understanding of how neighbour interactions vary temporally in different environmental conditions is required to inform predictive models of neighbour effects on plant growth in future climatic conditions.

Historically, research has focused on competitive (negative) interactions as the only, or most important, interaction type among plants (Connell, 1983; Grime, 1977). More recently, greater emphasis has been placed on the positive effects of neighbouring plants, termed facilitation (Bertness & Callaway, 1994; Brooker et al., 2008; Callaway et al., 2002). Facilitation among co-occurring plants, such as beneficial redistribution of soil water through hydraulic lift (Ludwig et al., 2004) or modifying the level of herbivory through associational defence (Champagne et al., 2016), can result in a positive neighbour effect on plant growth, survival or reproductive output (Callaway et al., 2002; Fajardo & McIntire, 2011; Gómez-Aparicio et al., 2004). While competition and facilitation are generally considered as distinct processes, it has been shown that the effect of a neighbour is not exclusively competitive or facilitative (Callaway & Walker, 1997). For example, shading by neighbours is generally considered as a competitive interaction for light (Schwinning & Weiner, 1998), but may also be facilitative under certain conditions if shading decreases leaf temperature, thereby reducing water loss via transpiration (Baumeister & Callaway, 2006). Thus, the net neighbourhood effect may shift in strength and direction depending on factors such as plant resource requirements and abiotic conditions.

The nature of interactions among neighbouring plants can be impacted by ontogeny and environmental conditions. As plants mature, their requirements for growth and survival differ and this can lead to changes in both the strength and direction of plant–plant interactions between different life-history stages (Goldberg et al., 2001; Howard & Goldberg, 2001; Miriti, 2006). Further, environmental conditions have a considerable impact on interaction strength and direction in plant neighbourhoods (Bimler et al., 2018). This concept is described by the stress-gradient hypothesis (SGH; Bertness & Callaway, 1994), which suggests that competition among neighbouring plants will dominate in benign and productive environmental conditions, but interactions will become increasingly facilitative as the environment becomes more stressful. While the SGH has predominately been applied to non-resource stressors such as temperature and salinity gradients (Bertness & Ewanchuk, 2002; Callaway et al., 2002), it has also been related to resource stressors such as gradients of water availability (He et al., 2013).

Temporal variation in climatic conditions, such as interannual differences in precipitation, can create a temporal water availability gradient and, thus, a particular habitat could move substantially along the "stress gradient" from year to year (Del Río et al., 2014). However, empirical support for the SGH in relation to temporal water stress gradients is mixed, whereby previous studies have found facilitation increased (Del Río et al., 2014; Sthultz et al., 2007), decreased (Tielbörger & Kadmon, 2000) or did not show clear differences (Soliveres et al., 2010) in lower rainfall (higher stress) periods compared to those with higher rainfall. Others have not directly tested the SGH but explored variation in neighbour effects on tree growth in response to temporal climate patterns, finding higher temperatures and reduced precipitation can either amplify (Diez et al., 2021) or reduce the strength of competitive neighbour effects (Luo et al., 2020). Thus, although there are clear indications that the neighbourhood effect varies temporally with climate, general patterns have not yet emerged. With regard to tree growth, this might be a product of limited research investigating abiotic and biotic drivers of tree growth simultaneously, compared to studies that consider the two drivers in isolation (Contreras et al., 2011; Das, 2012; Martín-Benito et al., 2008; Truettner et al., 2018).

Previous studies exploring temporal variation in neighbour effects on tree growth commonly focus on community-level neighbourhood metrics (NMs) such as stand basal area (Gleason et al., 2017; Rollinson et al., 2016) or broad groupings such as conspecific and heterospecific neighbours (Diez et al., 2021). While community-level metrics ignore the identity of neighbour species, con- and hetero-specific groupings are based on the assumption that intraspecific competition should always be stronger than interspecific competition because of greater niche overlap (i.e. limiting similarity; MacArthur & Levins, 1967). However, support for this theory in the literature is mixed (Adler et al., 2018; Goldberg & Barton, 1992; Gurevitch

et al., 1992). In forest communities specifically, a global analysis by Kunstler et al. (2015) used three common functional traits—wood density, specific leaf area and maximum height—to assess whether competition strength was primarily determined by the degree of trait similarity between interacting species or by particular trait values of neighbours that confer a competitive advantage. They found support for the latter, such as a negative relationship between neighbour competitive effect and specific leaf area, while finding limited evidence that trait similarity determined competition strength. This suggests that interaction strength between two species may not be related to their niche similarity alone but is also determined by species' morpho-physiological characteristics that determine their impact on the local environment and hence, neighbours in close proximity. For example, neighbours belonging to a species with xylem that is resistant to embolism (i.e. a more negative P_{50} value) can extract water from drier soil and hence, will have a stronger effect on neighbours during drought conditions when water is the most limiting resource (Britton et al., 2022). In contrast, a generally taller species may have a stronger competitive effect in wet years if competition for light is the dominant interaction force. Despite the clear theoretical importance of species-specific neighbour effects and the fact that they have previously been shown to vary with environmental conditions in annual plant communities (Bimler et al., 2018), they are relatively understudied in studies of tree growth (but see Fichtner et al., 2020).

Here, we explored how neighbouring plants impacted annual growth in two eucalypts, *Eucalyptus delegatensis* and *Eucalyptus regnans*, over a three-year period in the Australian Forest Evenness Experiment (AFEX; Gerwin et al., 2020) in south-east Tasmania, Australia. Previous work in the system has shown that the two eucalypts are sensitive to drought-induced canopy damage, and that damage is exacerbated at high densities of certain species, particularly in *E. delegatensis* (Britton et al., 2022). Specifically, we addressed the following research questions: (1) How are the annual growth rates of *E. delegatensis* and *E. regnans* influenced by neighbouring plants, and how important is the species identity of neighbours in determining growth? And (2) how does the strength of neighbour effects vary temporally in years with different climatic conditions?

We hypothesised that neighbours would have a strong competitive effect on eucalypt growth in this system as trees are older than saplings (5 years-old at the beginning of the study) and self-thinning has not yet occurred, so competition among neighbouring plants should be intense (Yoda et al., 1963). We also expected that the identity of neighbours would be a critical determinant of eucalypt growth, and that considering the identity, size and proximity of neighbours together would be the best predictor of growth. Our hypothesis regarding neighbour identity is based on the fact that species-specific neighbour effects have been shown in this system previously (Britton et al., 2022). Finally, in contrast to the SGH (Bertness & Callaway, 1994), we expect the effect of neighbours to be strongest in the driest and hottest year when competition for water will be most intense, as seen in other tests of the SGH to temporal variation in rainfall (Diez et al., 2021; Tielbörger & Kadmon, 2000, but see Sthultz et al., 2007).

