Effect of stand density on growth and allometry of marri (*Corymbia calophylla*) in the high rainfall zone of southwest Western Australia

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ABSTRACT

Marri (*Corymbia calophylla*), an endemic and keystone tree species of southwest Western Australia (SWWA), provides significant environmental, conservation, economic and cultural values. This study aims to analyse the effect of stand density, manipulated through thinning, on growth and allometry of marri-dominated forest. Although individual tree diameter (DHBUB, diameter at breast height under bark), basal area, height and crown-width (CW) growth was stimulated by thinning, stand basal-area growth was highest in denser (less thinned) stands. Stand density had a significant effect on the allometry between DBHUB and each of height and height-diameter ratio (HDR). Height and CW increased with an increase in DBHUB although the relationship with CW was not statistically significant; HDR was inversely related to DBHUB. Thinning has the potential to increase yields of merchantable timber, firewood, and enhance ecological values including tree hollows for arboreal fauna and marri-fruit production (important for cockatoos) that depend on retention of sufficient large old trees. Reduction of stand density through thinning reduces inter-tree competition and may help in reducing the risk of marri canker disease.

Keywords: Allometry; increment; marri; Mediterranean forest; stand density; thinning

INTRODUCTION

Marri (*Corymbia calophylla* (R. Br. ex Lindl.) K.D. Hill & L.A.S. Johnson), previously known as *Eucalyptus calophylla* (Hill & Johnson 1995), is one of the keystone and endemic tree species found in association with jarrah (*Eucalyptus marginata*) and karri (*Eucalyptus diversicolor*) in the forests of southwest Western Australia (SWWA). Marri is an evergreen broadleaved tree of a medium to large size (up to 40 m height and 1.5 m diameter at breast height (DBH)). The distribution of marri ranges north to south from Geraldton (28.77°S, 114.61°E) to Cape Riche (34.61°S, 118.76°E), and from Perth (31.95°S, 115.86°E) inland beyond Narrogin (32.93°S, 117.17°E) (Churchill 1968).

Marri has environmental, conservation, economic and cultural values. From an environmental and conservation point of view, it occurs within one of the 35 global biodiversity hotspots recognised by Conservation International (FPC 2018). Furthermore, the fruits and seeds of this species are important dietary constituents for the threatened Carnaby's black cockatoo (*Calyptorhynchus latirostris* Carnaby), Baudin's black cockatoo (*Calyptorhynchus baudinii* Lear) and Forest red-tailed black cockatoo (*Calyptorhynchus banksia)* (Johnstone & Kirkby 1999; Cooper *et al*. 2003; Johnstone *et al*. 2013; Lee *et al*. 2013). Marri is also used for nesting and roosting by these cockatoos (Whitford *et al*. 2015). Economic values derived from marri include honey, timber (for various uses including furniture, flooring, and firewood), food and medicine (CCWA 2013). Marri is a local indigenous Nyoongar word for "blood" after the red gum that exudes from wounds in the bark and has an important role in Nyoongar culture (Cunningham 1998). Marri trees have been affected by canker disease caused by *Quambalaria coyrecup* (Paap *et al*. 2008). This disease has caused a severe decline of marri trees in some places, including road verges and patches of remnant native vegetation in agricultural and urban landscapes (Paap *et al*. 2016). Decline in canopy condition and loss of large mature marri trees is of concern and may lead to detrimental impact on environmental, conservation, economic and cultural values.

Neighbouring trees compete for resources, affecting their growth rate (Stoneman *et al*. 1996; Koch & Ward 2005; Forrester *et al*. 2013). Reducing stand density through thinning can reduce intra-specific competition and regain growth potential (Grigg & Grant 2009). Thinning reduces competition, leaf-area index and water loss through transpiration (Ruprecht & Stoneman 1993; Stoneman *et al*. 1996; Reed *et al*. 2012; Qiu *et al*. 2013) and promotes access to light, water, and nutrients for retained trees (Stoneman *et al*. 1995; Stoneman *et al*. 1996). Thinning is also associated with increased water discharge from forest catchments (Reed *et al*. 2012), decreased fire hazard (Volkova *et al*. 2017), and increased drought resistance (Sohn *et al*. 2016; Vernon *et al*. 2018). Heavier thinning may promote regeneration through opening of the canopy (Wang *et al*. 2019).

It is well established that thinning increases the growth of individual trees; however, the effect of thinning on different specific aspects of individual tree growth is variable. For example, thinning to reduce stand density has been reported to positively influence stem diameter growth but the effect on height growth may not be consistent (Oliver 1997; Nogueira *et al*. 2015; Hébert *et al*. 2016). When thinning increases height growth, this effect is generally smaller than the effect on diameter growth (Zhang *et al*. 1997; Bhandari *et al*. 2021b; Bhandari *et al*. 2022). In cases where height growth is favoured more in un-thinned stands compared to thinned stands, this may be due to greater competition for sunlight leading to prioritization of vertical growth (Chaturvedi & Khanna 2011; Kim *et al*. 2016). Because of the different nature of diameter and height growth, and contrasting tree-growth strategies, it is always important to analyse the effect of thinning on diameter-height allometry.

Western Australia's public forests are managed under the authority of a ten-year forest management plan that applies the Montreal Process Criteria as the framework for ecologically sustainable forest management (CCWA 2013). The condition, structure and extent of these forests has been affected by clearing for agricultural production and urban development, timber harvesting, forest fire, drought, and pathogens (Kimber 1981; Bradshaw 2012; Taylor *et al*. 2012; Paap *et al*. 2016, 2017, 2018; Sapsford *et al*. 2021) and parts of the forest estate are fragmented. Silvicultural guidance documents that inform implementation of the forest management plan recognise the importance of marri trees as habitat and a food source for cockatoos and provide for retention of mature and senescent trees during timber harvesting operations. To sustainably manage these forests, it is important to understand the impact of thinning on growth and allometry. Previous research has investigated aspects of the biology and ecology of marri, but there is no published information about how thinning affects the growth and allometry of marri.

A thinning experiment was established in 1992 in an even-aged stand of karri, marri and jarrah regenerated from retained seed trees following timber harvesting in 1969 (White 1974). The aim of the experiment was to evaluate growth responses to different intensities of thinning from below (removal of smaller and slowly growing trees favour the growth of taller and fast-growing individual trees). The experiment has been measured on five occasions (1992, 1997, 2002, 2010 and 2018). The experimental design included examples of plots dominated by karri and plots dominated by marri with a secondary component of karri. This paper examines the effects of stand density on growth and allometry of marri in the marri dominant stands. We first examined the effect of stand density on individual tree and stand level variables at different time points (total DBH, total height, height-diameter ratio, crown width, stand basal area, stem number per ha), then investigated the effect of stand density on individual tree and stand-level growth. Furthermore, we fitted nine different allometric relationships between under bark DBH (DBHUB) and height. We also tested whether stand density affected allometric relationships between DBHUB and each of height, height-DBHUB ratio (HDR) and crown width (CW) at all five measurement times between plot establishment (1992) and the end of the study (2018).

