

**Predicting effects of thinning and neighbourhood competition on
growth of dominant endemic eucalypts**

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Jarrah (*Eucalyptus marginata*) forest at Inglehope, Western Australia (Phot: Shes Kanta Bhandari)

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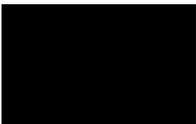
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ABSTRACT

Forests are structurally complex and dynamic, and consist of individual trees of different sizes, ages and species. Growth and development of individual trees in forests depend on several factors including age, size, stand density and competition for light, nutrients, and water. Competition is one of the most important factors influencing the growth and dynamics of forest trees. Competition negatively affects growth, but the magnitude of this effect depends on proximity and size of the neighbouring competitors. Above-ground competition for light may be more directional than below-ground competition, as light usually comes more from certain directions than others, and size-asymmetric, as taller trees may intercept more light than the shorter trees. Different management interventions, such as thinning and fertilization, can minimize competition and promote the growth of forest trees. Similar to forests in other parts of the world, forests in south-west Western Australia (SWWA) provide important commercial, ecological and conservation values. Jarrah (*Eucalyptus marginata*), karri (*Eucalyptus diversicolor*) and marri (*Corymbia calophylla*) are three of the most common forest tree species, and the areas in which they occur represent a large proportion of the forest area in SWWA. Sustainable and long-term management of these forests is of high priority. This thesis, therefore, aims to address these three objectives:

- i) to evaluate the effect of thinning treatments on the growth and allometry of jarrah, karri and marri separately;
- ii) to investigate factors affecting the growth of individual trees, especially competition from neighbouring trees; and
- iii) to examine the effect of azimuth of competitors as a potential indicator of the importance of above- versus below-ground competition in the jarrah, karri and marri forest.

For the first objective, mixed effect models were used to evaluate the effect of thinning on growth of each of the three species separately. Furthermore, we fitted allometric relationships

between DBH and each of height, height-DBH ratio (HDR) and crown width (CW), and tested whether thinning intensity affected these allometric relationships. For the second objective, we developed two new competition indices (CIs) and examined correlations between CIs (our new CIs plus several previously developed CIs) and DBH growth. Furthermore, models explaining diameter growth in terms of tree size and/or age at the beginning of the growth period were developed and then tested to determine whether they could be improved by also accounting for neighbourhood competition. We also investigated how many neighbouring trees or what neighbourhood distance needed to be considered when accounting for competition. For the third objective, we considered models of the DBH growth of three tree species (jarrah, karri and marri) and developed, applied and evaluated three new approaches to evaluate the effect of azimuthal effects of competition.

Thinning improved diameter growth in jarrah, karri and marri compared to the unthinned plots. Stand basal area growth was highest at an intermediate level of thinning in jarrah and karri, but in marri it was highest in unthinned plots. Thinning showed higher growth in DBH than in height and therefore a significant effect on allometry of DBH with each of height, HDR and CW.

The spatial CI we developed performed better than other non-spatial CIs. Diameter growth of the individual trees of jarrah, karri and marri could be predicted using size and/or age at the beginning of the growth period. This prediction was improved by 7% in karri, 8% in marri and 36% in thinned jarrah forest by accounting for neighbourhood competition. Prediction of diameter growth was optimized by accounting for competition from the 10 to 14 closest competitors or competitors within ~10 m from the base of the subject tree in jarrah, karri and marri forest. We found a significant effect of azimuth on competition among individual trees of jarrah, karri and marri, but the effect was small, suggesting that the major mode of competition is for below-ground resources rather than light.

Thinning can be a good management tool where the aim of management is to promote the growth of individual trees. We recommend accounting for neighbourhood competition when predicting individual tree growth, where possible. The modelling approaches developed in this thesis are likely to be useful methods for investigating individual tree growth of any species in the world where competition among trees restricts individual growth.

Keywords: Azimuth, Competition, Growth, Individual-based models, Eucalypt Forest, Thinning

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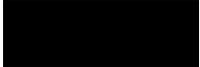
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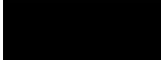
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CHAPTER 1

GENERAL INTRODUCTION

1 Individual trees, forests and forest growth dynamics

Forests are structurally complex and dynamic and consist of individual trees of different sizes (diameter, height, crown-width), stages (seedlings, saplings, poles, and trees), ages and species. After establishing as seedlings by germination from seed, or sprouting from coppice, trees become saplings, then become poles, and transition to the tree stage. The tree is generally categorised as a woody perennial plant with an erect stem or trunk, including branches and leaves. Although large variation is found in the definition of trees, the more general and comprehensive definition of a tree is “a woody perennial with a single main stem, or in the case of coppice, with several stems, and having a more or less definite crown” (FAO, 2020).