2 | METHODS

2.1 | Study site

The AFEX is in the Styx valley, southern Tasmania (42°46′49″ S 146°49′01″ E; Supporting Information Figure S1) on a north-facing slope from 530 to 590 m above sea-level (a.s.l.). The site has a mean summer (December to February) temperature of 12.3°C and mean summer precipitation of 65 mm. Winter (June to August) is substantially cooler and wetter with a mean temperature of 4.1°C and mean precipitation of 94 mm. The AFEX is located amid production eucalypt forest dominated by *Eucalyptus delegatensis* and *E. regnans*, and *Pinus radiata* plantation forest. Prior to clear-felling in 2010, the site was a native eucalypt forest co-dominated by *E. delegatensis* and *E. regnans*, along with *Acacia dealbata* as a sub-dominant and a mixed species understory that included *Pomaderris apetala*. The AFEX was established in April 2013 after a high-intensity regeneration fire. Locally sourced seeds of the four locally dominant native tree species—*E. delegatensis*, *E. regnans*, *Acacia dealbata* and *Pomaderris apetala*—were hand-sown 2 days post-burn to establish an orthogonal evenness × dominant species design. The AFEX experimental design included five different evenness levels for each of the four species (Gerwin et al., 2020), creating 20 treatments replicated four times across eighty 25 × 25 m plots, covering a total area of 5 ha. Seeds were sown at a target community density of 20 potential germinants m^{-2}. Permission to establish the experiment and to access the site for measurements was provided by Sustainable Timbers Tasmania who manage the site on behalf of the State Government of Tasmania, Australia.

2.2 | Neighbourhood plots

Mapped 2 m radius neighbourhood plots were established in the 2018 austral winter in a subset of the main treatment plots ($n = 23$) that were chosen to capture the range of community compositions observed across the site (Supporting Information Figures S2 and S3). Within each plot, we aimed to select a total of six focal trees (three each of *E. delegatensis* and *E. regnans* trees) but in some cases, three individuals of each *Eucalyptus* species were not present in a plot. This was due to the AFEX being designed to create specific monoculture treatments for each of the four species, meaning other species were only present due to germination from the seed bank and thus occurred at very low numbers. Therefore, a mean of 5 (range 1–6) focal trees per treatment plot were selected using randomised coordinates, around which we established the 2 m radius. Focal trees ranged in size from 0.5 to 5.2 cm in diameter at breast height (DBH) and were representative of the size of all plants of that species measured in the neighbourhoods (Supporting Information Figure S4). We recorded the height (m), DBH and GPS location (differential GPS; accuracy of <10 cm) of every tree in each neighbourhood plot area (12.6 m^2 total area). Trees shorter than 1.35 m were

assigned a constant diameter measurement of 0.25 cm, being half that of the smallest diameter value (0.5 cm) recorded for trees above this height. Plants smaller than 0.5 m were not measured or located, with the assumption that they played a negligible role in the neighbourhood. In total, we selected 114 focal trees of either *E. regnans* ($n = 58$) or *E. delegatensis* ($n = 56$) and mapped and measured 7854 neighbours. The 114 neighbourhood plots captured a range of community compositions and ranged in density from 0.8–13.5 plants m^{-2} (Supporting Information Figure S3). Additionally, in winter 2018, we measured the height and DBH of 34 trees growing without neighbours in their immediate 2 m radius, termed isolated focal trees.

Focal trees (isolated and non-isolated) were remeasured yearly in the winters of 2019, 2020 and 2021 to determine 3 years of annual incremental growth. Thus, the 3 year-long growth periods cover two calendar years and are referred to hereafter as 2018/19, 2019/20 and 2020/21. One *E. regnans* focal tree died before winter 2019, meaning its growth could not be measured and was thus removed from all analyses. In addition to the 2018 neighbourhood measurements, neighbours were remeasured at the beginning of the next two sampling periods (winter 2019, 2020) so that annual growth could be related to the relevant neighbourhood conditions at the beginning of each growth period.

2.3 | Focal tree growth

For each focal tree, we used absolute annual (BAI; cm^2) as the growth response variable (Britton et al., 2023a). Individual tree basal area was calculated using individual tree diameter (cm) measurements. Because the modelling approach required positive growth values, in the instances where we found non-positive growth (11.7%), we awarded those focal plants the lowest recorded annual BAI observed for that species in that year. In addition, we repeated the analysis with negative growth values removed, rather than replaced, and found no differences among our general findings (Supporting Information Table S1).

2.4 | Neighbourhood characteristics

To determine how neighbouring plants influenced focal tree growth, we described a focal plant's neighbourhood according to several NMs. First, we considered a simple abundance NM to assess how the number of neighbours within the 2 m radius neighbourhood impacted growth. Second, to capture neighbour size, we calculated the summed basal area (cm^2) of all neighbours within each focal plant's neighbourhood. Third, to include the proximity of neighbours to the focal tree, as well as neighbour size, we considered three neighbourhood indices that included the summed ratio of each neighbour's basal area (cm^2) divided by its distance (m) from the focal tree (Equation 1). The three indices took the general form:

$$NI_i = \sum_{j=1}^{n} \frac{BA_j}{d_{i,j}}, \quad (1)$$

where NI_i is the index associated with focal tree i, of which there are n. BA_j is the basal area of neighbour plant j, and $d_{i,j}$ is the distance metric separating focal plant i and neighbour j. The three indices differed only in how the distance term ($d_{i,j}$) was specified: linear (Britton et al., 2023a), squared or log-transformed.

We determined the importance of the neighbour identity by calculating NMs at the community-, functional group- and species-level. The community level NMs ignored the identity of neighbours and hence resulted in one term per neighbourhood. The functional group level calculated two terms per neighbourhood by determining NMs separately for neighbours that were eucalypts or non-eucalypts, whereby *P. apetala* and *A. dealbata* formed the non-eucalypt group. Finally, the species level NMs included four terms per neighbourhood, one for each of the four species: *E. delegatensis*, *E. regnans*, *P. apetala* and *A. dealbata*. Other species contributed just 1.5% of all trees measured so were excluded from all analyses. All NM terms were re-calculated following the yearly neighbour census to ensure they accurately described the current neighbourhood effect on focal tree growth.