MATERIALS AND METHODS

Study area

The study was conducted at Sutton forest block (34° 28' S, 116° 20' E) 38 km southeast of Manjimup, SWWA (Fig. 1). The area has a Mediterranean climate with an average annual rainfall of 986 mm (measured at the Manjimup station from 1915 to 2019, station number 9573). Average minimum and maximum temperature for February is 13.4°C and 27.2°C respectively and for July is 6.4°C and 14.4°C respectively (BOM 2020). The soils of the study site are mainly yellow and gravelly texture-contrast soils, formed on weathered mottled and pallid zone

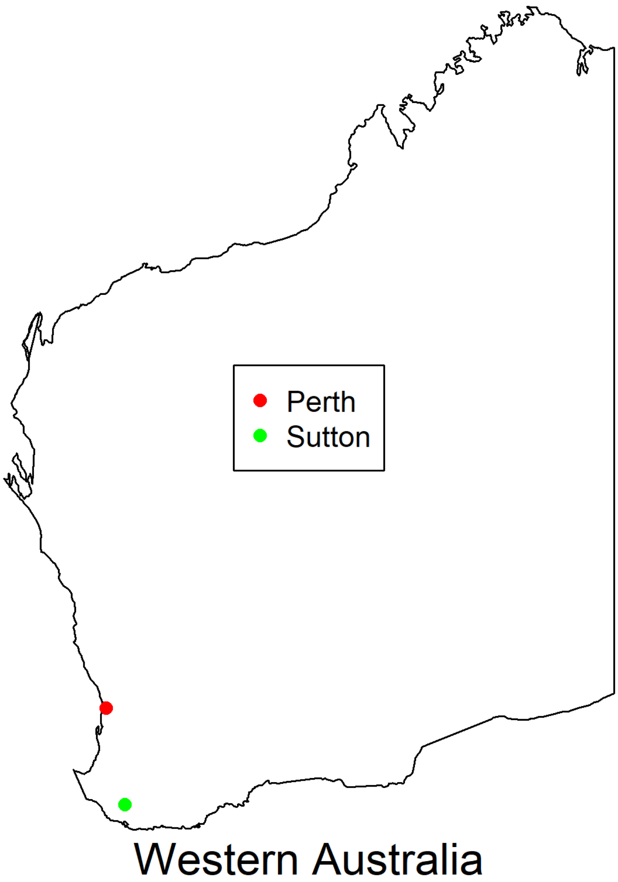

Figure 1. Location of the Sutton study site in Western Australia.

material (McArthur 2004). The regenerated forest at the experimental site remained unburnt prior to thinning and throughout the duration of the measurements reported in our study.

Treatment (thinning / stand densities)

The thinning trial at Sutton block consists of 27 plots (size 30 m × 30 m plus an outer 10 m buffer on all sides). The outer 10 m buffer was thinned to the same intensity as the inner plot, but tree measurements were carried out in the inner 30 m x 30 m. Thinning was undertaken manually with debris retained on site. Thinning plots were selected to represent marri forest where the over-bark basal area of marri was >60% of total stand basal area and top height was ≥18 m, as opposed to karri forest where the over-bark basal area of karri was >75% and top height was ≥20 m. This gave a total of eight plots for marri and 19 plots for karri. Separate experimental plots were not established for jarrah because of the small proportion of this species in the overall stand composition. In this paper, we analyse data from the eight plots dominated by marri. Results on effects of thinning and competition on growth and allometry based on karri-dominated plots are presented by Bhandari *et al*. (2021a) and Bhandari *et al*. (2022). Marri plots were managed at four different stand densities with two replicate plots placed randomly, which were established in 1992 as follows: 21.6 (T1), 11.6 (T2), 9.9 (T3) and 6.4 (T4) $m^2 ha^{-1}$ basal area under bark (BAUB, total for all species present). The BAUB of only marri trees in 1992 was 15.2 (T1), 9.4 (T2), 8.1 (T3) and 5.3 (T4) $m^2 ha^{-1}$. T1 is the un-thinned (control) and T2, T3 and T4 represent an increasing order of thinning intensity.

Data measurement

The location of each plot centre was measured using differential GPS in 1992 and the position of each tree mapped using direction and distance from the plot centre. The over bark DBH (DBHOB, cm) and bark thickness of each tree (including saplings, mm) and the total height (m) and crown radius (CR, m) of a subsample of trees of each plot was measured in 1992, 1997, 2002, 2010 and 2018. At least 10 trees located near the centre of each plot were selected for measurement of height and CR over the study period. The CR was measured as the horizontal distance from the base of the tree to the point vertically below the outward edge of the crown in the north, east, south and west orientations. Bark thickness at breast height of individual trees was measured using a syringe-type bark gauge, and the under bark DBH (DBHUB) was calculated by subtracting twice the average bark thickness from the over bark DBH. Under bark DBH (DBHUB), HDR and CW were calculated from the field measured variables. The HDR was calculated as the ratio of total height and DBH of the individual trees. The CW of each tree was calculated as twice the average of the four CR measurements. DBHUB of dominant trees (D-DOM) and height of dominant trees (H-DOM) of each plot were calculated as mean DBHUB and average height of the trees whose crowns extended above the general canopy level and thus received full light from above and some light from the sides and had the largest and fullest crowns in the stand (Smith 1962; Helms 1998). Dominance was assessed in 1992 when the trees were measured after establishment of the thinning trial.

DATA ANALYSIS

Effect of treatment on individual tree and stand level variables

The effect of thinning treatment on DBHUB, height, and CW of individual trees was evaluated using linear mixed effect models, fitted using maximum likelihood, in the R statistical software (R Core Team 2019) using the 'nlme' package (Pinheiro *et al*. 2018). Thinning treatment was included as a factor and a fixed effect (Table 1). A random effect for plot was also included to account for possible correlation among trees in the same plot. The effect of thinning treatment on stand BAUB and stem number per ha were evaluated at the plot level using standard ANOVA. The results of these plot-level ANOVA analyses should be treated with some caution, as the number of replicate plots was only two, and thus the assumption of equal variance among groups is difficult to test.

Effect of treatment on individual tree and stand-level growth

We evaluated the effect of thinning treatments on annual growth of individual DBHUB, height, CW and stand BAUB for the period of 1992 to 2018 using linear mixed effect models, fitted using maximum likelihood, in the R statistical software (R Core Team 2019) using the 'nlme' package (Pinheiro *et al*. 2018). Growth of DBHUB, height and CW of individual trees were evaluated for two different groups: all trees together and the cohort of dominant trees only. We used only marri trees to estimate the stand BAUB growth; however, the retained BAUB includes BAUB of all three species present in the plots. We included fixed effects for thinning treatment (as a factor), and random effects for plots, to account for possible spatial correlation among individual trees within the same plots, and individual trees, to account for the fact our data includes repeated measurement on the same trees at different measurement times. The effect of thinning treatment on growth of stand BAUB was evaluated at the plot level using standard ANOVA. The results of this plot-level ANOVA analyses should be treated with some caution, as the number of replicate plots was only two, and thus the assumption of equal variance among groups is difficult to test. We also tested whether the DBHUB growth varied between growth period (1992 to 1997, 1997 to 2002, 2002 to 2010 and 2010 to 2018) using growth period as fixed effect and plot as random effect.

