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### RESEARCH PAPER



## Grow wider canopies or thicker stems: Variable response of woody plants to increasing dryness

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### Abstract

**Aim:** Woody plants vary greatly from tall trees to branching shrubs with increasing dryness. Variation in plant allometry is driven by both biotic and abiotic factors, reflecting different plant adaptation strategies in different environments. Here, we explore how aboveground allometry of different woody plants responds to increasing dryness along an extensive aridity gradient.

**Global Ecology** 

Location: Eastern Australia.

Time period: 2018-2019.

Major taxa studied: Woody plants.

**Methods:** We surveyed the aboveground allometry of woody plants (e.g., canopy, height, stem diameter, branches) at 150 sites along a 1,500-km aridity gradient from humid to arid areas. We used regression analyses and structural equation modelling to explore the variation in woody allometry with increasing aridity, and the abiotic (resource availability) and biotic (aboveground competition) mechanisms driving such changes.

**Results:** Plant height declined, but branching, canopy width and canopy depth increased with increasing aridity. Woody responses to dryness varied among genera, with increasing aridity associated with wider canopies in *Eucalyptus* and *Callitris* spp., thicker stems in *Acacia* spp., but no clear differences in *Allocasuarina* spp. Biotic and abiotic factors exerted different effects on the allometry of different genera, with *Eucalyptus* and *Callitris* spp. constrained by resource availability, while *Acacia* and *Allocasuarina* spp. were regulated mainly by aboveground competition.

**Main conclusions:** As aridity increased, we found genus-specific responses in allometric changes and driving mechanisms (resource availability cf. aboveground competition). Rather than merely shrinking in size, our results suggest that woody plants allocate resources to either canopies or stems to cope with increasing dryness. Increasing stem or canopy size, and altering branching might be a useful strategy for woody plants to compensate for biomass reduction and maintain functions while growing shorter under hotter and drier climates.

### KEYWORDS

aboveground allometry, aboveground competition, allometric variation, aridity gradient, climate change adaptation, resource availability, stress trade-off hypothesis

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### 1 | INTRODUCTION

Woody plants are widely distributed across most terrestrial ecosystems, with growth forms ranging from tall, thin trees in humid forests to short, branching shrubs in arid environments (Lines et al., 2012; Roa-Fuentes et al., 2012). Allometry represents the result of complex trade-offs among a number of plant requirements such as resource acquisition, reproduction, and resilience against disturbances (Henry & Aarssen, 1999; Küppers, 1989) and is driven by environmental factors that operate across all the plant growth stages (Archibald & Bond, 2003). Plants are likely to exhibit distinct growth forms under different climates, which reflect a range of strategies to adapt to various environments (Lines et al., 2012). For example, species growing in hot, dry environments generally have leaves with a smaller specific leaf area to minimize transpiration losses (Read et al., 2014) and denser wood with slower growth rates to cope with drought (Anderegg et al., 2020). The presence of these idiosyncratic features of plants in different environments suggests that longterm environmental changes might select for different allometries of mature plants. While much is known about the response of plant functional traits (e.g., seed mass, leaf area, growth rates) to declining rainfall (Schulze et al., 2006), less is known about how aboveground allometry (e.g., canopy size, height, stems, branching characteristics) of woody plants might respond to increasing dryness as Earth's climate becomes hotter and drier. This knowledge is important, as predicted climate change will present substantial challenges for the survival and functioning of woody plants. These changes will likely have profound effects on biomass production, nutrient cycling, hydrological function, habitat provision for a diverse array of fauna (e.g., mammals, bird and invertebrates) and landscape stability across large scales (Kissling et al., 2008).

Plants are known to be shorter in drier environments to reduce the risk of hydraulic failure (Givnish et al., 2014). Rather than simply contracting in size, other components of aboveground allometry such as stem and canopy may also change systematically in response to increasing dryness (Lines et al., 2012). Stem diameter is positively associated with water transporting efficiency and resistance to disturbance (e.g., grazing, fire; Dantas & Pausas, 2013), thus thicker stems strengthen the capacity of plants to adapt to drier environments (Jacobsen et al., 2007; Nelson et al., 2020). Increases in canopy size give plants a competitive advantage under harsh environmental conditions by maximizing photosynthetic revenue over construction costs (Togashi et al., 2015; Westoby et al., 2012) and increasing water harvesting through rainfall accumulation (e.g., via interception and stem flow; Kermavnar & Vilhar, 2017). However, the extent to which woody plants preferentially allocate biomass to canopy expansion or stem thickening in drier regions likely varies among genera due to interspecific differences in their ability to utilize water resources (e.g., variable rooting depth, phenotypic plasticity, adaptation ability; Anderegg et al., 2020; Jacobsen et al., 2007; Lehmann et al., 2014; Lines et al., 2012). For example, in resource-poor environments, eucalypts, which have well-developed rooting systems, might increase the depth of root penetration for scavenging resources, compared

with Acacia spp., which might increase the allocation of biomass to foliage growth due to their ability to fix nitrogen (Forrester et al., 2006). Despite these potential genus-specific allometric changes, we have little empirical evidence of whether aboveground allometry changes as environments become drier and whether different genera of woody plants exhibit divergent trends in relation to their allometry. This information is important because it can provide insights into the adaptation of woody plants to increasing dryness and the alternative growth forms we might expect across woody species as we move to a drier, hotter climate.