2.5 | Climate

We calculated climate metrics at the AFEX during the sampling period to explain year-to-year variation in the strength of neighbourhood effects on focal tree growth. Using climate data collected at the closest government-run weather station to the AFEX (Bushy Park, Tasmania; ~10 km from the study site), we determined the mean daily temperature (°C), total daily precipitation (mm) and mean daily potential evapotranspiration (PET; mm/month) during the sampling period (Supporting Information Table S2). From these data, we determined the standardised evapotranspiration index (SPEI; Vicente-Serrano et al., 2010), a commonly used drought index that encapsulates temperature, precipitation and PET that can be calculated over different time scales, such as within a year. The SPEI ranges from −3 to +3 whereby negative values indicate hot/dry conditions, and positive values indicate cool/wet conditions compared to the long-term average. We calculated SPEI values on a 6-month analysis period to capture growing season (October to March) climatic conditions. SPEI values were determined in March and thus represent the weather conditions in the preceding 6-month growing season.

2.6 | Statistical analyses

All data analyses were performed using the R programming language (v4.0.4; R Development Core Team, 2021).

2.6.1 | Neighbourhood metric selection

First, to determine which NM best described eucalypt growth and to reduce the number of competing models, we fit five linear mixed-effect models (LMMs) that differed in their NM (i.e. neighbourhood

abundance, neighbourhood basal area and the three versions of the neighbourhood index; Equation 1). Log-transformed BAI was the response variable in all models, focal tree species (*E. delegatensis* or *E. regnans*) and sampling year were included as fixed factors, and individual tree BA and NMs were included as continuous predictors. The five models were ranked based on Akaike's information criterion (AIC). We found that the summed neighbourhood basal area metric, which ignores the distance of neighbours to the focal tree, best described our data (Supporting Information Table S3) and was thus used as our NM hereafter.

2.6.2 | Assessing climate and neighbourhood effects

In all subsequent analyses, *Eucalyptus regnans* and *E. delegatensis* were analysed separately to assess how the combined influence of neighbouring plants and growing season climatic conditions impacted each species' annual growth rate. We fit multiple growth models that differed in whether and/or how NMs and SPEI values were incorporated into the model, being either omitted, included as main effects alone or with an interaction between the two predictors. Specifically, we fit 11 LMMs; (Supporting Information Table S4) for each eucalypt species (lme4 R package; Bates et al., 2014). We used log-transformed absolute BAI as the response variable and size-dependent growth was accounted for in all models by including log-transformed focal tree basal area (BA) at the beginning of each sampling period as a continuous predictor. BAI and BA were log-transformed as we observed a power-relation between the two variables. Neighbour effects were investigated by including the NMs defined previously: community, functional group or species neighbourhood basal area values. The influence of growing season climatic conditions on tree growth was determined by including the growing season SPEI value as a continuous predictor. Finally, we included the interaction between the SPEI and the NMs to assess whether climatic differences influenced the strength of neighbour interactions. Neighbourhood number, nested within plot, was included as an observation-level random effect to account for repeated sampling of focal trees and unmeasured environmental differences among treatment plots.

For each eucalypt, we ranked models based on AIC and ignored all models with $\Delta AIC > 6$ than the best model or with a higher AIC than a simpler nested model (Richards, 2008). This approach ensures that more complex models are only selected when they substantially improve model fit beyond the penalty of additional terms.

The net neighbourhood effect on tree growth, for both eucalypt species during each of the three growing seasons, was estimated by comparing predictions of growth of the non-isolated trees according to the best AIC model with and without the competition term (i.e. when setting the NMs to zero). In addition, to visualise the relationship between annual BAI and a given predictor (e.g. the NMs), we extracted partial residuals and partial slopes (visreg R package; Breheny & Burchett, 2017) from the best-fitting model in each species.

3 | RESULTS

Both eucalypts grew substantially over the three-year period with an average annual BAI of $5.62 \pm 0.65\,cm^2$ (mean ± SE) in *E. delegatensis* and $7.05 \pm 0.74\,cm^2$ in *E. regnans*. In both species, absolute BAI was positively size-dependent (Supporting Information Figure S5), such that initial BA was the strongest single influence on BAI. In addition, *E. delegatensis* and *E. regnans* annual BAI was strongly influenced by neighbouring plants and the climatic conditions during the growing season (Table 1).

The best-fitting model in both species contained a NM, the SPEI term and their interaction (Table 1), indicating that the strength of the neighbourhood effect on eucalypt growth depended on the growing season climatic conditions (Table 1, Figure 1). However, the best-fitting model differed slightly between the two species according to how neighbours were grouped (Table 1): *E. delegatensis* BAI was best described by the summed neighbourhood basal area at the community-level, whereas *E. regnans* BAI was better described by calculating the neighbourhood basal area separately according to functional group (eucalypt or non-eucalypt). The BAI of both species was negatively related to the NMs in both models, indicating that neighbours had a competitive effect on eucalypt growth irrespective of their identity (Figure 1). The best-fitting model for *Eucalyptus regnans*, in which neighbours were categorised by functional group, was only marginally better at describing variation in *E. regnans* growth compared with the same model that was selected for *E. delegatensis* (neighbours grouped at the community-level; Table 1). Importantly, irrespective of how neighbours were categorised, model parsimony improved dramatically in both species when the interaction between the NMs and the SPEI value was included (Table 1), providing strong evidence that the influence of neighbours and climate on tree growth were dependent on one another.

Regardless of the NM used in the model, its influence on annual BAI was strongest in 2018/19 (Figure 1) when the climatic conditions were hot and dry, evident in the lowest SPEI value of all three growing seasons (Figure 2). This effect was weaker in 2019/20 (intermediate SPEI) and weaker again in 2020/21 (highest SPEI; Figure 1) as conditions became progressively cooler and wetter (Figure 2). Thus, the competitive effect of neighbours on eucalypt growth was strongest when conditions were hot and dry, and substantially weaker when conditions were generally cooler and wetter (Figure 1).