Allometric relationship between DBH and height

Nine different linear and non-linear allometric equations (Table A1) were fitted to DBH and height data for all time points. After a preliminary analysis of all nine equations, the three best equations were selected for further analysis (Table 2). Parameters and fit statistics for each model were estimated in R using the nls and nlsLM functions in the minpack.lm package (Timur *et al*. 2016; R Core Team 2019), and models were evaluated and compared using different criteria including significance of estimated parameters (at 95% confidence level), coefficient of determination (R^2; higher values indicated better models), root mean squared error (RMSE; lower values indicate better models) (Montgomery *et al*. 2001), and Akaike

Information Criterion (AIC; lower values indicate better models) (Akaike 1972; Burnham & Anderson 2002). The distribution of residuals was also considered in selecting the best model.

Effect of treatment on allometric relationships

We also tested whether stand density (thinning treatment) affected allometric relationships between DBHUB and each of height, HDR and CW. For height, we fitted a model predicting height as a power function (Huxley & Teissier 1936) of DBHUB using a linear model including an interaction: log(height)~log(DBHUB)*T, where T was the thinning treatment as a categorical factor. We then tested whether the effect of treatment was significant in the model. The same approach was used for HDR and CW.

RESULTS

Effect of treatment on individual tree and stand level variables

Decreasing stand density resulted in a significant ($p<0.05$) increase in diameter and CW over the period 1992 to 2018 (Table 1). However, HDR, stand BAUB and number of trees per ha decreased significantly ($p<0.05$) with a decrease in stand density. Stand density had a significant effect on DBHUB, CW, height, stand BAUB, number of individual trees per ha and HDR at all five measurement times ($p<0.05$) (Table 1, Table A2, Fig. A4) except the CW in 1992 and height in 1992, 1997, 2010 and 2018. Unthinned plots of marri had 32% fewer individual live trees in 2018 than in 1992, a net change of 1.22% yr^{-1}.

Effect of treatments on individual tree and stand level growth

Growth in DBHUB, height and CW of individual trees increased with a decrease in stand density for all trees and for dominant trees, but the rate of growth was higher for dominant trees than for all trees (Fig. 2a, b, c). The DBHUB, height and CW growth of all trees in the lowest density (T4) treatment were 108%, 41% and 82% higher than the growth in the highest density (T1) treatment respectively. Growth in stand BAUB increased with an increase in stand density (Fig. 2d). The growth of DBHUB and height increased with an increase in DBHUB (Fig. 3a, b) and the growth of DBHUB and height varied significantly with thinning treatment. Growth of CW decreased with an increase in DBHUB and varied significantly with thinning (Fig. 3c). Growth in DBHUB during the first five-year period following thinning (1992 to 1997) was significantly faster than during all subsequent periods ($p<0.05$) (Fig. 3d).

Allometric relationship between DBHUB and height

All parameters of nine height-DBHUB allometric equations were highly significant ($p<0.001$) (Table 2, Appendix Table A1) but equations M1, M2 and M3 produced higher R^2, lower RMSE and lower AIC (Table 2, Appendix Table A1) than other equations. The difference in fit statistics among these three equations was very small (Table 2), but the residuals produced by M3 are smaller and more consistent than M1 and M2 (Fig. 4b), and so M3 was considered as the best equation for the prediction of height from DBHUB.

Effect of treatment on allometric relationship

The height-DBHUB allometry varied significantly among thinning treatments in 1992 ($p=0.01$), 1997 ($p=0.003$) and 2002 ($p=0.002$) but not in 2010 ($p=0.17$) and 2018 ($p=0.24$) (Figs 4c, A3). The differences among thinning treatments were similar for 1992, 1997 and 2002. Allometry of HDR with DBHUB differed significantly with stand density in 1992 ($p=0.03$), 1997 ($p=0.003$), 2002 ($p=0.004$), but not in 2010 ($p=0.14$) and 2018 ($p=0.11$) (Figs 4d, A3). Allometry of CW and DBHUB did not differ significantly with stand density in any of the measurement years (Figs 4e, A3). Height and CW increased with an increase in DBHUB, however, HDR decreased (Fig. 4a, c, d, e).

Table 1. Arithmetic mean±standard error values of individual tree and stand characteristics according to thinning treatment for the most recent measurement (2018). For each variable, the degrees of freedom (numerator/denominator), f-value and p-value from the mixed effect model ANOVA is also shown. Note: all variables except BAUB ($m^2\ ha^{-1}$) and Stem number per hectare (ha^{-1}) are presented for only marri trees. BAUB ($m^2\ ha^{-1}$) and stem number per hectare given in the table includes all tree species present in the plots. Marri represents 70%, 73.1%, 74.9%, and 79.7% of the plot total basal area in T1, T2, T3 and T4 respectively.

Characteristics	Thinning (BAUB in 1992 after thinning)						
	T1 (21.6)	T2 (11.6)	T3 (9.9)	T4 (6.4)	df	F-value	p-value
DBHUB (cm)	15.7±0.5	21.8±0.5	27.8±0.8	30.2±1.2	3/4	44.5	0.001
DBHUB of dominant trees (cm)	26.5±1.0	27.5±0.8	33.3±1.4	34.2±2.0	3/4	15.7	0.007
Height (m)	20.4±0.6	21.1±0.6	23.7±0.7	25.8±1.1	3/4	5.1	0.075 ^{ns}
Height of dominant trees (m)	23.8±1.0	24.1±0.9	27.2±1.2	28.5±1.0	3/4	13.3	0.010
Height-DBHUB ratio ($m\ cm^{-1}$)	1.1±0.02	1±0.02	0.9±0.02	0.8±0.03	3/4	11.6	0.019
Crown width (m)	3.3±0.2	3.3±0.2	4.5±0.3	4.7±0.4	3/4	6.8	0.047
BAUB all species ($m^2\ ha^{-1}$)	42.7±4.7	29.8±2.8	26.5±3.4	19.0±1.2	3/4	175.0	<0.001
Stem number per hectare all species (ha^{-1})	1905±383	655±67	361±28	238±39	3/4	14.7	0.012