Irrespective of the overriding effect of water availability driven by climate (Lehmann et al., 2014; Moles et al., 2009; Scholtz et al., 2018), other soil resources and aboveground species competition also shape plant growth and, therefore, aboveground allometry. For example, sandy soils with a low water holding capacity can impose water stress on plant metabolic activities, and infertile soils (e.g., nitrogen, phosphorus depletion) would likely constrain biomass allocation to productive leaf tissues (Givnish et al., 2014). Woody plants also adjust their allometry to the local competitive environment, with relatively more biomass being invested to height growth to avoid overshadowing under crowded conditions (Henry & Aarssen, 1999). The magnitude of these factors might vary with increasing dryness, with plant allometry potentially constrained by biotic stress (e.g., aboveground competition) in benign environments where soil and water resources do not limit plant growth (e.g., mesic areas), but by abiotic stress (e.g., resource availability) in harsher (e.g., drier, nutrient-poor) environments (stress trade-off hypothesis; Louthan et al., 2015). Few studies, however, have examined the effects of both resource availability and aboveground competition on woody plant allometry across entire climatic gradients, though abiotic constraints on tree growth have been demonstrated in harsh elevational areas (Anderegg & HilleRisLambers, 2019). Further, it remains unknown whether the aboveground allometry of different woody genera is also constrained by abiotic stress (e.g., resources availability) in drier environments.

To address these issues, we conducted an analysis of the aboveground allometry of woody plants, from multiple genera, and the impacts of both biotic and abiotic constraints at 150 sites along an extensive aridity gradient (1,500 km), extending from mesic coastal forests to arid open woodland in eastern Australia. Australia has a diversified native woody flora that is widely distributed across all climatic regions, with aboveground structure ranging from tall, dense eucalypt forests to multiple-stemmed mallees and branched acacia shrubs, which provide a proxy of worldwide variation in woody plant allometry (Givnish et al., 2014). In this study, we used a combination of regression analyses and structural equation modelling to address two predictions. First, we expected that woody plants would grow shorter and have either wider canopies or thicker stems to enhance water capture or transport under drier conditions, and the allometric response would vary across woody genera, which differ in growth rates, phenology and their ability to adapt to dryness (Figure 1; Figure S1.1 in Supporting Information Appendix S1, Pathway 2). Second, we expected that resource availability (i.e., climate, soil

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properties) would be the major factor constraining woody allometry. This mechanism might be either direct (Figure S1.1 in Supporting Information Appendix S1, Pathways 2, 5 or 8), or indirect, via



**FIGURE 1** Theoretical model of how we expect changes in aboveground allometry to vary along the aridity gradient in (a) woody plants overall and (b) different genera

aboveground species competition (Figure S1.1 in Supporting Information Appendix S1, Pathway 9 via 3, 6 or 7). For this, we assessed abiotic stress using an aridity gradient, and assessed the aboveground competition for light and space based on measures of woody plant density and basal area.

### 2 | METHODS

### 2.1 | Study area

Our study was conducted along an extensive aridity gradient in eastern Australia from the east coast to the dry interior. covering humid, dry subhumid, semiarid and arid zones (29.0 to 35.1° S, 140.7 to 151.4° E; Figure 2). We surveyed 150 sites at regular intervals along the aridity gradient, which ranged from -0.2 (humid) to 0.9 (arid) in terms of aridity. Aridity was determined as 1 -(precipitation/potential evapotranspiration) (unitless; United Nations Environment Programme, 1992). Aridity data were obtained from the CGIAR Consortium for Spatial Information (CGIAR-CSI) averaged over the 1950-2000 period (Zomer et al., 2008; https://cgiarcsi.community/2019/01/24/global-aridity-index-andpotential-evapotranspiration-climate-database-v2/). Average annual rainfall ranged from 1,299 to 184 mm and average annual temperature varied from 13 to 21°C along the gradient based on data obtained from the WorldClim database averaged across 1970-2000 with 30-s resolution (https://www.worldclim.org/). Rainfall seasonality changed from summer dominant in the north



FIGURE 2 (a) Location of the 150 sample sites in relation to aridity, and images of woodland in (b) humid, (c) dry subhumid, (d) semiarid, (e) arid areas in eastern Australia

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and east, uniform in the centre, to predominantly winter dominant in the south-west, with the lowest rainfall in the north-west (Bureau of Meteorology, 2019). Soil textures ranged from loams near the coast to clay loams in the semiarid and to loamy sands in the arid areas with acid soils near coasts (pH  $5.1 \pm 0.1$ ; mean  $\pm$  SE), and alkaline soils in more arid regions (pH  $7.5 \pm 0.1$ ). Plant communities across the gradient changed from coastal forests to semiarid woodlands and shrublands dominated by *Eucalyptus* spp., *Callitris* spp., *Acacia* spp. and *Allocasuarina* spp.