The reduction in annual BAI of both species due to neighbours was more pronounced as the neighbourhood basal area increased (Figure 1). This was particularly evident in the relationship between *E. delegatensis* BAI and the community-level neighbourhood basal area, and *E. regnans* BAI and eucalypt neighbourhood basal area (Figure 1). In *E. delegatensis*, we did not find evidence that the strength of the neighbour effect on growth differed substantially between functional groups. Instead, we found that *E. delegatensis* BAI decreased as the cumulative neighbourhood basal area increased, regardless of neighbour identity. In contrast, eucalypt neighbours had a greater suppressive effect on *E. regnans* BAI than did non-eucalypt neighbours (*A. dealbata* and *P. apetala*; Figure 1). However, in general, the growth rates of

TABLE 1 Summary of AIC analysis of 11 LMMs of *E. delegatensis* and *E. regnans* annual . Each row describes the model and parameters included and rows are arranged in increasing complexity in terms of how the standardised precipitation evapotranspiration index (SPEI) and/or (NMs; i.e. neighbourhood basal area) are incorporated into the model. NM indicates how neighbours were described: grouped irrespective of their species identity (community BA), by their functional group (functional BA) or their species identity (species BA). SPEI and NM × SPEI terms indicate whether SPEI was included as a fixed effect and whether an interaction was included, respectively. *K* is the number of estimated parameters, ln*L* is the maximum log-likelihood and ΔAIC is the AIC of the model relative to the best-AIC model, shown in bold. Selected models are highlighted in grey-shading and include the best-AIC model, as well as any additional models with ΔAIC <6 that are not a nested and more complex version of the best-AIC model. Here, species BA models are nested within their respective functional BA models, which are themselves nested within the respective community BA models. This approach follows the selection criterion outlined in Richards (2008). All models included log-transformed basal area as a predictor, and neighbourhood number, nested within plot as an observation-level random effect.

Neighbourhood metric (NM)	SPEI	NM × SPEI term	*K*	ln*L*	ΔAIC
Eucalyptus delegatensis					
None	No	–	5	−298.1	42.1
None	Yes	No	7	−298.1	44.0
Community BA	No	–	6	−288.2	24.1
Functional BA	No	–	7	−287.1	24.0
Species BA	No	–	9	−286.0	25.7
Community BA	Yes	No	7	−286.3	22.3
Functional BA	Yes	No	8	−284.4	23.2
Species BA	Yes	No	10	−287.5	24.6
Community BA	**Yes**	**Yes**	**8**	**−279.0**	**0.0**
Functional BA	Yes	Yes	10	−286.0	3.4
Species BA	Yes	Yes	14	−271.4	6.7
Eucalyptus regnans					
None	No	–	5	−279.7	25.7
None	Yes	No	7	−279.5	27.4
Community BA	No	–	6	−274.2	16.7
Functional BA	No	–	7	−274.0	18.5
Species BA	No	–	9	−273.9	22.3
Community BA	Yes	No	7	−272.2	14.7
Functional BA	Yes	No	8	−272.2	16.7
Species BA	Yes	No	10	−272.1	20.5
Community BA	Yes	Yes	8	−264.5	1.5
Functional BA	**Yes**	**Yes**	**10**	**−261.8**	**0.0**
Species BA	Yes	Yes	14	−259.6	3.5

both eucalypts were lower in neighbourhoods where neighbours were larger and more abundant.

The best-fitting models in both species explained a similar amount of variation in BAI in both *E. delegatensis* ($R^2 = 0.70$) and *E. regnans* ($R^2 = 0.68$), however, the contribution of neighbourhood effects was stronger in *E. delegatensis*. The best-fitting model explained 31% more variation in annual BAI in *E. delegatensis* than the model that excluded all neighbour effects and included only initial BA and SPEI as predictors. In contrast, *E. regnans* best fitting model explained an additional 14% in annual BAI compared to the simpler model containing no neighbour effects.

For all non-isolated trees, the reduction in annual BA growth due to neighbours, when estimated by the best AIC model, was significant (Figure 3). For *Eucalyptus delegatensis*, competition from neighbours was greatest in 2018/19 (66.3% reduction in mean growth) and became progressively weaker in 2019/20 (61.6%) and 2020/21 (53.6%; Figure 3a). The competitive effect of neighbours on *E. regnans* growth followed the same trend; neighbours reduced growth strongly in 2018/19 (63.1% mean growth reduction) and 2019/20 (53.1%) but had a substantially weaker effect in 2020/21 (28.4%; Figure 3b).

4 | DISCUSSION

This study clearly shows that neighbouring plants impacted eucalypt growth between 2018 and 2021 in the AFEX. Neighbours had a consistent, competitive effect on the growth of both *E. delegatensis* and *E. regnans* in all three growing seasons. The strength of the competitive effect of neighbours was strongly related to their combined size and was less influenced by their proximity to the focal tree, which held true in both focal species. However, the identity of neighbours was important in determining *E. regnans* growth only, whereby distinguishing neighbours according to functional group adequately captured differences in their competitive effect on growth. The strength of the neighbourhood effect was also dependent on the climatic conditions of the growing season. The growth of focal trees with neighbours was lowest during the hotter/drier growing seasons and highest during the coolest/wettest season. This supported our hypothesis that the competitive effect of neighbours on tree growth would be strongest in hot, dry climatic conditions.

The net neighbourhood effect on eucalypt growth was consistently competitive, however, the strength of this effect varied among growing seasons, being strongest in 2018/19 and weakest in 2020/21. Although this decreasing trend in competition strength over the three growing seasons suggests that competition is decreasing with tree age, this is unlikely because the site is yet to experience substantial self-thinning (Yoda et al., 1963) and the intensity of competition, as indicated by the values of the neighbourhood basal area metrics (Figure 1), increased from 2018/19 to 2020/21. However, it is possible that the ability of the eucalypt focal trees to tolerate competition (i.e. their competitive response; Goldberg, 1996) increased over the three growing seasons, thereby reducing the degree to which neighbours suppressed growth. For example, the two eucalypts are the canopy-forming species in this system, so as they mature, the difference in plant size compared to the sub-canopy species (*P. apetala* and *A. dealbata*) becomes pronounced, potentially reducing light competition. Alternatively,