Individual trees in a forest increase gradually in size (diameter, height, crown) and some of the individual trees die due to insufficient resources. The continuous change in these parameters modifies forest structure over time and is defined as forest dynamics (Shen et al., 2013). This change is governed by natural regeneration, growth, death and disturbance. Forest disturbance refers to mechanisms or phenomena other than natural regeneration, growth and death of individual trees, which drive change in the structure and composition of a forest. Common examples of forest disturbances are fire, landslides, outbreaks of insects and pathogens, grazing, browsing, volcanic eruptions and anthropogenic disturbances such as logging/thinning, mining and urbanization (Seidl et al., 2017). High intensity disturbance such as logging or mining may result in slower rates of recovery. Mine site restoration activities are commonly practiced to speed up recovery of the forest following mining (Koch and Samsa, 2007).

Individual trees growing in a forest interact with each other and the interaction may be positive, neutral, or negative. Positive interaction may be due to factors such as: i) protection against epidemic disease, grazing, wind or lodging; ii) increased availability of specific resources such as nitrogen; iii) reduction in over-abundant but harmful resources (Weiner, 1993). Positive interactions are generally much less prevalent than negative (competition) interactions. Interactions may be asymmetric eg. one tree may positively or negatively affect another tree, but neutrally affected by that tree.

Negative interaction between individual trees may inhibit the growth and existence of certain individuals, while favouring others (Lang and Benbow, 2013). Negative interaction among individual trees may be due to competition for light, water and nutrients (Opie, 1968; Weiner, 1993). Competition generally has a negative effect on the growth of individual trees; however, the magnitude of competition varies with resource availability, size and proximity of competitors (Forrester et al., 2011). Self-thinning (tree mortality leading to reduced tree density) occurs as an outcome of inter-tree competition in almost all tree species, but the rate (the number of trees that die per unit time) may vary greatly with species, stand density, light and nutrient availability (Yoda et al., 1963; Westoby, 1984; Weller, 1987; Lonsdale, 1990). Self-thinning results in a hierarchy of dominance and suppression.

2 Forests in Australia

Australia has 134 million hectares (ha) of forests (17% of the total land area of Australia; 3% of the total forests in the world; seventh-largest reported forest area in the world) (ABARES, 2018). Forest resources in Australia have been divided into three categories (native forest, commercial plantation, and other forests). Native forests in Australia cover the largest proportion (132 million ha)

of the total forest area. The native forest is dominated by eucalypts forests (101 million ha; or 77% of native forest area), acacia forests (11 million ha; or 8% of native forest area) and rainforests (3.6 million ha; or 3% of native forest area) (ABARES, 2018).

Commercial plantations in Australia cover 1.95 million ha and include both softwoods (1.01 million ha) and hardwoods (0.92 million ha), mainly eucalypts. A small proportion of the total forest is categorized as other forests (comprises non-commercial plantations and planted forests that are not reported through the National Plantation Inventory but that satisfy the definition of forest) and covers 0.47 million ha (ABARES, 2018). Queensland has the largest area of forest (39% of Australia's forest), followed by the Northern Territory (18%), Western Australia (16%), and New South Wales (15%) (ABARES, 2018). Western Australia has about 18 million ha of forests and woodland. The major tree species found in the forests of Western Australia are the eucalypts jarrah, karri and marri (Stoneman et al. 1996; Bradshaw, 2015a; Bradshaw, 2015b).

3 Jarrah, karri and marri forests

Jarrah (*Eucalyptus marginata* Donn ex. Smith) forest is one of the most widespread native forest types of Southwest Western Australia (SWWA). Jarrah grows in association with marri (*Corymbia calophylla* (R. Br. ex Lindl.) K.D. Hill and L.A.S. Johnson) throughout its range and with wandoo (*Eucalyptus wandoo*) and powderbark wandoo (*Eucalyptus accedens*) on the drier eastern edge; with blackbutt (*Eucalyptus patens*) in moister sites; and with karri (*Eucalyptus diversicolor* F. Muell.) and yellow tingle (*Eucalyptus guilfoylei*) in the cooler southern forests (Bradshaw, 2015a). Jarrah, karri and marri forests occur within one of the 35 global biodiversity hotspots recognised by Conservation International (Myers et al., 2000; Mittermeier et al., 2011). Jarrah grows relatively slowly compared to karri and marri (Abbott and Loneragan, 1983a; Abbott and Loneragan, 1983b; Stoneman et al., 1996), and attains a mature structural stage at an age of about 130 years and continues

in this stage until about 250 years of age (Bradshaw, 2015a). Jarrah forest is well known for its environmental, conservation, economic and cultural values. Jarrah provides nesting sites and food (fruits and seeds) for threatened cockatoos (Johnstone et al., 2013; Lee et al., 2013). Jarrah forests have also been used by other taxonomic groups (terrestrial vertebrates, birds, macro-invertebrates, vascular flora, lichens, bryophyte, macrofungi, cryptogams) for their habitat (Whitford and Williams, 2002; Abbott and Williams, 2011; Whitford et al., 2015). In addition, jarrah forest catchments contribute to regulating local hydrology and provide drinking water to urban centres. The jarrah forest also provides protection against water salinity, stores carbon (Bradshaw, 2015a) and is economically important for timber, fuelwood, drinking water and honey (CCWA, 2013).