### 2.2 | Inventory data and environmental variables

Biotic and abiotic data were collected between February 2018 and August 2019. To avoid confounding any potential effects of differences in herbivore grazing and browsing among sites, and differences in wildfire history on the aboveground allometry of woody plants, we only surveyed in conservation areas or reserves (e.g., national parks, nature reserves, state forests) that have been unburned for the past 30 years or more with kangaroos as the major herbivores, which account for 74% of the total amount of dung collected across the gradient in this study. To minimize potential impacts of supplementary water supply on plant allometry, we avoided sampling near large water bodies (e.g., rivers, swamps or lakes), to ensure moisture availability for plants followed our aridity gradient. Except for the large-scale shift in aridity, the allometry of individual plants could potentially respond to idiosyncratic site-level effects such as differences in soil properties (e.g., texture, phosphorus, moisture, profile depth) or species interactions (e.g., species competition), which are accounted for in the structural equation models.

At each site, we measured the aboveground allometry of woody plants along a transect of variable width. Woody plant density varied from 720.6  $\pm$  60.0 per ha in mesic areas to 146.9  $\pm$  11.2 per ha in arid areas. The transects were generally 100 m long and 10 m wide at densely timbered sites, but the width was adjusted, up to 40 m wide, in order to sample at least 30 woody plants at each site. To ensure that the sampling regime captured differences in woody plant allometry, we focused on mature woody plants taller than 4 m. Coordinates for the beginning and end of the transect were recorded by GPS. Woody plant density and richness were recorded for each site. For each woody plant, we measured five allometric attributes: (a) plant height (m); (b) height of the first branch (m); (c) canopy diameter (m); (d) stem diameter at breast height (DBH, cm); (e) branching number (i.e., number of branches from the main stem, after Borchert & Slade, 1981). Across the entire gradient we surveyed 6,353 woody plants of 127 species from four major genera (see Table S2.2 in Supporting Information Appendix S2; 67% Eucalyptus spp., 12% Callitris spp., 6% Acacia spp. and 4% Allocasuarina spp.), covering a representative part of Australian native woody species (c. 3,000 species total; Beadle, 1981) and the major growth forms of woody plants (e.g., tree and shrub growth form with single and multiple stems). Height was

measured using a Haglöf ECII-D electronic clinometer (ASICS Crop., Torsång, Sweden). Canopy depth (%) was calculated as the proportion of the canopy (plant height minus height of the first branch) to the plant height. The ratio of the canopy diameter to DBH (canopy : DBH, m/m) was calculated as the allometric adaptation ratio in order to evaluate whether plants tended to have wider canopies or thicker stems along the aridity gradient. For woody plants with multiple stems (i.e., mallee growth forms, tall shrubs with low branching points and trees with low forks), we calculated the DBH of the whole plant based on the total crosssectional area of all stems. The basal area of each woody plant was estimated from its DBH based on the area of a circle. We used (a) woody plant density, (b) stand basal area (m<sup>2</sup>/ha, total basal area of all woody plants within a site) and (c) basal area of larger woody plants (m<sup>2</sup>/ha; those larger in DBH than the target woody plant, Wykoff, 1990) as three measures of aboveground competition. In addition, both aboveground competition (competition for light and space; Henry & Aarssen, 1999) and belowground competition (root competition for water and nutrients; Coomes & Grubb, 2000) are critical determinants of plant growth and allometry through their effects on resource availability. However, due to the difficulties in assessing root competition of woody plants across an extensive aridity gradient, we restricted our study to an examination of aboveground competition (i.e., light and space competition), and used soil resource availability (e.g., soil water availability, soil total phosphorus) to illustrate variation in belowground resources along the aridity gradient.

For variables related to resource availability, we collected data on climatic conditions, soil physical properties and soil nutrients at each site. We obtained data on soil profile depth, soil water availability, soil clay content and soil total phosphorus at 100–200 cm depth as measures of soil resources from the deep soil layer that woody plants rely on, from the Soil and Landscape Grid of Australia database (30-s resolution; https://www.clw.csiro.au/aclep/soila ndlandscapegrid/). Climatic variables, such as temperature range, temperature seasonality, rainfall seasonality and wettest month of precipitation, were derived from the WorldClim v.2 database averaged across 1970–2000 with 30-s resolution (https://www.world clim.org/).