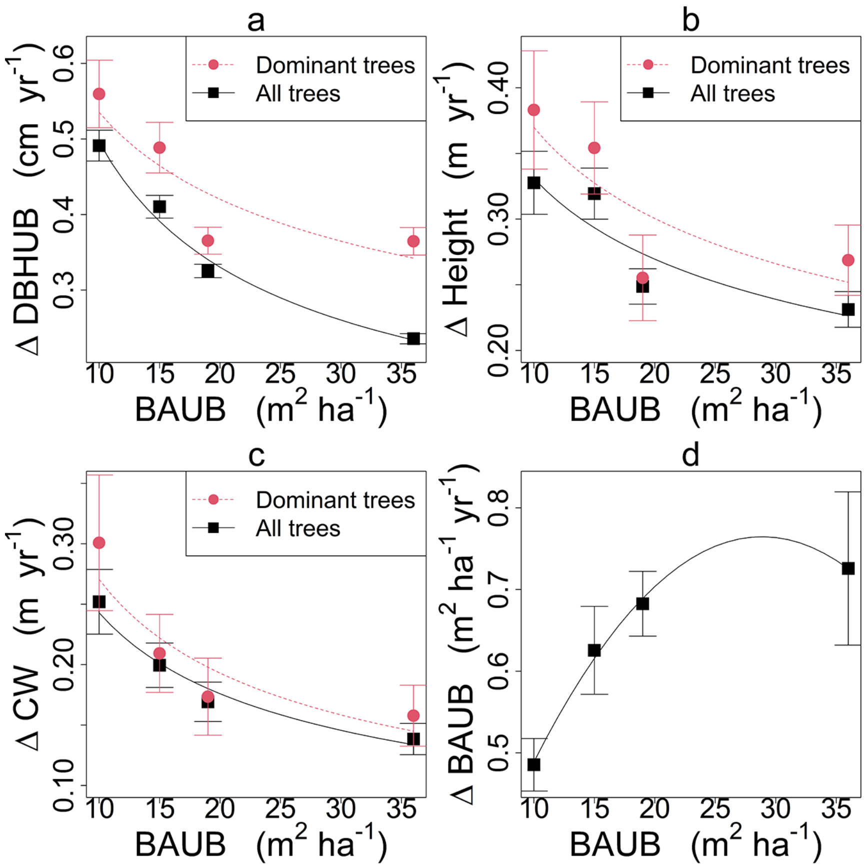

Figure 2. Effect of stand density on annual growth (1992-2018) of (a) DBHUB, (b) height, (c) CW, (d) stand BAUB**.** Δ denotes annual growth. Error bars denote standard error. Stand density presented in the x-axis was measured in 1992, 1997, 2002 and 2010 and the growth was from initial measurement to the next measurement year for example growth from 1992 to 1997 was plotted against stand density of 1992. The growth presented is only of marri but the BAUB presented in the x-axis is of all trees presented in the plots.

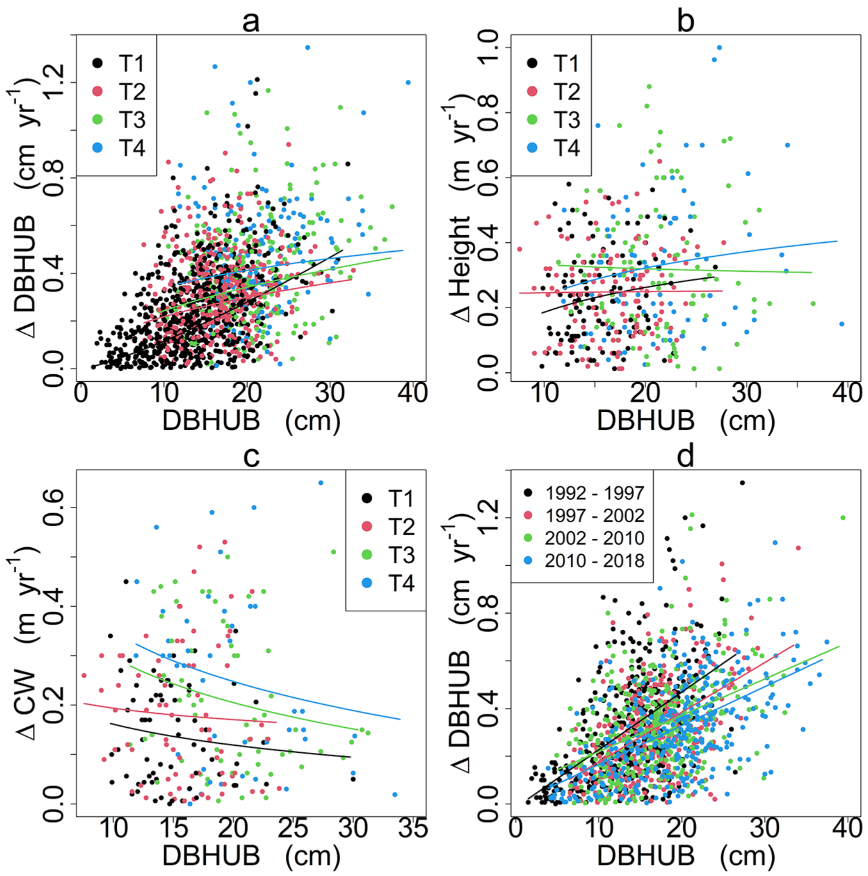

Figure 3. Effect of stand density on annual growth (1992-2018) with respect to DBHUB; (a) DBHUB, (b) height, (c) CW, (d) Effect of time period on DBHUB growth of marri only. Δ denotes annual growth. T1 (21.6 m^2ha^{-1}), T2 (11.6 m^2ha^{-1}), T3 (9.9 m^2ha^{-1}) and T4 (6.4 m^2ha^{-1}) (according to 1992 data) are thinning treatments (stand densities) in an increasing order of thinning intensity.

Table 2. Parameter values and fit statistics of different allometric equations for tree height and DBHUB (H=height in m, D=DBHUB in cm, b_1 and b_2 are parameters that were estimated). The constant value 1.3 is the height of the stem above the ground level at which DBH was measured.

Model	Equation	References	Parameter value	R^2	RMSE	AIC
M1	$H = 1.3 + b_1 + b_2 D + \varepsilon_{ij}$	Linear model	b_1=6.71 b_2=0.56	0.751	1.89	2252
M2	$H = 1.3 + b_1 \left\{\frac{D}{(D+1)}\right\} + b_2 D + \varepsilon_{ij}$	Watts (1983)	b_1=7.47 b_2=0.54	0.751	1.89	2251
M3	$H = 1.3 + b_1 D^{b2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	b_1=2.78 b_2=0.62	0.752	1.89	2251