Karri is one of the tallest hardwoods in the world (Munks and Mann, 2017) and is mostly confined to high rainfall areas (>1100 mm yr⁻¹) of SWWA (Bradshaw, 2015b; Gentili 1989). Approximately one-third of the karri forest (35%) occurs as pure karri and the remaining forest occurs in mixture with marri and to a lesser extent with the jarrah (Bradshaw, 2015b). Karri also occurs in mixture with red tingle (*Eucalyptus jacksonii*), yellow tingle (*Eucalyptus guilfoylei*) and rates tingle (*Eucalyptus brevistylis*) in the cooler south-east of its range (Bradshaw and Lush, 1981; Wardell-Johnson et al., 1996; Bradshaw et al., 1997). The initial extent (European settlement period) of karri forest was 232,000 ha. At present, 82% of that original forest remains, with approximately 174,000 ha occurring on public land (CCWA, 2013). In Western Australia, approximately 1% of the current total area of karri forest is harvested each year (400 ha yr⁻¹ is clear-felled and 1000 ha yr⁻¹ is thinned). Of 0.19 million ha of karri forest in Western Australia, 53% is in formal reserves and 13% is in informal reserves (Munks and Mann, 2017). Karri forest is important in terms of the timber, wildlife habitat, tourism, conservation, environmental amenity, water catchments and for carbon storage.

Marri is a keystone and endemic tree species and occurs in association with jarrah and karri forest of SWWA. Marri occurs 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) to inland beyond Narrogin (32.93°S 117.17°E) (Churchill, 1968). Marri trees provide nesting sites and food (fruits and seeds) for threatened cockatoos (Johnstone and Kirkby 1999; Johnstone et al. 2013; Lee et al. 2013; Whitford et al. 2015). Marri is economically important for its role in honey production, furniture, flooring, food and medicine (CCWA, 2013). A canker disease caused by *Quambalaria coyrecup* has caused decline (population size and/or health) of marri in some places, including road verges and patches of remnant native vegetation in agricultural and urban landscapes (Paap et al., 2008; Sapsford, 2017).

The forests of jarrah, karri and marri are adapted to the Mediterranean climate and nutrient-poor soil of SWWA. Jarrah has a slow growth rate and extensive root system. Jarrah has a leafy crown that forms a shady canopy which inhibits the growth of new seedlings (Bradshaw, 2015a). This controls forest density, keeping it in balance with the limited supply of water and minerals. Karri occurs on relatively more fertile soil than that of jarrah. The long tap roots of karri can go down to 50 m. In general, karri forest has dense understory which helps retain moisture for as long as possible over summer and helps to moderate the summer temperature too (Bradshaw, 2015b).

4 Forest thinning

Thinning is a process of reduction in the number of individual trees to provide additional nutrients, water, light and space for the growth of remaining trees, either naturally or through human intervention (Khanna, 1996; Ashton and Kelty, 2018). Various methods of thinning exist, however two main categories are in common use: thinning from below and thinning from above. Thinning from below, also called low thinning, removes small-sized and slow-growing trees and retains large trees. Thinning from above, also called high thinning, removes individual tall and dominant trees

from the upper canopy and retains small-sized trees. Thinning, irrespective of method, reduces stand density and thus competition among individual trees and results in higher growth of retained trees (Forrester et al., 2003; Forrester and Baker, 2012; Parrott et al., 2012; Forrester et al. 2013a; Forrester et al. 2013b; Hackworth et al., 2020). However, the rate of increment varies with the intensity of thinning and/or retained stand density. Response of individual trees to thinning also depends on their stage of life and the degree and duration of suppression a tree has experienced. For example, thinning at the sapling and pole stage increases diameter growth rapidly as these stages are the most responsive to thinning treatments in the life of the forest. Thinning has also been reported to improve forest health (Meadows et al., 2013), temporarily increase water yield and discharge from forest catchments (Stoneman and Schofield, 1989, Bari et al., 1996; Bari and Ruprecht, 2003, CSIRO, 2009; Hawthorne et al., 2013), increase drought resistance (Vernon et al., 2018), promote regeneration (Peacock, 2008) and may under some circumstances reduce fire hazard (Volkova et al., 2017).