#### 2.3 | Statistical analysis

We first explored the general variation in woody plant allometry based on all woody plants surveyed. Due to few woody species covering most of the aridity gradient (i.e., 9 of 127 species) and the lack of sufficient samples of each species (Table S2.2 in Supporting Information Appendix S2), we instead explored allometric changes at the genus level. We used regression analyses to explore how the allometric attributes changed along the aridity gradient. We first used quantile regression by fitting 5th, 50th and 95th percentiles to identify the trend and boundaries of woody allometry (i.e., height, DBH, canopy diameter, canopy depth, branch number, basal area of larger woody plants, canopy : DBH) along the aridity gradient using the inventory data on all individual woody plants. Quantile regression is widely used in ecology to document the changes in linear relationships and quantify the edges of scatter plots against environmental gradients, particularly for large datasets (Moles et al., 2009). Linear regression was then used to explore changes in woody plant density, Wood

regression was then used to explore changes in woody plant density, woody plant richness and variability of canopy : DBH (CV%, coefficient of variation) along the aridity gradient for all the woody species surveyed at the site level. We also used linear regression to explore changes in allometry attributes for the four major genera (i.e., *Acacia* spp., *Allocasuarina* spp., *Callitris* spp. and *Eucalyptus* spp.) along the aridity gradient, with allometry attributes being averaged at the site level to avoid potentially confounding effects due to different sample sizes among genera within each site. Analyses and figures were performed using the 'quantreg' (Koenker, 2019) and 'ggplot2' (Wickham, 2016) packages in R 3.4.1 version (R Core Team, 2018).

We then used structural equation modelling (SEM; Grace, 2006) to explore the direct and indirect effects of water availability (temperature range, temperature seasonality, wettest month of precipitation, rainfall seasonality, aridity, soil water availability, soil profile depth) and nutrient availability (soil clay content, soil total phosphorus), and aboveground competition (stand basal area, basal area of larger woody plants, woody plant density) on canopy : DBH for the four genera. After excluding collinear predictors based on the variance inflation factor (VIF) test (Tables S3.3-S3.5 in Supporting Information Appendix S3), our final list of predictors were aridity, rainfall seasonality, soil properties (soil water availability, soil profile depth, soil clay content and soil total phosphorus), and aboveground competition (woody plant density and basal area of larger woody plants). We used a site-level dataset in the structural equation modelling, in which the canopy : DBH data were averaged at the site level for each genus. Structural equation modelling allowed us to test hypothesized relationships among the predictors and canopy : DBH based on an a priori model (see Figure S1.1 in Supporting Information Appendix S1) that constructs pathways among model terms based on a priori knowledge (Table S1.1 in Supporting Information Appendix S1). We allowed aridity and rainfall seasonality to covary in our models. As the path coefficients in the structural equation model represent partial correlations, we are able to explore the effect of each driver after accounting for the effects of other attributes included in our model. Overall goodness-of-fit probability tests were performed to determine the absolute fit of the best models, using the  $\chi^2$  statistic. The goodness-of-fit test estimates the likelihood of the observed data given an a priori model structure. Thus, high probability values indicate that these models have highly plausible causal structures underlying the observed correlation. Models with low  $\chi^2$  and root mean square error of approximation (RMSEA < .05), and high goodness-of-fit index (GFI) and  $R^2$  were selected as the best-fit models for our data. In addition, we calculated the standardized total effects of each predictor to show its total effect on canopy : DBH, the allometric adaptation ratio. Analyses were performed using AMOS 22 (IBM, Chicago, IL) software.

### 3 | RESULTS

### 3.1 | Woody plant allometry changes along aridity gradient

Woody plants tended to be shorter (Figure 3a), have deeper canopies (Figure 3b) and experience less aboveground competition from their neighbours (i.e., lower basal area of larger woody neighbours) with increasing aridity (Figure 3c, Table S4.6 in Supporting Information Appendix S4). The allometric adaptation ratio increased slightly, with canopy diameter increasing but DBH not changing significantly along the aridity gradient (Figure 3e-g, Table S4.6 in Supporting Information Appendix S4). We also found some variability in plant allometry along the gradient. For example, plant height, canopy depth and aboveground competition were more homogenous (Figure 3a-c), but branching number was more heterogenous, with increasing aridity (Figure 3d). Site-level variability in the allometric adaptation ratio declined, and woody plant density and richness also declined with increasing aridity (Figure 3h and i, Table S4.7 in Supporting Information Appendix S4).