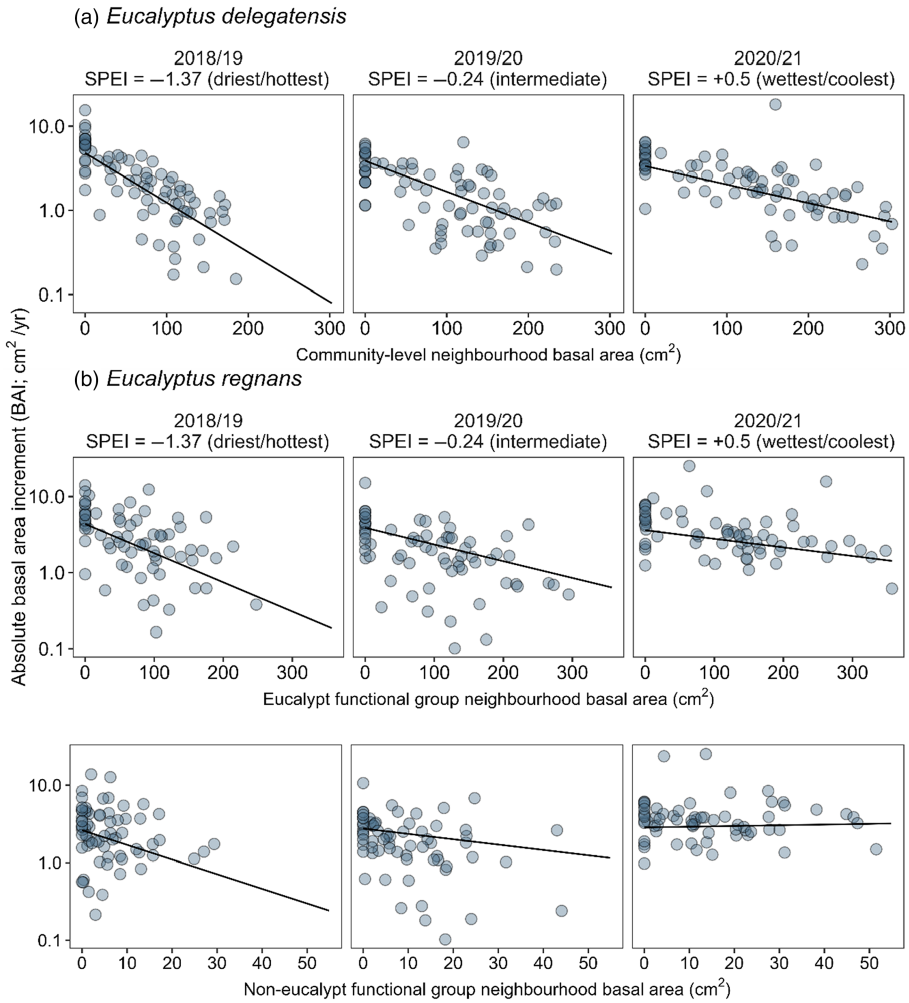


FIGURE 1 Partial residual plots depicting the relationship between (a) *Eucalyptus delegatensis* and (b) *Eucalyptus regnans* annual absolute basal area increment (BAI) (cm^2) and neighbourhood metrics (NMs) (community- and functional group-level neighbourhood basal area; cm^2) in three sampling periods with different climatic conditions. Points indicate partial regressions and black lines represent the partial slope between BAI and the NMs in that year, determined from the best-fitting model for each species (Table 1). NMs (a) weight all species equally or (b) calculate separate metrics for eucalypts and non-eucalypts. Note the log-scale on the *y*-axis.

several growing seasons of strong competition, as observed here, may have initiated a plastic response by the focal trees. This could be a response such as focal trees increasing their water-use efficiency by allocating more nitrogen to leaves to increase their carboxylation capacity (i.e. increasing leaf Rubisco content), thereby reducing their transpiration rate and thus, water requirements (Weih et al., 2011; Wright et al., 2003). While determining which, if any, of these responses occurred over the three growing seasons is outside the scope of this study, future work could explore traits related to these specific functions and compare trait shifts between isolated and non-isolated focal plants for evidence of a competitive response in the two species. Nevertheless, it is probable that differences in competition strength among growing seasons are due, at least in part, to distinct differences in climatic conditions and highlights the need to quantify neighbour effects over several time periods.

The strength of the competitive neighbourhood effect on eucalypt growth was related to the SPEI of the growing season and suggests that water-limitation is a key determinant of interaction strength in the AFEX. Our results indicate that the strength of competition was negatively related to environmental severity (water stress), whereby the strongest and weakest neighbour effects were observed in the hot/dry and cool/wet growing seasons, respectively. This finding contradicts predictions of the SGH (Bertness & Callaway, 1994) and contributes to an increasing body of evidence that in severely water-limited environments, plant–plant interactions often become increasingly competitive, rather than facilitative (Barron-Gafford et al., 2017; Maestre & Cortina, 2004; O'Brien et al., 2017; Tielbörger & Kadmon, 2000). Further, our finding that stronger competition was associated with reduced precipitation is supported by previous similar studies that assess how temporal variation in rainfall determines the nature of plant–plant interactions (Diez et al., 2021; Tielbörger & Kadmon, 2000) and by a recent study that found drought tended to increase competition-induced tree mortality across parts of Europe (Kulha et al., 2023). Stronger competition in dry conditions has important implications for tree

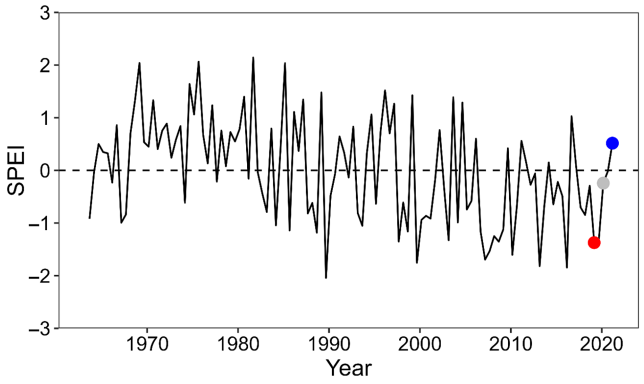


FIGURE 2 Time series of 6-month standardised precipitation evapotranspiration index (SPEI) at Bushy Park Estates weather station ~10 km from the Australian Forest Evenness Experiment site (1963–2021). The black line depicts March and October SPEI values, which represent the deficit/surplus in the austral growing season (November–March) and the remainder of the year (April–October). Coloured points indicate the growing seasons in this study: 2018/19 (red), 2019/20 (grey) and 2020/21 (blue). Climate data sourced from the Australian Bureau of Meteorology: http://bom.gov.au/climate/data/.

growth in future climatic conditions, in which drought frequency and severity is expected to increase (Dai, 2013; Reichstein et al., 2013).

In contrast to our expectations, we did not find the species identity of neighbouring plants to be a strong determinant of their impact on eucalypt growth. However, our results did lend some support to the classic ecological theory of limiting similarity (MacArthur & Levins, 1967). We found that *E. regnans* experienced greater competition from conspecific and *E. delegatensis* neighbours (eucalypt functional group) compared to the non-eucalypt functional group. While this result was observed in only one of our focal species and did not distinguish between the effect of the two eucalypts, it does suggest that the strength of competition increases with increasing phenotypic similarity due to greater niche overlap (Abrams, 1983; MacArthur & Levins, 1967). This supports previous research that shows grouping species into relatively broad categories, such as a grass or forb (Martyn et al., 2021) and canopy or sub-canopy trees as seen here, can capture important differences in how species interact. However, we note that this finding is in contrast to a previous study in this system which found strong species-specific effects on drought damage in *E. delegatensis* and *E. regnans*, predominantly from *P. apetala* neighbours