5 Forest growth models

Models are abstract representations of real-world systems that help us understand them better. Models can be in the form of mathematical equations, tables, figures and symbols (Vanclay, 1994; Haefner, 1996; Grimm and Railsback, 2005; Borner et al., 2012). Forest growth models are mathematical or computer models that represent or predict the current and/or future status of the individual trees or the whole forest stand (Vanclay, 1994; Weiskittel et al., 2011). Forest growth models can be developed for a whole stand, or for a group of certain sized trees, or for individual trees depending on the level of detail required (Orellana et al., 2017; Burkhart and Tome, 2012). Broadly, forest models are either mechanistic (i.e., process-based), phenomenological (i.e., empirical), or a combination of the two (i.e., hybrid models) (Makela and Valentine, 2020). Due to the long-life span of forest trees, new silvicultural treatments cannot be tested experimentally over short time-periods. Forest growth models developed and validated using data obtained from

previously established trial plots can provide a good basis for strategic and operational planning and forest valuation, making rational forest management decisions, and predicting the financial and ecological consequences of new management regimes or disturbances without establishing new experiments (Burkhardt and Tome, 2012; Pretzsch, 2009).

Different statistical modelling approaches (least squares regression, mixed effect models, logistic models, generalized models) have also been used depending on the nature of the data to model forest growth and yield. The least squares regression modelling approach is generally used where the data are distributed randomly. Data for forest growth analysis and modelling are often clustered in plots, hierarchical in nature and measured repeatedly. To account for the nature of data in forest growth and yield modelling, mixed effect modelling approaches are more suitable (Goldstein, 1986; Morris et al., 2006; Wang et al., 2019). Mixed effect models include both fixed and random effects. Fixed effects deal with covariate or treatment effects and random effects explain the different sources of stochastic variability (Calama and Montero, 2005; Zobel et al., 2011).

5.1 Stand level growth models

Stand level models use stand-level variables (e.g., average stand age, site index, stand basal area (BA) ha^{-1} , number of trees ha^{-1}) to predict and/or explain and/or describe the growth and yield of the forests (Palahi et al., 2003; Stankova, 2016). These models have been categorised into different generations (Pretzsch, 2009) and have various applications (Vanclay, 1994). Stand-level models are useful for simulating expected stand development when scarcity of long-term data precludes the use of more complex modelling approaches (Stankova, 2016) and to predict the annual volume growth of a forest (Gasparini et al., 2017). These models are generally used for relatively even-aged forests (Castedo-Dorado et al., 2007) and may not be effectively applied where variation between individual trees is high in terms of the species, age or size (Zhang and Lei, 2010). However, there are some

examples of application of stand level models to uneven-aged forests that contain many size classes (Forrester et al., 2021).

5.2 Size class models

In this modelling approach, the whole population is divided into groups, commonly called cohorts, based on diameter or height or a combination of these variables (Burkhardt and Tome, 2012). Size class models aim to predict the growth of similar-sized individual trees through time (Twery and Weiskittel, 2013). They simulate the growth for each diameter class based on the average-sized tree in each size class. Some commonly used size-class models are stand table projection (Trincado et al., 2003), matrix-based models (Picard et al., 2002), diameter-distribution models (Qin et al., 2007). Stand table projection is the more commonly used model in size class models. In stand table projection, the number of individual trees and their growth in each diameter class is determined. The volume for each diameter class is estimated separately and then summed up to obtain stand-level values. Future growth is predicted based on the past growth rate of individual trees in each diameter class. When predicting future growth, mortality, harvest and ingrowth (the number of individual trees that achieved the minimum measurable size during the growth period but were not at that size during the previous growth period) must be considered. Two basic assumptions are made when predicting future growth: i) all tree diameters in a diameter class equal the midpoint diameter for that class; and ii) all individual trees of a particular diameter class grow at the same average rate. Size-class models have been developed for even-aged, uneven-aged, single species, mixed-species and natural forests.

5.3 Individual-based models (IBMs)

Individual-based models (IBMs) are those models which describe the behaviour of autonomous individuals and are exclusively developed for the prediction of traits of individual organisms (Huston et al., 1988; Grimm, 1999; Grimm and Railsback, 2005, Grimm et al., 2006).

Individual-based modelling is one of the most comprehensive and accurate modelling approaches for predicting the traits of individuals. Forest IBM represents trees individually, and thus allows individual trees and their interactions to be represented in greater detail than would be possible in more aggregated modelling approaches, such as stand-level modelling (DeAngelis and Grimm, 2014; Zhang and Lei, 2010). As information regarding each individual tree is used in the modelling, it is a relatively detailed and complex modelling approach (DeAngelis and Grimm, 2014). IBM can account for the fact that the individual trees of a forest or stand are often different, interact locally and adapt differently to their varying local environments (DeAngelis and Grimm, 2014; Berger et al., 2008). Even more detailed and complex modelling approaches exist, such as functional–structural plant models that describe the development of the three-dimensional architecture and structure of plants at the scale of individual tree organs (Guo et al., 2011; Xu et al., 2011), but these may be overly complex for representing the growth and interactions between large numbers of trees.