### 3.2 | Adaptation strategy to dryness vary with genera

The allometric adaptation ratio differed among genera, with declines (thicker stems) in *Acacia* spp., increases (wider canopies) in *Callitris* spp. and *Eucalyptus* spp., but no trend in *Allocasuarina* spp. along the aridity gradient (Figure 4, Table S4.6 in Supporting Information Appendix S4). Generally, either increases in DBH or canopy diameter were associated with reductions in plant height (*Eucalyptus* spp., *Acacia* spp. Figure 5a,e,f, Table S4.7 in Supporting Information Appendix S4) and our measure of aboveground competition (basal area of larger woody plants) declined with increasing aridity across all genera (Figure 5c, Table S4.7 in Supporting Information Appendix S4).

There were also some other differences in allometry among the four genera. For example, canopy depth of *Eucalyptus* spp. and *Acacia* spp. increased with increasing aridity (Figure 5b, Table S4.8 in Supporting Information Appendix S4) and the number of branches of *Callitris* spp. declined along the aridity gradient (Figure 5d, Table S4.8 in Supporting Information Appendix S4). Although the allometric adaptation ratio of *Allocasuarina* spp. remained constant, they had deeper canopies with more branches as aridity increased (Figure 5b,d, Table S4.8 in Supporting Information Appendix S4).

### 3.3 | Genus-specific drivers of different adaptation strategies

We found that the dominant drivers of the allometric adaptation ratio varied among the adaptation strategies. Based on standardized

![](_page_5_Figure_0.jpeg)

**FIGURE 3** Changes of woody plant (a) height, (b) canopy depth, (c) basal area of larger woody plants (BA), (d) branching number, (e) canopy diameter, (f) stem diameter at breast height (DBH), (g) allometric adaptation ratio (canopy : DBH), (h) coefficient of variation (CV%) of allometric adaptation ratio [canopy : stem diameter at breast height (DBH)] for each site, and (i) woody plant density and richness for each site along the aridity gradient. Blue broken lines in (a)–(g) are the 5th and the 95th percentile, red line is the 50th percentile and each point represents an individual woody plant (Table S4.6 in Supporting Information Appendix S4). Solid lines in (h) and (i) are fitted by linear regression (Table S4.7 in Supporting Information Appendix S4) with each point representing a site, and the grey shading zone is the 95% confidence interval

total effects, the wider canopy strategy of *Callitris* and *Eucalyptus* spp. was mainly driven by changes in resource availability (i.e., climate, soil), while the thicker stem strategy of *Acacia* spp. was predominantly regulated by aboveground competition (Figures 6 and 7).

Aridity was the major factor associated with the allometric adaptation ratio of *Eucalyptus* spp. (Figure 6d). Aridity was associated with an increase in the ratio directly, and indirectly, by enhancing the positive effect of soil phosphorus on the ratio. Increasing aridity was mainly associated with a weak increase in the allometric adaptation ratio of *Callitris* spp. (Figure 7), with direct negative effects from rainfall seasonality (Figure 6c). The allometric adaptation ratios for *Acacia* and *Allocasuarina* spp. were mainly associated with aboveground competition and to a lesser extent, aridity or soil clay content (Figure 7). Although the allometric adaptation ratio of *Acacia* spp. declined with increasing aridity (Figure 4a), and aboveground competition (i.e., basal area of larger woody plants) had the largest standardized total effect (Figure 7), the impact of either aridity or aboveground competition was not significant after accounting for the effects of other factors such as soil properties and rainfall seasonality (Figure 6a). For *Allocasuarina* spp., any positive effects of aridity were mitigated by a suppressive effect on aboveground competition, which resulted in an overall merely effect of aridity on the allometric adaptation ratio (Figures 6b and 7).

### 4 | DISCUSSION

In our study, plant height and aboveground competition declined, but branching number, canopy width and canopy depth increased, with increasing aridity, providing strong empirical evidence that woody plants respond to dryness by altering their aboveground allometry. Differences in allometry, however, varied among genera,

![](_page_6_Figure_1.jpeg)

**FIGURE 4** Changes of allometric adaptation ratio [canopy : stem diameter at breast height (DBH)] along aridity gradient for (a) *Acacia* spp., (b) *Allocasuarina* spp., (c) *Callitris* spp., (d) *Eucalyptus* spp. Blue broken lines are the 5th and the 95th percentile, red line is the 50th percentile and each point represents an individual woody plant (Table S4.6 in Supporting Information Appendix S4). Icons at each top right corner represent allometry changes for each genus

with increasing aridity associated with wider canopies in Eucalyptus and Callitris spp., thicker stems in Acacia spp., but no clear differences in Allocasuarina spp. Major environmental variables associated with these allometric changes were related to different effects of resource availability (e.g., water, soil phosphorus) and aboveground competition (e.g., competition for light and space) from larger plants. Overall, our results suggest that woody plants reduce plant height and allocate biomass to either canopy or stem as a result of tradeoffs between light competition and water acquisition as environments become drier. In addition, different genera exhibited different strategies, regulated by resource availability or aboveground competition, in response to increasing dryness. This study extends our understanding of allometric trade-offs, highlighting how different woody genera might respond to increasing dryness, and how associated ecological functions might change under future climate change scenarios.