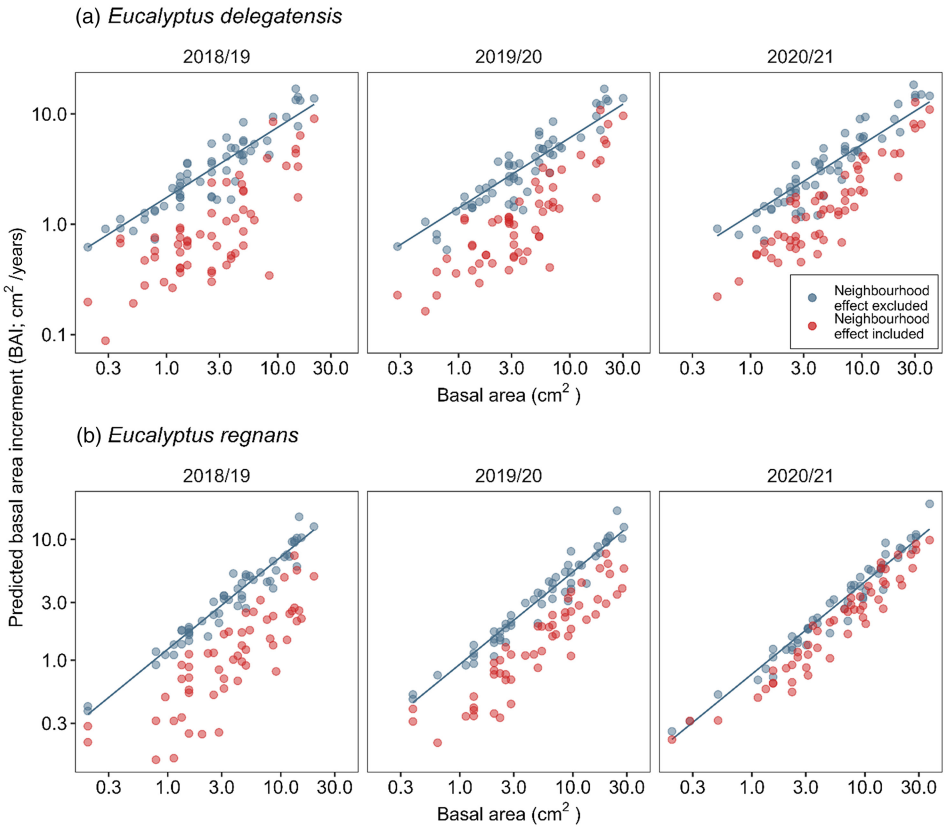


FIGURE 3 Model predicted annual change in basal area of non-isolated focal trees in relation to individual tree basal area. Blue points show predicted growth when neighbourhood metrics (NMs) are excluded (i.e. set to zero) and red points show predicted growth when NMs are considered for (a) *Eucalyptus delegatensis* ($n = 58$) and (b) *Eucalyptus regnans* ($n = 55$) over three separate growing seasons. Variation in the predictions is due to between-tree variation in their neighbours and the random effect term in the model, which describes individual-level variation estimated from the repeated measurements of trees. The solid lines are predictions when the random effect is removed and thus depict predicted growth for a typical tree of the size indicated in the absence of neighbours.

(Britton et al., 2022). Britton et al. (2022) suggested that the strong effect of *P. apetala* neighbours was due to their xylem being more resistant to embolism than the eucalypts, allowing *P. apetala* plants to remove water from drier soil and hence, have a stronger impact on the local water availability during drought. While we cannot determine why we did not detect this same effect on eucalypt growth in the present study, it is possible that the strong competitive effect of *P. apetala* on eucalypt canopy damage was an acute effect during the most water-stressed period of the year and that this effect may have been dampened over the longer measurement period of this study. Nevertheless, these contrasting results contribute to increasing evidence that multiple plant performance metrics, such as plant survival and growth, can respond differently to neighbour interactions in the same system (Fajardo & McIntire, 2011; Hastwell & Facelli, 2003).

4.1 | Conclusions

Here, we show that tree growth is controlled by a complex interplay between growing season climatic conditions and the cumulative biomass of neighbouring plants. While we did not find the identity of neighbouring plants to be a strong determinant of their effect on the growth of co-occurring plants, our findings lend some support to the notion that grouping neighbours by functional group can capture variation in their competitive effects on tree growth. The net effect of neighbours, while always competitive in this system, varied in strength substantially among growing seasons but in a predictable way. The strength of competition was negatively related to the growing season SPEI value, indicating that competition is more intense in hot and dry than cold and wet conditions in the AFEX. Given the consistent results observed in two co-occurring eucalypts, our findings suggest that drier and hotter climatic conditions projected for this region will increase the frequency of strong competitive effects on tree growth, with worrying implications for future forest productivity.

AUTHOR CONTRIBUTIONS

Travis G. Britton and Mark J. Hovenden conceived the study. Melissa R. Gerwin established the neighbourhood plots with assistance from Travis G. Britton and Mark J. Hovenden. Travis G. Britton conducted the remaining data collection with major contributions from Rose E. Brinkhoff. Travis G. Britton, Shane A. Richards and Mark J. Hovenden analysed the data. Travis G. Britton wrote the manuscript with contributions from all authors.

ACKNOWLEDGEMENTS

We acknowledge the traditional custodians of the land on which this research was undertaken, the palawa people of lutruwita/Tasmania, and recognise the lairmairrener people as the traditional custodians of the AFEX field site. We pay respects to elders past and present. We thank Sustainable Timbers Tasmania for providing access to the study site. TGB was supported by an Australian Government Research Training Program (RTP) scholarship, and acknowledges provision of scholarship support from the Gottstein Trust and fieldwork funding by the Holsworth Wildlife Research Endowment—Equity Trustees Charitable Foundation and the Ecological Society of Australia. Open access publishing facilitated by Western Sydney University, as part of the Wiley - Western Sydney University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14214.

DATA AVAILABILITY STATEMENT

All data used in this study is available from the Dryad Digital Repository https://doi.org/10.5061/dryad.tmpg4.f53b (Britton et al., 2023b).

ORCID

Travis G. Britton https://orcid.org/0000-0003-1202-116X
Shane A. Richards https://orcid.org/0000-0002-9638-5827
Melissa R. Gerwin https://orcid.org/0000-0003-0072-2786
Rose E. Brinkhoff https://orcid.org/0000-0001-9089-6661
Mark J. Hovenden https://orcid.org/0000-0001-7208-9700

REFERENCES

Abrams, P. (1983). The theory of limiting similarity. *Annual Review of Ecology and Systematics*, *14*, 359–376.

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T., & Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, *21*, 1319–1329.