The application of IBM to forest growth simulation began in the 1960s (Newnham, 1964), after which several IBMs for pure stands (Lee, 1967; Ledig, 1969; Mitchell, 1975) and mixed stands (Ek and Monserud, 1974; Monserud, 1975) were developed. An important milestone in forest growth IBM was the development of JABOWA (Botkin et al., 1972) to simulate the population dynamics of trees in mixed-species forests including competition, secondary succession and elevation. Other forest IBMs include PROGNOSIS (Stage, 1973), FORET (Shugart and West, 1977), FORTNITE (Aber and Melillo, 1982), STEMS (Belcher et al., 1982), SORTIE (Pacala et al., 1993); FORMIND (Kohler and Huth, 1998), GLOBTREE (Soares and Tome, 2003), ODD (Grimm et al., 2006) and UVAFME-VOC (Wang et al., 2017). The growth of trees depends on light, stand density, soil moisture, soil nutrients, topography and temperature and type of species (Wagner et al., 2014; Herault et al., 2010). Competition, one of the major determinants of growth, affects the radial and vertical growth of trees and always reduces growth from its maximum potential (Nakagawa et al., 2015).

While some IBM have not included competition (Gasparini et al., 2017; Wang et al., 2017) many others do (Contreras et al., 2011; Orellana et al., 2017). These competition-inclusive IBM can be distance independent (non-spatial) or dependent (spatial) based on whether the model uses tree location and distance of competitor from the subject tree (Contreras et al., 2011; Lhotka and Loewenstein, 2011; Burkhardt and Tome, 2012; Forrester et al., 2013a; Lhotka, 2017). Non-spatial IBMs have also been recognized as tree-list models and used in several parts of the world. However, they have very different architectures and data requirements compared to spatial IBMs, which require location information of each tree, therefore increasing the time and cost of data collection.

6 Predictor variables in individual based models

A number of predictor variables have been used in individual-based modelling for predicting individual tree growth. Predictor variables used in the individual-based modelling include diameter at breast height (DBH), height, individual tree basal area, crown measures (crown diameter/crown width, crown length, crown height, crown ratio and crown projection area and crown volume), slenderness coefficient (height-diameter ratio, HDR) and age of the individual trees (Cole and Lorimer, 1994; Coomes and Allen, 2007; Lhotka and Loewenstein, 2011; Gyawali et al., 2015; Lhotka, 2017; Zhang et al., 2017). Of these variables, DBH and height are the most commonly used predictors (Martins et al., 2014; Lhotka, 2017). Nevertheless, the use of DBH as a predictor variable is more common than height (Gyawali et al., 2015; Ou et al., 2019) because it is cost-effective and readily measured to a high level of accuracy (Sileshi, 2014; Kuyah and Rosenstock, 2015). Stand level variables such as stand basal area per ha, number of trees per ha, site index, and average age of the stand have also been used in predicting the growth of individual trees (Lhotka and Loewenstein, 2011; Lhotka, 2017).

Some of the individual-based modelling approaches also use competition indices as one of the predictor variables along with other commonly used predictor variables (Contreras et al., 2011; Forrester et al., 2011; Lhotka and Loewenstein, 2011; Lhotka, 2017; Ou et al., 2019). Competition indices may be spatial or non-spatial. Models with non-spatial indices predict growth based on the characteristics of individual trees and effectively assume that the location of individual trees is uniformly distributed throughout the stand (Weiskittel et al., 2011). These models are usually applied to even-aged and homogeneous forests but may also be useful for uneven-aged and mixed forests. Their prediction accuracy may be relatively low in uneven-aged and mixed forest because the complexity of species composition and stand structure is quite high in this type of forest. Bridging models between distance-independent and dependent models were developed to simulate the growth of mixed forests in which distance-independent models could not perform well; however, these bridging models are limited (Perot et al., 2010).

To overcome the limitation of distance independent models, distance-dependent models can be better options. The distance-dependent models analyse local interactions, individual variability, adaptive behaviour and heterogeneous distribution of resources and environmental factors. The distance between the subject tree and its competitors can provide one of the strongest indicators of competition faced by a subject tree from its competitors, although the use of distance-dependent models is likely to increase the cost and time. Contreras et al. (2011) evaluated four distance-independent, nine distance-dependent and three light-value competition indices and found that distance-dependent competition indices described a larger proportion of BA increment. Including distance-dependent indices improved the BA growth model for loblolly pine plantation in northern Louisiana (Daniels et al., 1986). The distance-dependent indices were shown to explain about 50% of the variation of radial growth for Scots pine in Finland (Pukkala and Kolstrom, 1987) and 72% for

western larch in the USA (Contreras et al., 2011). Forrester et al. (2011) reported that 52% to 60% variability in basal area growth was explained by the distance dependent competition indices.