### 4.1 | Plant shape changes with increasing aridity

We found that woody plants were shorter as resource limitation shifted from light to water, consistent with global studies (Lehmann et al., 2014; Liu et al., 2019; Moles et al., 2009), providing evidence that the upper limit of plant height is likely constrained by water availability. In mesic areas, high plant density and crowding between neighbours force woody plants to invest relatively more resources in increasing their height in order to compete for light and aboveground space (Archibald & Bond, 2003; Henry & Aarssen, 1999). As water becomes limiting and belowground root competition intensifies in drier environments (Coomes & Grubb, 2000), allocation to plant height is constrained in order to reduce the cost of water transportation and to avoid the risk of xylem embolism and cavitation (Liu et al., 2019). In addition, sparser plant communities in drier environments release woody plants from both light and aboveground space competition, making it possible for them to reduce investment in vertical growth and allocate biomass to other organs (Shipley & Meziane, 2002).

As aridity increases, aboveground allometry also changed in a systematic way rather than simply scaling down, consistent with our hypothesis. Complementing previous findings on increases in belowground structures with increasing dryness (Roa-Fuentes et al., 2012), we found that aboveground plant components such as canopy and branches also increased as the environment became drier. Allometric changes reflect a balance between different requirements (e.g., light assimilation, resource acquisition, drought tolerance) and it is well recognized in the balanced-growth hypothesis that plant biomass would preferentially be allocated to organs that harvest limited resources (Shipley & Meziane, 2002). As dryness

![](_page_7_Figure_0.jpeg)

**FIGURE 5** Changes along the aridity gradient of (a) height, (b) canopy depth, (c) basal area of larger woody plants (BA), (d) branching number, (e) canopy diameter, (f) stem diameter at breast height (DBH) for the four genera. Lines are fitted by linear regression (Table S4.7 in Supporting Information Appendix S4) with each point representing the averaged value for each site, and the grey shading zone is the 95% confidence interval

increases, increasing canopy width with declining height reflects the trade-offs between light competition and water acquisition, with more biomass being allocated to lateral growth instead of vertical growth to maximize the chances of survival of plants in water stressed environments (Küppers, 1989). For example, a larger canopy would increase the efficiency of light assimilation and carbon fixation (Archibald & Bond, 2003; Küppers, 1989), thus increasing the net photosynthetic revenue of plants to support a greater volume of roots and branches (Crockford & Richardson, 2000). Larger canopies also increase rainfall accumulation by interception and stem flow, whereby water is channelled to deeper soils, enhancing water availability for plants surviving under water stress (Crockford & Richardson, 2000; Pressland, 1976). In drier areas, increases in the number of branches can promote canopy expansion at a lower water cost, and reduce the risk of mortality compared to increases in stem numbers. For example, a greater branching number in Prosopis spp. growing in the Chihuahuan Desert ensures that branch death or shedding induced by intensive water stress does not compromise the survival of the whole plant under drier conditions (Martínez & López-Portillo, 2003).

### 4.2 | Genus-specific strategies to adapt to dryness

Despite general trends in biomass allocation to the canopy, each genus responded differently to increasing dryness, as we expected.

As dryness increases, increasing vapour pressure deficit and radiation increase the demand for both photosynthesis and transpiration (Barkhordarian et al., 2019), with species increasing either their leaf area for canopy expansion, or sapwood area for stem thickening, in order to maximize photosynthetic revenue or reduce the risk of hydraulic failure. Eucalyptus spp., the dominant woody genus, had wider canopies rather than thicker stems, as aridity increased. Eucalypts are typically shade intolerant (Bauhus et al., 2004) and light likely imposes a selection pressure on their allometry by promoting rapid vertical height growth at the expense of lateral canopy growth under intensive aboveground competition in crowded stands (Henry & Aarssen, 1999). As species interactions shift to belowground competition for water and nutrients, and the plant community becomes sparser with increasing aridity (Coomes & Grubb, 2000), the crown is less constrained by local competition for either light or aboveground space. Therefore, more biomass is allocated to canopy growth at the expense of height to maximize net photosynthetic returns and rainfall capture, in order to increase the competitive advantage of woody plants in drier environments (Crockford & Richardson, 2000; Küppers, 1989). As no single eucalypt species spanned the entire aridity gradient, differences in stem diameter could potentially be confounded by intraspecific variation in water use efficiency of eucalypts along the gradient (Anderegg et al., 2020; Schulze et al., 2006). Rather than increasing stem diameter, eucalypts can also cope with dryness by other mechanisms such as reducing leaf area, and increasing hydraulic conductivity and rooting depth

![](_page_8_Figure_0.jpeg)