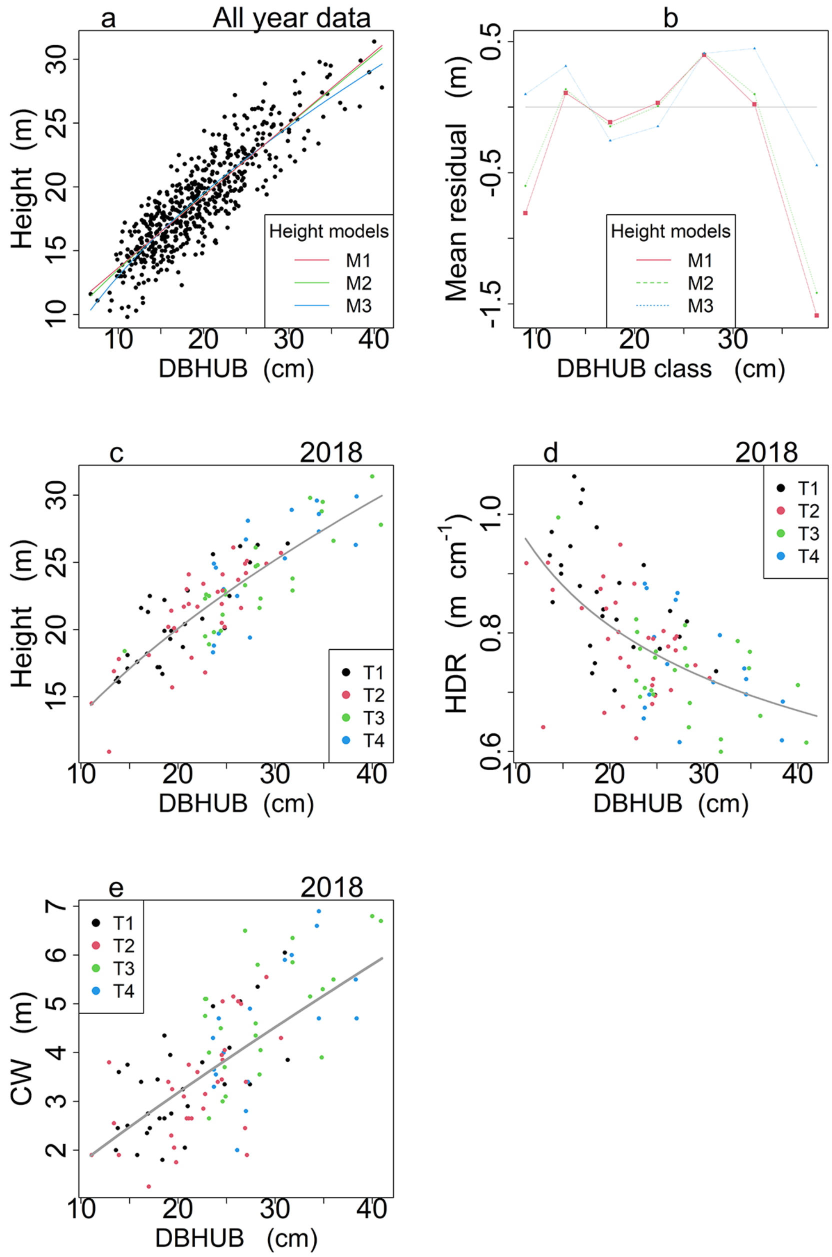

Figure 4. (a) Curves of the different DBHUB height allometry models overlaid on the observed data (data from all years), (b) Mean residual from predicted height by DBHUB class of height DBHUB allometry models, (c) Effect of stand density on allometry of DBHUB with height, (d) Effect of stand density on allometry of DBHUB with HDR, (e) Effect of stand density on allometry of DBHUB with CW. Meanings of T1 to T4 are described in Figure 3.

DISCUSSION

Effect of treatments on individual tree and stand-level variables

Low stand densities resulting from heavier thinning led to higher values of average DBHUB, height and CW at the end of the 26-year study period. In contrast, plots with low stand density resulted in lower values of HDR, stand BAUB and number of individual trees per ha. It is well established in both theory and experimental research that individual trees grow faster when competition is reduced and have greater access to light, nutrients, and water. The higher values for DBHUB and height in plots with low stand density and lower values of HDR, stand BAUB and number of individual trees per ha are consistent with the results reported for jarrah by Stoneman *et al*. (1996) and Bhandari *et al*. (2021b). Bhandari *et al*. (2022) also found similar results in the 26-year thinning experiment in karri plots at the same experimental site as this study.

Effect of treatments on individual tree and stand-level growth

Our study showed an increase in growth of DBHUB, height and CW with a decrease in stand density for the period of 1992 to 2018. Other studies have also found an increase in growth of DBH and height with a decrease in stand density (Stoneman *et al*. 1996; Grigg & Grant 2009; Forrester *et al*. 2013; Acuna *et al*. 2017; Bhandari *et al*. 2021b; Bhandari *et al*. 2022). Decreasing stand density reduces competition and increases the access to light, nutrients, and soil moisture. A similar study in *Eucalyptus* stands in Brazil found a positive effect of thinning on DBH growth but no effect on height growth of dominant trees (Medeiros *et al*. 2017). In a study carried out in jarrah forest of SWWA, Bhandari *et al*. (2021b) found that DBH growth increased continuously with an increase in thinning intensity, but the same effect was not observed consistently for height growth. Results similar to jarrah forest were also reported for the karri forest of SWWA (Bhandari *et al*. 2022). The inconsistent effect of thinning on height growth is the result of two opposing responses: 1, Thinning increases resource availability, causing remaining trees to grow faster (accumulate biomass faster); 2, Height growth is less favoured in high-light environments because more biomass is invested in diameter, branches and perhaps roots. The first is a matter of primary productivity, the second is a morphological/allometric effect. In dense plots, the individual trees tend to increase more in height in search of sunlight and thus increase their HDR. Our study also showed a lower HDR in heavily thinned plots (0.85) and higher HDR in un-thinned plots (1.05). Height growth of dominant trees was higher than that of all trees in all thinning treatments. Dominant trees even in dense stands are less influenced by light competition; however, their potential growth may be limited by below-ground competition for water and nutrients (Bhandari *et al*. 2021a, c, 2023).

Consistent with other studies (Janik *et al*. 2018; Bhandari *et al*. 2021b; Bhandari 2022), we also found that trees with greater DBHUB had greater DBHUB growth. This suggests that the DBHUB growth of individual trees of marri are still increasing and have not reached their peak. It is to be expected that DBH growth will not further increase at a certain tree DBH and will even decrease beyond that point (Gove *et al*. 2019; Chaturvedi & Khanna 2011).

Diameter growth was greatest in the first growth period after thinning (1992-1997) but decreased gradually in later growth periods. The decreasing trend in growth after the first growth period can be explained by at least two factors; the first being increased basal area in thinned plots leading to a steady increase in the inter-tree competition. A second factor leading to reduced growth over time is the decreasing trend of rainfall at the study site. Mean annual precipitation at the nearest weather station from the study site from 1992 to 1997 was 934 mm; 1997 to 2002 was 932 mm; 2002 to 2010 was 909 mm; and 2010 to 2018 was 735 mm (BOM 2020). The difference in the mean annual precipitation in the first three growth periods was small, however the significantly lower mean annual precipitation in the fourth growth period might have played a greater role in reducing the growth, along with the increased stand density.

The present study showed an increase in growth of stand BAUB with an increase in stand density. Despite the higher growth in individual tree BAUB in plots with lower stand density, we observed lower growth in stand BAUB in plots with lower stand density, primarily because of the reduction in number of individual trees. However, a trend for increasing stand BAUB growth with an increase in stand density is not likely to persist indefinitely. As inter-tree competition starts to limit growth in dense stands, growth rate starts to decrease (Bradshaw 2015a). The result of this study (increase in growth of stand BAUB with an increase in stand density) is inconsistent with observations reported by Moller (1954), Stoneman *et al*. (1996), Grigg & Grant (2009) and Bradshaw (2015a, 2015b). Studies carried out in jarrah forest (Bhandari *et al*. (2021b) and in karri forest (Bhandari *et al*. 2022) showed that stand basal area increases with an increase in stand density at stand densities below the critical threshold, but reported peak growth followed by reduced growth with further increase in stand density. Two reasons may explain our result with respect to stand density for marri in this study. The first reason for not observing reduced basal area growth in the highest density (un-thinned) stand in our study may be because this regrowth forest of relatively young age had not yet reached the critical density of trees where competition and tree allometry reduce growth rates. The second reason might be that marri is relatively tolerant of competition, perhaps due to efficient use of resources (light, moisture, and nutrients) compared to other species, but we have no direct evidence for this at present. The experimental design favoured heavier thinning treatments and did not include a treatment with a retained basal area in the range of 22-35 m^2 ha^{-1} which was the basal area range where the other studies (Bhandari *et al*. 2021b) found reduced tree growth and so the relationship between stand density and basal-area increment in denser marri stands remains uncertain.