7 Above-ground and below-ground competition

Competition amongst individual trees largely occurs for two broad categories of resources i.e., above-ground and below-ground. Above-ground resources such as light generally come more from certain directions than others, and taller trees intercept more light than the shorter trees when they are growing together though several other factors affect light availability to individual trees (Aerts, 1999; McPhee and Aarssen, 2001; Forester, 2019). Previous studies have considered below-ground competition for water and soil nutrients as size-symmetric but, in reality, it probably lies somewhere between size-asymmetric and size-symmetric competition (Forrester, 2019). Identifying whether individual trees are competing above-ground or below-ground or both, is generally difficult, and a relatively small number of studies have focused on this aspect, especially in West Australian forests.

8 Application of forest growth models

Various kinds of forest growth models have been useful in conserving and managing forest resources for a long time (Twery, 2004). A simple version of forest growth models provides information on the quantity of a product present in the forest and how much can be removed without negatively affecting the forest's condition. It may predict how much economic value can be achieved in the market if one sells those forest products. Forest growth models provide support to foresters, forest managers, forest entrepreneurs and investors in examining forest condition and developing optimal strategies for the management of the forest resources (Gunn, 2007; Weiskittel et al., 2016). Forest growth models are a key element in prediction of current yield and future yield and in designing and implementing strategies to optimize yield from a particular forest stand (Lhotka and Loewenstein,

2011; Forrester et al., 2013a; Lhotka, 2017; Vospernik, 2017). Forest growth models are also useful tools in predicting and comparing the outcomes of different forest management systems, predicting climate change impact on forest productivity and nutrient cycling, predicting the availability of wildlife habitat, determining what action is required to improve wildlife habit in a region (Vospernik and Reimoser, 2008; Seely et al., 2015) and carbon accounting and quantification of the amount of carbon held in above-ground and below-ground fractions of different size classes, e.g., FullCAM (DEE, 2014).

9 Knowledge gap

Forest resources in Western Australia have been managed for a long period. The management of these forests is guided by ten-year forest management plans prepared by the Conservation and Parks Commission of Western Australia (CCWA, 2013). The forest management plan is based on principles of ecologically sustainable forest management and emphasizes the health, vitality and productive capacity of ecosystems to conserve and manage the forest resources in Western Australia. Past management plans have used information from previous studies (especially short-term thinning experiments and other studies) on West Australian forests but results from long-term thinning experiments, from individual-tree models predicting growth from tree size, age and competition, and from models of above-ground or below-ground competition or both, are expected to provide important and valuable information to strengthen more for future management plans.

Jarrah, karri and marri forests form the dominant forest types in SWWA and are an important source of commercial, ecological and conservation values. Therefore, sustainable and long-term management of these forests is of high priority. Forest management activities such as thinning and control burning have been used extensively in these forests (CCWA, 2013). Studies of tree growth have been carried out and published to inform the management of jarrah forest, but these studies

mostly focused on stand level growth dynamics and for a relatively short period of up to two decades (Abbott and Loneragan 1983a; Abbott and Loneragan 1983b; Stoneman et al., 1996; Koch and Ward, 2005; Grigg and Grant, 2009). A thinning experiment for karri and marri (regenerated in 1969) was started in 1992 at Sutton, SWWA and has been measured on five occasions (1992, 1997, 2002, 2010 and 2018). Bradshaw (2015b) reported higher growth of stand basal area at an intermediate level of thinning when these stands were 32 years of age. However, the long-term response to thinning of slow growing tree species such as jarrah, karri and marri, and the effect of thinning on the allometric relationship between DBH and each of the height, CW, HDR, had not yet been studied and published.

Although several IBMs have been developed for different species in different parts of the world (Botkin et al., 1972; Grimm et al., 2006; Soares and Tome, 2003; Contreras et al., 2011; Hann, 2011; Lhotka and Loewenstein, 2011; Forrester et al., 2013a; Lhotka, 2017; Wang et al., 2017), no IBM for jarrah and marri growth has been developed. Growth models developed for karri include stand level models to predict stand height (Rayner 1991) and timber yield (Rayner, 1992a), and an individual-tree distance independent simulator called KARSIM (karri regrowth simulator) for karri trees (Rayner, 1992b). However, no IBMs for karri using a distance-dependent approach have been developed and published.

Several CIs have been developed and published for forests in other parts of the world to investigate the effect of competition on forest growth (Reineke, 1933; Krajicek et al. 1961; Hegyi, 1974; Corona and Ferrara, 1989; Wykoff, 1990; Rouvinen and Kuuluvainen, 1997; Forrester et al., 2013a), but no CI has been developed and published specifically using primary data from the jarrah, karri and marri forest of SWWA. In addition, no studies had been carried out to determine the optimum number and optimum distance of competitors from the base of the subject tree while predicting the growth of jarrah, karri and marri.