**FIGURE 6** Structural equation model assessing the direct and indirect effects of aridity, rainfall seasonality (Rain Season), soil, and aboveground (AG) competition on the allometric adaptation ratio [canopy : stem diameter at breast height (Canopy : DBH)] for (a) *Acacia* spp., (b) *Allocasuarina* spp., (c) *Callitris* spp., (d) *Eucalyptus* spp. 'Soil' comprises data on clay content (CLAY), soil profile depth (SDEP), soil water availability (SWA) and soil phosphorus at 100–200 cm depth (P). 'AG Competition' contains woody plant density (DENS) and basal area of larger woody plants (BA). Standardized path coefficients, adjacent to the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Pathways are significant negative (red unbroken line), significant positive (blue unbroken line) or mixed significant negative and significant positive (black unbroken lines). Non-significant pathways were not shown in the models. Model fit: *Acacia* spp.:  $\chi^2 = 5.04$ , df = 5, p = .41,  $R^2 = .12$ , root mean square error of approximation (RMSEA) = .01, Bollen-Stine = .34 (2,000 bootstrap). *Allocasuarina* spp.:  $\chi^2 = 5.69$ , df = 5, p = .34,  $R^2 = .32$ , RMSEA = .07, Bollen-Stine = .44 (2,000 bootstrap). *Callitris* spp.:  $\chi^2 = 4.80$ , df = 3, p = .19,  $R^2 = .30$ , RMSEA = .12, Bollen-Stine = .29 (2,000 bootstrap). *Eucalyptus* spp.:  $\chi^2 = 6.04$ , df = 5, p = .30,  $R^2 = .40$ , RMSEA = .04, Bollen-Stine = .34 (2,000 bootstrap)

(Schulze et al., 2006; Whitehead & Beadle, 2004). We found that *Callitris* spp. tended to have wider canopies, but branching number declined with increasing aridity. *Callitris* spp. are generally slow growing (Schwilk, 2003) and fail to resprout following fire (Cohn et al., 2011). Having fewer low branches could reduce the vertical continuity of fuels, enhancing the survival of trees in drier, fire-prone environments (Dantas & Pausas, 2013).

In contrast, Acacia spp. tended to allocate more biomass to stem thickening than canopy enlargement as aridity increased. This is consistent with physiological findings that the ratio of sapwood area to leaf area in acacias is greater under drier environments (Anderegg et al., 2020). Compared to eucalypts, acacias are generally shade tolerant, midstorey species, and are less constrained by light availability beneath taller trees. Instead, the crown morphology of acacias is more likely to be constrained by intraspecific competition (Bauhus et al., 2004), which might complicate the trend of canopy expansion as aridity increases. As dryness increases, biomass in Acacia spp. is preferentially allocated to stem thickening rather than height or canopy, reflecting the trade-offs between plant requirements for carbon assimilation and drought tolerance (Küppers, 1989; Shipley & Meziane, 2002). As aridity increases, intensified vapour pressure deficit suggests that plants need to maintain greater transpiration rates for a given rate of photosynthesis, leading to greater allocation of biomass to sapwood (Westoby et al., 2012). Stem thickening in acacias, which is also a conservative water use strategy under drier conditions, increases xylem density, enhances water stress tolerance, and reduces the risk of embolism (Dantas & Pausas, 2013; Jacobsen et al., 2007). Finally, we failed to detect any clear strategy in relation to canopy width or stem size for Allocasuarina spp., while their canopy depth and branching numbers increased along the aridity gradient. Unlike Callitris spp., Allocasuarina spp. are fire adapted (Schwilk, 2003), with their seedling recruitment largely dependent

![](_page_9_Figure_1.jpeg)

**FIGURE 7** Heatmap illustrating the standardized total effects (sum of direct plus indirect effects) of driving factors derived from the structural equation modelling for the allometric adaptation ratio of *Acacia* spp., *Allocasuarina* spp., *Callitris* spp., *Eucalyptus* spp. AG Competition = aboveground competition; Larger basal area = basal area of larger woody plants

on fire. Thick canopies and branched structures in *Allocasuarina* spp. are selected for, and enhances a site's flammability by increasing fuel connectivity, which ensures the release of seeds for recruitment after fire (Lunt, 1998; Schwilk, 2003).