Barron-Gafford, G. A., Sanchez-Cañete, E. P., Minor, R. L., Hendryx, S. M., Lee, E., Sutter, L. F., Tran, N., Parra, E., Colella, T., & Murphy, P. C. (2017). Impacts of hydraulic redistribution on grass–tree competition vs facilitation in a semi-arid savanna. *New Phytologist*, *215*, 1451–1461.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Baumeister, D., & Callaway, R. M. (2006). Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. *Ecology*, *87*, 1816–1830.

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*, 191–193.

Bertness, M. D., & Ewanchuk, P. J. (2002). Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, *132*, 392–401.

Bimler, M. D., Stouffer, D. B., Lai, H. R., & Mayfield, M. M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, *106*, 1839–1852.

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*, 56–71.

Britton, T. G., Brodribb, T. J., Richards, S. A., Ridley, C., & Hovenden, M. J. (2022). Canopy damage during a natural drought depends on species

identity, physiology and stand composition. *New Phytologist*, *233*, 2058–2070.

Britton, T. G., Hovenden, M. J., Porter, M., Flittner, A., Brinkhoff, R., & Mayfield, M. M. (2021). Plant communities, populations and individuals have distinct responses to short-term warming and neighbour biomass removal in two montane grasslands. *Applied Vegetation Science*, *24*, e12557.

Britton, T. G., Richards, S. A., & Hovenden, M. J. (2023a). Quantifying neighbour effects on tree growth: Are common "competition" indices biased?*Journal of Ecology*, *111*, 1270–1280.

Britton, T. G., Richards, S. A., & Hovenden, M. J. (2023b). Data from: Quantifying neighbour effects on tree growth: Are common "competition" indices biased?*Dryad Digital Repository*. https://doi.org/10.5061/dryad.tmpg4f53b

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M., & Anthelme, F. (2008). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, *96*, 18–34.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., & Aschehoug, E. T. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*, 844–848.

Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology*, *78*, 1958–1965.

Champagne, E., Tremblay, J. P., & Cote, S. D. (2016). Spatial extent of neighboring plants influences the strength of associational effects on mammal herbivory. *Ecosphere*, *7*, e01371.

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist*, *122*, 661–696.

Contreras, M. A., Affleck, D., & Chung, W. (2011). Evaluating tree competition indices as predictors of in western Montana forests. *Forest Ecology and Management*, *262*, 1939–1949.

Criddle, R. S., Smith, B. N., & Hansen, L. D. (1997). A respiration based description of plant growth rate responses to temperature. *Planta*, *201*, 441–445.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*, 52–58.

Das, A. (2012). The effect of size and competition on tree growth rate in old-growth coniferous forests. *Canadian Journal of Forest Research*, *42*, 1983–1995.

Del Río, M., Schütze, G., & Pretzsch, H. (2014). Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology*, *16*, 166–176.

Diez, J. M., Boone, R., Bohner, T., & Godoy, O. (2021). Frequency-dependent tree growth depends on climate. *Ecology*, *102*, e03284.

Fajardo, A., & McIntire, E. J. (2011). Under strong niche overlap conspecifics do not compete but help each other to survive: Facilitation at the intraspecific level. *Journal of Ecology*, *99*, 642–650.

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

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

Gleason, K. E., Bradford, J. B., Bottero, A., D'Amato, A. W., Fraver, S., Palik, B. J., Battaglia, M. A., Iverson, L., Kenefic, L., & Kern, C. C. (2017). Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere*, *8*, e01849.

Goldberg, D. E. (1996). Competitive ability: Definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*, 1377–1385.

Goldberg, D. E., & Barton, A. M. (1992). Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *The American Naturalist*, *139*, 771–801.

Goldberg, D. E., Turkington, R., Olsvig-Whittaker, L., & Dyer, A. R. (2001). Density dependence in an annual plant community: Variation among life history stages. *Ecological Monographs*, *71*, 423–446.

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & Baraza, E. (2004). Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, *14*, 1128–1138.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, *111*, 1169–1194.

Gurevitch, J., Morrow, L. L., Wallace, A., & Walsh, J. S. (1992). A meta-analysis of competition in field experiments. *The American Naturalist*, *140*, 539–572.

Hastwell, G. T., & Facelli, J. M. (2003). Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. *Journal of Ecology*, *91*, 941–950.

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters*, *16*, 695–706.

Howard, T. G., & Goldberg, D. E. (2001). Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology*, *82*, 979–990.

Kulha, N., Honkaniemi, J., Barrere, J., Brandl, S., Cordonnier, T., Korhonen, K. T., Kunstler, G., Paul, C., Reineking, B., & Peltoniemi, M. (2023). Competition-induced tree mortality across Europe is driven by shade tolerance, proportion of conspecifics and drought. *Journal of Ecology*, *111*, 2310–2323.

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., … Westoby, M. (2015). Plant functional traits have globally consistent effects on competition. *Nature*, *529*, 204–207.

Le Roux, P. C., & McGeoch, M. A. (2010). Interaction intensity and importance along two stress gradients: Adding shape to the stress-gradient hypothesis. *Oecologia*, *162*, 733–745.

Ludwig, F., Dawson, T., Prins, H., Berendse, F., & De Kroon, H. (2004). Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, *7*, 623–631.

Luo, Y., McIntire, E. J., Boisvenue, C., Nikiema, P. P., & Chen, H. Y. (2020). Climatic change only stimulated growth for trees under weak competition in central boreal forests. *Journal of Ecology*, *108*, 36–46.

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

Maestre, F. T., & Cortina, J. (2004). Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, S331–S333.

Martín-Benito, D., Cherubini, P., Del Río, M., & Cañellas, I. (2008). Growth response to climate and drought in *Pinus nigra* Arn. Trees of different crown classes. *Trees*, *22*, 363–373.

Martyn, T. E., Stouffer, D. B., Godoy, O., Bartomeus, I., Pastore, A. I., & Mayfield, M. M. (2021). Identifying "useful" fitness models: Balancing the benefits of added complexity with realistic data requirements in models of individual plant fitness. *The American Naturalist*, *197*, 415–433.

Miriti, M. N. (2006). Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, *94*, 973–979.

Montgomery, R. A., Reich, P. B., & Palik, B. J. (2010). Untangling positive and negative biotic interactions: Views from above and below ground in a forest ecosystem. *Ecology*, *91*, 3641–3655.