Because of the directional nature of light, the above-ground competitive effect of neighbouring trees may depend on their azimuths (north, south, east and west). For example, in the southern hemisphere, we can assume that competitor trees to the north of the subject tree might impose greater competition to the subject tree than the competitor trees from other azimuths. To our knowledge, this assumption has not yet been tested for tree species in West Australian forests. In addition, the relative importance of above-ground and below-ground competition to the growth of jarrah, karri and marri forest has not been studied extensively.

10 Thesis objective, aims and structure

My overall research objective was to investigate the effects of thinning and neighbourhood competition on the growth of dominant endemic eucalypts. The specific aims of this thesis were:

1. To evaluate the effect of thinning on growth and allometry of jarrah, karri and marri;
2. To investigate the factors affecting the growth of individual trees of jarrah, karri and marri, especially the competition from neighbouring trees; and
3. To examine the effect of azimuth of competitors as a potential indicator of the importance of above- vs. below-ground competition in jarrah, karri and marri forests.

To achieve these aims, the following four hypotheses have been addressed in this thesis:

- i) Thinning reduces inter-tree competition, improves the growth of retained trees and has a significant effect on allometry of DBH and each of height, CW and HDR in jarrah, karri and marri forests.
- ii) Size and age of individual trees at the beginning of the growth period are important predictors of the growth of individual trees, and this prediction can be improved by

including neighbourhood competition effects based on size and distance of neighbours in jarrah, karri and marri forests.

- iii) The predictive ability of individual tree growth models including competition effects based on size and distance of neighbours will increase as the number of competitors or radius from the base of the subject tree is increased, up to a point where considering additional trees does not improve models any further.
- iv) Competitors to the north of the subject tree have higher growth predictive ability than competitors to the other azimuths in jarrah, karri and marri forests.

The thesis is structured as a series of papers intended for publication. As such, a degree of repetition, particularly with regards to methods is unavoidable, e.g., in Chapters 2, 3 and 4, and in Chapters 5 and 6. Chapters included for examination are:

Chapter 1: this general introduction;

Chapter 2: addresses the aim of evaluating the effect of thinning on growth and allometry of jarrah (Aim 1). The effect of fertilizer is also considered;

Chapter 3: addresses the aim of evaluating the effect of thinning on growth and allometry of karri (Aim 1);

Chapter 4: addresses the aim of evaluating the effect of thinning (stand density) on growth and allometry of marri (Aim 1);

Chapter 5: addresses the aim of investigating the factors affecting the growth of individual trees of jarrah, especially the competition from neighbouring trees (Aim 2);

Chapter 6: addresses the aim of investigating the factors affecting the growth of individual trees of karri and marri, especially the competition from neighbouring trees (Aim 2);

Chapter 7: addresses the aim of investigating above- vs. below-ground competition by accounting for azimuth of competitors in jarrah, karri and marri forests (Aim 3); and

Chapter 8: provides a general discussion.

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CHAPTER 2

Effect of thinning and fertilizer on growth and allometry of *Eucalyptus marginata*

PREAMBLE

This chapter presents the long-term effect of thinning and fertilizer on individual tree and stand level growth and allometry between diameter at breast height (DBH) and each of height, crown width and height diameter ratio of *Eucalyptus marginata*.

It is presented as the manuscript published at Forest Ecology and Management (<https://doi.org/10.1016/j.foreco.2020.118594>). Formatting is that specified by the journal with the exception of minor editing and page numbering. Supplementary material S1 is the materials for online publication with the published manuscript.

Effect of thinning and fertilizer on growth and allometry of *Eucalyptus marginata*

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Abstract

Jarrah (*Eucalyptus marginata*) forest is one of the most widespread native forest types of southwest Western Australia (SWWA) and provides timber, firewood, wildlife habitat, water production, catchment protection and recreation. To inform management aimed at optimizing these values, a thinning trial in even aged regrowth forest was commenced in 1965. A second thinning and N and P fertilizer treatment was applied in 1986. The effect of thinning and fertilizer on tree and stand level growth and allometry was evaluated. Thinning resulted in higher values of under bark diameter at breast height (DBHUB) and tree height, and lower values of height diameter ratio (HDR), stand basal area under bark (BAUB) and stem number per unit area. Growth of DBHUB increased with a decrease in stand density. Growth of stand BAUB peaked at intermediate stand densities. Fertilizer increased growth in DBHUB and stand BAUB. Height growth was significantly greater in thinned plots. Thinning had a significant effect on the allometric relation between diameter at breast height over bark (DBHOB) and each of height, HDR and crown width (CW) while fertilizer had a significant effect on the allometric relation between DBHOB and each of height and HDR. Height and CW

increased with an increase in DBHOB but HDR decreased. Larger sized trees resulting from thinning and addition of fertilizer are likely to provide a higher volume of timber, firewood, fruits (important food for threatened cockatoos), and improved visual amenity. As thinning had a positive effect on diameter and height growth and self-thinning in jarrah is relatively low ($0.20\% \text{ yr}^{-1}$), thinning may be a valuable management tool to accelerate development of larger trees which can be beneficial for both timber production and conservation.