### 4.3 | Variable effects of resource availability and aboveground competition on allometry

We found that allometric adaptation in woody plants was associated with mechanisms related to both biotic (aboveground competition) and abiotic (resource) factors, with the magnitude of impacts of aboveground competition and resource availability on the allometric adaptation ratio varying with adaptation strategies. Consistent with the stress trade-off hypothesis (Anderegg & HilleRisLambers, 2019), water availability is the major factor driving a wider canopy strategy (Eucalyptus and Callitris spp.) as belowground resource competition intensifies in drier environments. Aridity positively affected the canopy width of eucalypts directly, and indirectly, by enhancing its positive association with soil phosphorus. As aridity increases, there is an increasing requirement for water harvesting and photosynthesis, and more open communities provide an impetus and available space for canopy enlargement (Bauhus et al., 2004). Soil phosphorus increases with aridity due to enhanced regolith weathering and reduced nutrient uptake from plants (Delgado-Baquerizo et al., 2013), which promotes carbon assimilation for leaf growth

and, therefore, crown expansion (Crous et al., 2015). We also found that the canopy width of *Callitris* spp. was negatively associated with rainfall seasonality. Higher rainfall seasonality will increase the frequency of prolonged droughts or wet periods, which could impede the activity of *Callitris* roots that are concentrated in the top 0.2 m (Thompson & Eldridge, 2005), thereby constraining canopy development. Competition for light and aboveground space are unlikely to affect canopy development in *Callitris* spp., which fail to self-thin (Wells, 2011) and are generally shade tolerant and, therefore, less likely to be influenced by their neighbouring conspecifics.

Contrary to our prediction, stem thickening in acacias was mainly regulated by aboveground competition for light and space from larger woody plants rather than resource availability in drier environments. The weak effects of resource availability could possibly be explained by the ability of acacias to adapt to drought and fix nitrogen in drier environments. Acacias typically have lower rates of transpiration (Kumar et al., 1998), which minimizes the effect of water limitation on their aboveground growth in xeric environments (Munzbergova & Ward, 2002). Furthermore, their ability to fix nitrogen results in high leaf N and P, giving them a photosynthetic advantage under conditions of low rainfall or infertile soils (Schulze et al., 2014). However, our SEM failed to identify the significant effect of aboveground competition on the allometric changes in acacias after taking account of other abiotic drivers, suggesting substantial variation in environmental conditions among sites and unmeasured factors such as intraspecific phenotypic plasticity or potential response

to disturbance regimes (e.g., browsing, wind exposure; Dantas & Pausas, 2013). Aboveground competition also largely accounts for the allometric changes in *Allocasuarina* spp., which are generally semi-shade intolerant and would be more likely to have constrained crown or stem development under conditions of intense competition for light and aboveground space (Henry & Aarssen, 1999; Williams & Woinarski, 1997).

### 5 | CONCLUSIONS

Our study reveals that rather than merely shrinking in size (miniaturization), aboveground allometry (e.g., canopy, stem, branches) of woody plants systematically changes as environments become drier. Aboveground allometric relationships are important for estimating biomass and modelling community succession (Purves et al., 2008). Changes in allometric relationships highlight the necessity of adopting different scaling algorithms to improve the precision of models for assessing carbon stocks (Fayolle et al., 2013) and predicting vegetation dynamics across wide environmental gradients. Furthermore, our study highlights the fact that plant strategies of coping with increasing dryness are genus-specific and associated with different mechanisms from resource availability to aboveground competition. Compared to Eucalyptus and Callitris spp., allometric changes in Acacia and Allocasuarina spp. are mainly regulated by competition for light and aboveground space, indicating that resource availability (i.e., abiotic stress) may not be the major factor constraining the growth of all woody species in drylands. However, as few woody species are distributed across all the climatic zones (from humid to arid) along the aridity gradient, our study failed to explore allometric variations at the species level, which could be compensated by studies focusing on species level allometric changes (e.g., Anderegg et al., 2020). Apart from aboveground competition, competition among roots for water and nutrients also regulates aboveground allometry, particularly in infertile soils and in drier regions (Coomes & Grubb, 2000). The effects of belowground competition on plant allometry need further study if we are to improve our understanding of the impacts of species interactions on plant allometry under drier climates. Under projected increases in aridity, future woody plants are likely to be shorter, have wider canopies with more branches, and occur in sparser stands with fewer associated species. In addition, increases in aboveground allometric attributes such as canopy size, stem size, and branching number in woody plants could potentially compensate for reductions in ecosystem functions (e.g., productivity, carbon fixation, habitat provision) as aridity increases, thereby ensuring the maintenance of functional woody communities under predicted drier climate (Sherwood & Fu, 2014).

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### AUTHOR CONTRIBUTIONS

JD, DE and ST designed the research. JD, DE and ST conducted the field survey and JD performed the statistical analyses. JD wrote the manuscript draft. DE and ST critically revised the manuscript.

#### DATA AVAILABILITY STATEMENT

Data used in the study have been archived in the Figshare repository (https://figshare.com/projects/Response\_of\_woody\_allometry\_to\_dryness/89045; https://doi.org/10.6084/m9.figshare.12941525.v1).

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clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment, 126, 67–80.* 

### BIOSKETCH

Our research team focuses on understanding the impacts of climate change on woody plant communities using field surveys and meta-analysis. Specifically, our research seeks to understand the effects of land use change on plants, biocrusts, microbes and soil processes from site to global scales (website: http://www. aridecologylab.com.au/).

### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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