Canker disease caused by *Quambalaria coyrecup* represents a potential threat to the health of marri forest (Paap *et al*. 2008). In a study carried out in a marri forest of SWWA, Sapsford (2017) found stand basal area was positively correlated with the proportion of trees with canker, and thus recommended thinning as an option for controlling canker disease in marri trees. Further experiments would be helpful to validate the hypothesis that reducing basal area of marri reduces the incidence of canker disease. However, thinning may increase the frequency of root diseases in some tree species such as karri (Robinson 2003). Disturbances, especially anthropogenic, need to be minimized to reduce canker disease in marri as the disturbances have a positive correlation with canker (Sapsford *et al*. 2021). Overstory species diversity was negatively correlated with the proportion of marri trees with canker (Paap *et al.* 2017; Paap *et al.* 2018). Heterogeneous forests having higher species diversity have been reported to suffer less damage from pathogens (Haas *et al.* 2011; Jactel *et al*. 2017). Thus, forest management strategies that promote species diversity may be one of the potential options for reducing the susceptibility of forest to pathogens (Holdenrieder *et al*. 2004).

Thinning resulted in a higher proportion of larger marri trees in the forest. Larger trees are likely to produce a greater quantity of fruits and seeds (Cargill *et al*. 2016), which contribute to the diet of the threatened cockatoos (Johnstone & Kirkby 1999; Cooper *et al*. 2003; Lee *et al*. 2013). In the longer term, larger trees are also likely to provide more habitat for wildlife. The formation of hollows in marri and other eucalypts is a slow process and highly dependent on age and disturbance events, natural or anthropogenic (Whitford *et al*. 2015). Older trees with larger canopies are likely to have more hollows suitable for use as nesting sites by various arboreal animals including cockatoos (Whitford 2002; Whitford & Williams 2002; Johnstone *et al*. 2013; Whitford *et al*. 2015). Marri trees are more likely to bear hollows than jarrah trees of equivalent size (Whitford & Williams 2001). At the time of writing, the maximum age of the marri trees in this study site is about 50 years and the availability of tree hollows would be expected to increase progressively over the next four to six decades. In stands comprised of a mixture of mature and regrowth trees, retention of mature trees that have a greater probability of containing large hollows is desirable from a wildlife conservation perspective even though these trees may suppress the growth of younger regeneration (Rotheram 1983)

Positive effects of a reduced number of trees due to thinning may include an increase in water yield and water discharge in a forest catchment, which may be a source of water for wildlife and may favour aquatic fauna in the forest (Stoneman & Schofield 1989; Bari & Ruprecht 2003). Thinning has also been reported to reduce fire hazard under some circumstances (Volkova *et al*. 2017; Volkova & Weston 2019). Thinning operations should be managed carefully to minimise soil disturbance and damage to retained trees and other habitat elements including mid-storey trees and large ground logs. Changes to forest management policy implemented by the Western Australian government mean that commercial timber harvesting in public native forests in SWWA will cease at the end of 2023. Thinning of younger regrowth forests to maintain and enhance ecosystem health has been identified as an option in the draft forest management plan that will apply from 2024 onwards, although the scale and nature of thinning has yet to be confirmed by government.

Effect of treatments on allometry

The allometry of DBHUB with height and HDR was significantly different among different stand densities even immediately after thinning in 1992, indicating that these differences were either introduced by bias in selection of trees for thinning, or possibly reflect random pre-existing differences among plots. This is further supported by the fact that differences in allometry between thinning treatments were not in logical order according to thinning intensity. The biggest difference was in the lowest thinning treatment (T2) and is driven by the presence of a cohort of thinner and especially shorter trees that were retained to achieve the target basal area for the thinning treatments. The significance and patterns of the differences in allometry were maintained in 1997 and 2002, but not significant in 2010 and 2018, suggesting a slow return to a more even allometry over this longer period. We did not see a clear effect of thinning treatment (stand density) on the allometric relationships between DBHUB and each of height, HDR, and CW in this study. This contrasts to the clearer effect of thinning on the allometric relationship between DBH and height reported by Deng *et al*. (2019) in *Pinus massoniana* in China; between DBH and each of height, HDR and CW reported by Bhandari *et al*. (2021b) in *Eucalyptus marginata* in SWWA and Bhandari *et al*. (2022) in *Eucalyptus diversicolor* in SWWA. The strength of the effect of thinning on allometric relationships likely depends on species, thinning intensity, inter-tree competition and time after thinning. The initial impact of thinning on inter-tree competition was reduced over the period of study as trees matured. Marri trees growing in the study area are also affected by neighbouring karri trees which contributed 20-30% of total BAUB at the start of the measurement period. Karri trees typically grow more rapidly than marri and may influence the overall growth of the marri trees, potentially attenuating the effect of thinning. The average height of karri trees was 30.8 m (Bhandari *et al*. 2022) and marri was only 22.8 m at the age of 49 years. As the number of individual trees per unit area is different in different thinning treatments, the level of competition exerted on individual trees is also different. Inter-tree competition has a crucial role in allometry of DBH and height (Lines *et al*. 2012; Forrester *et al*. 2017).

In all thinned plots, at lower stand density, height growth increased and HDR decreased with an increase in DBHUB. The HDR of un-thinned stands was higher than that of thinned stands. As described by Metzger's theory (Metzger 1893), trees growing in a low stand density prioritise girth/diameter growth even at the cost of height growth. On the other hand, trees prioritise height growth in a dense stand to improve access to light from above, as light from the side is obstructed by neighbouring competing trees. Therefore, HDR becomes smaller in thinned or open stands than in un-thinned or dense stands. Individual trees having lower HDR are stronger and therefore less prone to external forces such as wind and weight of the crown than are trees with higher HDR (Wonn & O'Hara 2001; Bobinac *et al*. 2018).

CONCLUSION

The study, using data spanning 26 years, showed that thinning reduced competition and promoted the growth of individual marri trees. Trees in heavily thinned plots had 108% higher DBHUB growth than those in un-thinned plots but un-thinned plots had higher stand basal area growth than thinned plots. Stand density affected DBHUB and height growth of individual marri trees, which in turn had a significant effect on allometry between DBHUB and each of height and HDR but not on CW. Thinning provides a technique to enable an accelerated transition from dense stands of even-aged regrowth to more open stands of larger trees that may benefit a range of forest values including water catchment management, timber production and wildlife conservation. Large-sized trees resulting from thinning are likely to provide a higher quality habitat and food resource for arboreal fauna and birds including threatened cockatoos, and more visually appealing forests.

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

ACKNOWLEDGEMENTS

Much of the data for this study was provided by Department of Biodiversity, Conservation and Attraction (DBCA), Western Australia. We thank Ray Leemans for his cooperation in data collection. The financial support for this study was provided by Research and Training Program (RTP) and University Post Graduate Award (UPA) of University of Western Australia. We also acknowledge the constructive comments provided by two anonymous referees.