O'Brien, M. J., Pugnaire, F. I., Armas, C., Rodríguez-Echeverría, S., & Schöb, C. (2017). The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. *Ecology and Evolution*, *7*, 2441–2448.
R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van derVelde, M., Vicca, S., Walz, A., & Wattenbach, M. (2013). Climate extremes and the carbon cycle. *Nature*, *500*, 287–295.
Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, *45*, 218–227.
Rollinson, C. R., Kaye, M. W., & Canham, C. D. (2016). Interspecific variation in growth responses to climate and competition of five eastern tree species. *Ecology*, *97*, 1003–1011.
Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, *113*, 447–455.
Soliveres, S., DeSoto, L., Maestre, F. T., & Olano, J. M. (2010). Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*, 227–234.
Sthultz, C. M., Gehring, C. A., & Whitham, T. G. (2007). Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist*, *173*, 135–145.
Tielbörger, K., & Kadmon, R. (2000). Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, *81*, 1544–1553.
Trinder, C. J., Brooker, R. W., & Robinson, D. (2013). Plant ecology's guilty little secret: Understanding the dynamics of plant competition. *Functional Ecology*, *27*, 918–929.
Truettner, C., Anderegg, W. R., Biondi, F., Koch, G. W., Ogle, K., Schwalm, C., Litvak, M. E., Shaw, J. D., & Ziaco, E. (2018). Conifer radial growth response to recent seasonal warming and drought from the southwestern USA. *Forest Ecology and Management*, *418*, 55–62.
Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, *23*, 1696–1718.
Weih, M., Bonosi, L., Ghelardini, L., & Rönnberg-Wästljung, A. C. (2011). Optimizing nitrogen economy under drought: Increased leaf nitrogen is an acclimation to water stress in willow (*Salix* spp.). *Annals of Botany*, *108*, 1347–1353.
Wright, I. J., Reich, P. B., & Westoby, M. (2003). Least-cost input mixtures of water and nitrogen for photosynthesis. *The American Naturalist*, *161*, 98–111.
Yoda, K., Kira, T., Ogawa, H., & Hozumi, K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology*, *14*, 107–129.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Location of the Australian Forest Evenness Experiment (AFEX; 42°46′49″ S 146°49′01″ E) in the lower Styx valley, south-eastern Tasmania, Australia (Gerwin et al., 2020).

Figure S2. (a) The Australian Forest Evenness (AFEX) site and neighbourhood plot layout. Squares represent the 25×25 m treatment plots. Points indicate the location of the 2 m radius neighbourhood plots surrounding a *Eucalyptus delegatensis* (red) or *Eucalyptus regnans* (black) focal plant. (b) Example of a mapped neighbourhood plot surrounding a focal plant, indicated by the black point. Size of the coloured points of each species represent plant size in diameter at breast height (not to scale).

Figure S3. Neighbourhood density of the four species in the 113 AFEX neighbourhoods of either *Eucalyptus delegatensis* ($n = 58$) and *Eucalyptus regnans* ($n = 56$) focal trees, ordered in decreasing density from 0.79 to 13.49 plants m^{-2}.

Figure S4. Observed relationship between diameter at breast height and tree height of all (a) *Eucalyptus delegatensis* and (b) *Eucalyptus regnans* focal trees (black points) and (a–d) all neighbour plants (grey points) in the four species (*Eucalyptus delegatensis*, *Eucalyptus regnans*, *Pomaderris apetala* and *Acacia dealbata*) at the Australian Forest Evenness Experiment in 2018, the beginning of the study.

Figure S5. Relationship between absolute annual (BAI; cm2) and initial tree basal area (BA; cm^2) in (a) *Eucalyptus delegatensis* and (b) *Eucalyptus regnans* isolated (open points) and non-isolated (filled points) focal trees. Data shown are pooled over the three annual growth periods. Note the log-scale. The approximate linear relationship depicted here for the isolated trees supports the assumption of a power relationship between annual BAI and basal area adopted by all the fitted statistical models.

Table S1. Summary of AIC analysis of eleven LMMs of *E. delegatensis* and *E. regnans* annual (BAI) when negative growth is excluded, rather than awarded the lowest growth value for that species in each year (Table 1 in the main text). Each row describes the model and parameters included and rows are arranged in increasing complexity in terms of how the standardised precipitation evapotranspiration index (SPEI) and/or neighbourhood metrics (NM; i.e. neighbourhood basal area) are incorporated into the model. NM indicates how neighbours were described: grouped irrespective of their species identity (community BA), by their functional group (functional BA) or their species identity (species BA). SPEI and NM × SPEI terms indicate whether SPEI was included as a fixed effect and whether an interaction was included, respectively. *K* is the number of estimated parameters, lnL is the maximum log-likelihood and ΔAIC is the AIC of the model relative to the best-AIC model, shown in bold. Selected models are highlighted in grey-shading and include the best-AIC model, as well as any additional models with ΔAIC <6 that are not a nested and more complex version of the best-AIC model. Here, species BA models are nested within their respective functional BA models, which are themselves nested within the respective community BA models. This approach follows the criterion outlined in Richards (2008). All models included log-transformed basal area as a predictor, and neighbourhood, nested within plot as a random effect.

Table S2. Growing season climate data over the three sampling periods. Data shown are for the closest weather station (Bushy Park, Tasmania, Australia) ~10 km from the AFEX and are calculated over the 6-month growing season (October to March). Climate metrics are the Standardised Precipitation Evapotranspiration Index (SPEI), mean daily temperature (°C), total precipitation (mm) and mean Potential Evapotranspiration (PET; mm/month).

Table S3. AIC analysis of five different neighbourhood metrics (NMs) describing *Eucalyptus delegatensis* and *E. regnans* growth in the Australia Forest Evenness Experiment. Five identical linear mixed-effect models[1] were compared that differed only in their chosen NM: neighbourhood abundance, summed neighbourhood basal area, and three indices (Equation 1 in the main text) that consider neighbour size and their distance from the focal tree with either a linear, squared or log-transformed distance term. NM describes which NM was included in the respective model, AIC provides the raw AIC value of each model, and ΔAIC describes the AIC of each model relative to the best-AIC model, shown in grey shading.

Table S4. Description of eleven LMMs used in the AIC analyses of *Eucalyptus delegatensis* and *E. regnans* growth in the Australian Forest Evenness Experiment, presented in Table 1. Each row describes the model by detailing which predictors—neighbourhood basal area (BA), standardised precipitation evapotranspiration index (SPEI)—are used and whether/how interactions are included. The two eucalypts were analysed separately and al models included neighbourhood number, nested within plot, as an observation-level random effect.

How to cite this article: Britton, T. G., Richards, S. A., Gerwin, M. R., Brinkhoff, R. E., & Hovenden, M. J. (2023). The competitive effect of neighbouring plants on the growth of two eucalypts is stronger in dry conditions. *Journal of Ecology*, *111*, 2721–2732. https://doi.org/10.1111/1365-2745.14214