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APPENDIX

Table A1. Parameter values and fit statistics of different height DBHUB allometric equations of marri (H = height in m, D= DBHUB in cm, b_1, b_2, b_3 are parameters that were estimated). The constant value 1.3 is the height of the stem above the ground level at which DBH was measured.

Model	Equation	References	Parameter value	R2	RMSE	AIC
M1	$H = 1.3 + b_1 + b_2D + \varepsilon_{ij}$	Linear model	b_1=6.71 b_2=0.56	0.751	1.89	2252
M2	$H = 1.3 + b_1\left\{\frac{D}{(D+1)}\right\} + b_2 D + \varepsilon_{ij}$	Watts (1983)	b_1=7.47 b_2=0.54	0.751	1.89	2251
M3	$H = 1.3 + b_1D^{b2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	b_1=2.78 b_2=0.62	0.752	1.89	2251
M4	$H = 1.3 + b_1 \{1\text{-exp}(-b_2D)\} + \varepsilon_{ij}$	Meyer (1940)	b_1=45.44 b_2=0.02	0.730	1.95	2312
M5	$H = 1.3 + \left\{\frac{D}{b_1 + b_2D}\right\}^3 + \varepsilon_{ij}$	Naslund (1936)	b_1=1.02 b_2=0.003	0.730	1.95	2312
M6	$H = 1.3 + \frac{b_1D^2}{(D+b_2)^2} + \varepsilon_{ij}$	Hossfeld (1822)	b_1=46.73 b_2=14.96	0.720	1.99	2332
M7	$H = 1.3 + exp\left\{b_1 + \frac{b_2}{(D+1)}\right\} + \varepsilon_{ij}$	Wykoff *et al*. (1982)	b_1=3.66 b_2=-19.53	0.708	2.03	2355
M8	$H = 1.3 + b_1\, exp\left(\frac{b_2}{D}\right) + \varepsilon_{ij}$	Buford (1986)	b_1=37.69 b_2= -17.89	0.704	2.05	2362
M9	$H = 1.3 + b_1 \{1\text{-}exp(-b_2D)\}^3 + \varepsilon_{ij}$	Bertalanffy (1949)	b_1=25.17 b_2=0.09	0.674	2.15	2415

Table A2. Effect of stand density on growth of marri at different time periods (Note: ns is not significant). For each variable, the degrees of freedom (numerator/denominator) and p-value from the mixed effect model ANOVA is also shown. P-value (growth) means p-value generated in Anova analysis on change of variables between two consecutive growth periods. P-value (retained) means p-value generated in Anova analysis on the retained values of the variables at the beginning of each growth period.T1 (21.6 m^2ha^{-1}), T2 (11.6 m^2ha^{-1}), T3 (9.9 m^2ha^{-1}) and T4 (6.4 m^2ha^{-1}) (according to 1992 data) are thinning treatments (stand densities) in an increasing order of thinning intensity.

Year	variables	Thinning					p-value	p-value
		T1	T2	T3	T4	df	(growth)	(retained)
1992	DBHUB (cm)	9.90	14.12	17.69	17.57	3/4		0.001
	Height (m)	15.39	15.14	16.27	17.55	3/4		0.209^{ns}
	Crown Width (m)	2.50	2.35	3.17	2.87	3/4		0.147^{ns}
	BAUB all species (m^2ha^{-1})	21.62	11.65	9.91	6.44	3/4		<0.001
	Stem number per ha all species (ha^{-1})	2794	672	366	255	3/4		0.011
1997	DBHUB (cm)	10.72	15.47	19.52	20.54	3/4	0.019	0.001
	Height (m)	16.55	16.44	17.92	19.36	3/4	0.252^{ns}	0.158^{ns}
	Crown Width (m)	3.60	3.72	4.72	4.74	3/4	0.039	0.019
	BAUB all species (m^2ha^{-1})	24.13	14.48	12.72	9.11	3/4	0.980^{ns}	<0.001
	Stem number per ha all species (ha^{-1})	2544	661	366	250	3/4	0.048	0.008
2002	DBHUB (cm)	13.93	17.03	21.49	22.84	3/4	0.001	<0.001
	Height (m)	17.52	17.44	20.26	21.54	3/4	0.011	0.041
	Crown Width (m)	3.46	3.96	4.94	4.98	3/4	0.252^{ns}	0.049
	BAUB all species (m^2ha^{-1})	25.18	17.78	15.66	11.41	3/4	0.0972^{ns}	0.003
	Stem number per ha all species (ha^{-1})	2400	655	366	250	3/4	0.057^{ns}	<0.001
2010	DBHUB (cm)	13.79	19.44	24.77	25.97	3/4	0.030	<0.001
	Height (m)	19.02	19.36	22.28	23.06	3/4	0.601^{ns}	0.062^{ns}
	Crown Width (m)	3.21	3.42	4.82	4.59	3/4	0.330^{ns}	0.017
	BAUB all species (m^2ha^{-1})	35.26	23.39	21.05	15.16	3/4	0.0124	<0.001
	Stem number per ha all species (ha^{-1})	2150	655	366	250	3/4	0.121^{ns}	0.009
2018	DBHUB (cm)	15.68	21.76	27.78	30.21	3/4	0.004	0.001
	Height (m)	20.44	21.08	23.75	25.76	3/4	0.165^{ns}	0.075^{ns}
	Crown Width (m)	3.33	3.28	4.80	4.69	3/4	0.670^{ns}	0.047
	BAUB all species (m^2ha^{-1})	42.71	29.81	26.47	19.00	3/4	0.030	<0.001
	Stem number per ha all species (ha^{-1})	1905	655	361	238	3/4	0.003	0.012

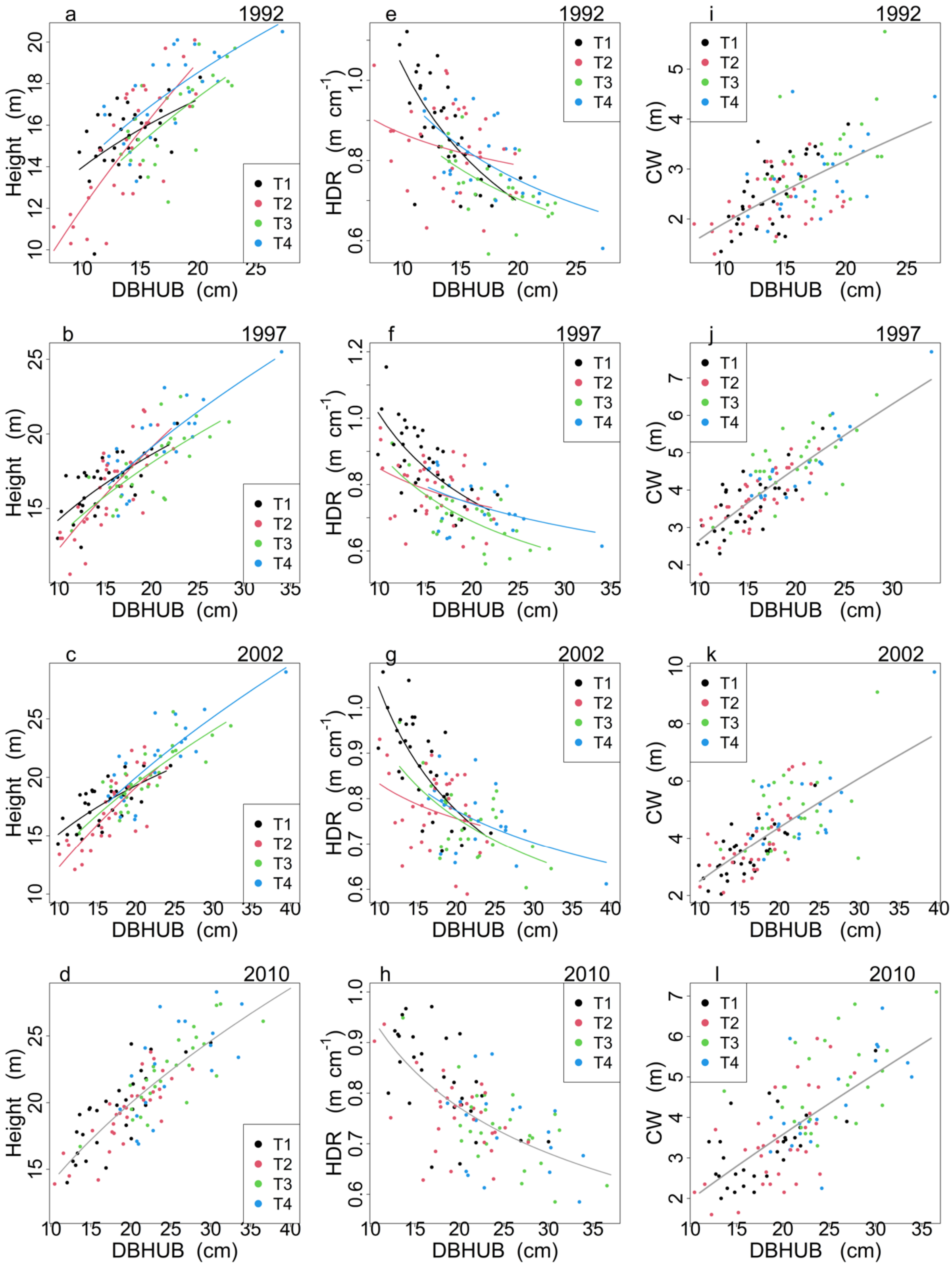

Figure A3. Effect of stand density on allometry of DBHUB with (a) height in 1992; (b) height in 1997; (c) height in 2002; (d) height in 2010; (e) HDR in 1992; (f) HDR in 1997; (g) HDR in 2002; (h) HDR in 2010; (i) CW in 1992; (j) CW in 1997; (k) CW in 2002; (l) CW in 2010. T1 (21.6 m^2ha^{-1}), T2 (11.6 m^2ha^{-1}), T3 (9.9 m^2ha^{-1}) and T4 (6.4 m^2ha^{-1}) (according to 1992 data) are thinning treatments (stand densities) in an increasing order of thinning intensity.

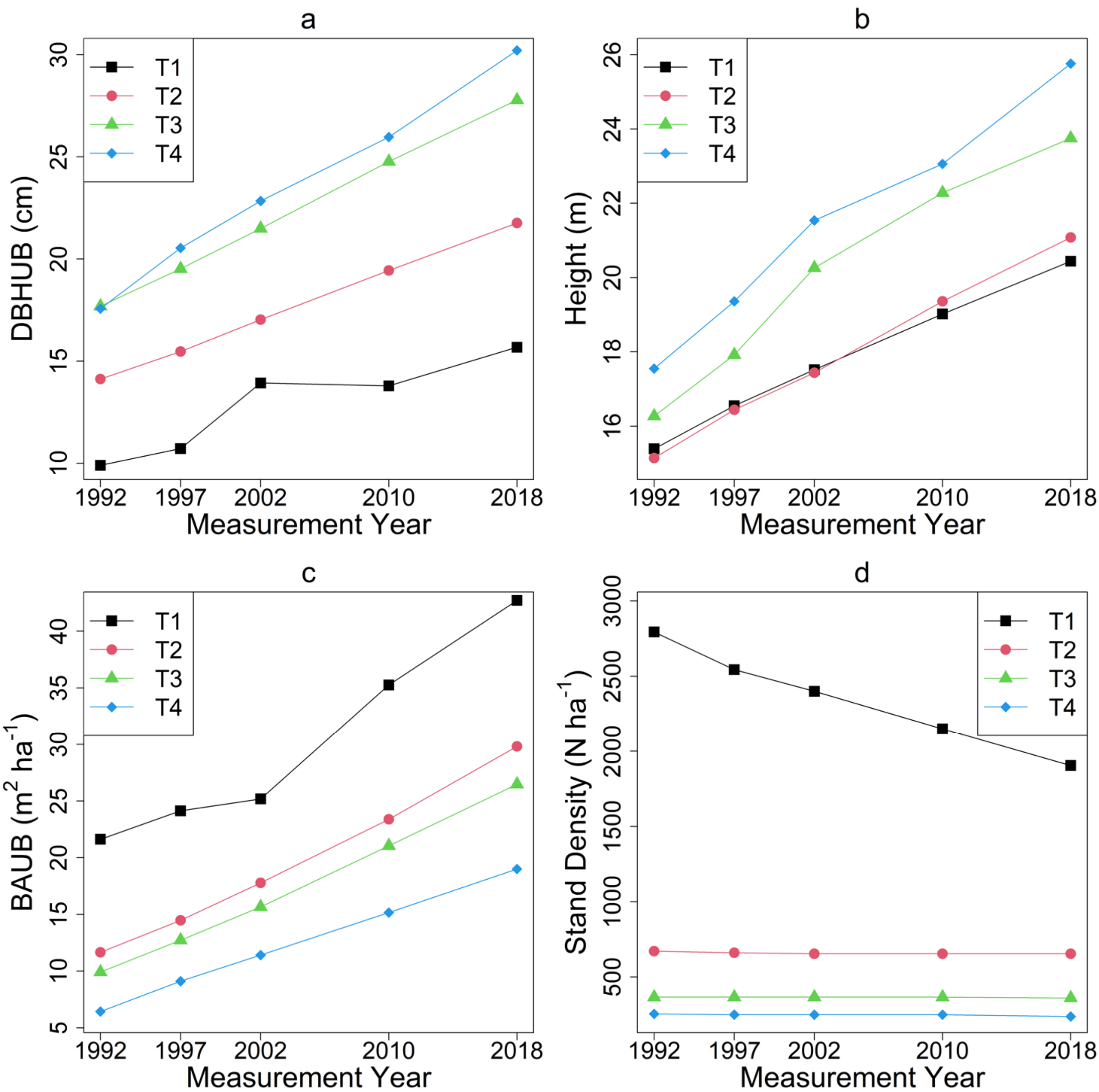

Figure A4. Variation of individual tree and stand level variables at different measurement year for different levels of stand density: (a) DBHUB; (b) height; (c) BAUB, (d) stand density. Meanings of T1 to T4 are described in Figure A2.