Key words: Growth, Allometry, Thinning, Fertilizer, Stand density

1 Introduction

Jarrah (*Eucalyptus marginata* Donn ex. Smith) forest is one of the most widespread native forest types of Southwest Western Australia (SWWA), with 80% of 2.25 million hectare (ha) of native forest being dominated by jarrah. Jarrah occurs in mixture with marri (*Corymbia calophylla*) throughout its range and with wandoo (*E. wandoo*) and powderbark wandoo (*E. accedens*) on the drier eastern edge; with blackbutt (*E. patens*) in moister sites; and with karri (*E. diversicolor*) and yellow tingle (*E. guilfoylei*) in the cooler southern forests (Bradshaw, 2015a). Of 1.8 million ha of jarrah forest in Western Australia, 1.57 million ha is publicly owned and 48% of this publicly owned forest is available for timber production (CCWA, 2013).

Jarrah forest has environmental, conservation, economic and cultural values. The fruits and seeds of this species are important constituents of the diet of the threatened cockatoos (Johnstone et al., 2013; Lee et al., 2013). Jarrah trees are also used as nesting sites by these cockatoos and other taxonomic groups (terrestrial vertebrates, birds, macro-invertebrates, vascular flora, lichens, bryophyte, macro fungi, cryptogams) (Whitford and Williams, 2002; Abbott and Williams, 2011; Whitford et al., 2015). In addition, jarrah forest regulates local hydrology with benefits for drinking

water and salinity protection, and stores carbon (Bradshaw, 2015a). Its economic values include timber, fuel wood, drinking water and honey (CCWA, 2013).

Jarraah is a slow growing tree species (Abbott and Loneragan, 1983) and attains a mature structural stage at an age of about 130 years and continues in this stage until about 250 years of age (Bradshaw, 2015a). In good conditions, jarraah can grow up to 50 m in height and 3.2 m in diameter at breast height (DBH) (Abbott et al., 1989). Jarraah tolerates high levels of intra-specific competition and the natural rate of mortality is relatively low ($0.12\% \text{ yr}^{-1}$) (Burrows et al., 2010). Growth and development of this species is influenced by site (Abbott and Loneragan, 1986), topography, drought (Stoneman et al., 1996), genetic characteristics and provenance (Abbott and Loneragan, 1986), dominance and stand structure (Koch and Ward, 2005), competition (Ward and Koch, 1995), fire (Burrows et al., 2010), fertilizer (Stoneman et al., 1996), rainfall (Standish et al., 2015) and management intervention (Abbott and Loneragan, 1986).

Individual tree growth rate of jarraah tends to increase with age but can decrease if adjacent trees become too close, leading to competition for light, space and nutrients (Ryan et al., 1996; Stoneman et al., 1996). Thinning of densely stocked stands can be used as a management tool to regain growth potential and improve tree quality (Grigg and Grant, 2009). Furthermore, overstorey removal increases soil temperature, which along with irradiance has been shown to increase the growth of jarraah seedlings in controlled environments (Stoneman and Dell, 1993). The effect of thinning on tree growth generally varies with thinning intensity and with tree age (Gallway et al., 2001). Thinning has a positive influence on DBH growth and sometimes on height growth (Nogueira et al., 2015; Štefančík et al., 2018). Diameter growth is highly dependent on stand density (Hébert et al., 2016), but height growth is more sensitive to site (Zhang et al., 1997). As the effect of thinning on DBH and height growth differs, it is interesting to assess the effect of thinning on the allometric

relationship between DBH and height, which is a fundamental factor in determining forest and ecosystem structure, as well as in quantifying tree volume, biomass and carbon stocks (Deng et al., 2019).

The soils of SWWA are considered some of the most ancient and nutrient poor soils in the world, with plant growth often limited by low availability of phosphorus (Handreck, 1997). In an area near to the study site of this study, organic matter content was about 5% in the surface 5 cm, 4% at 5-10 cm and between 1% and 2% at 1 m, with very low net rates of nitrogen mineralization (Hingston et al., 1981). Application of fertilizer has been shown to have a positive impact on growth of jarrah, with the growth response dependent on stand structure and thinning strategy. For example, when fertilizer was applied, the rate of diameter growth was higher in a stand with low stem density than a stand with higher stem density (Stoneman et al., 1996), and the use of fertilizer increased the shoot growth of jarrah seedlings at a higher rate in plots where the overstorey was removed (Stoneman et al., 1995).

This study evaluated the effect of thinning and N and P fertilizer on growth and allometry of jarrah using data gathered from a thinning experiment established in 1965 and subsequently re-thinned in 1986. We examined the effect of thinning and fertilizer on individual tree and stand level variables and on individual tree and stand level growth, predicting that thinning and fertilizer would increase diameter growth and that thinning would decrease height diameter ratio. Furthermore, we developed an allometric relationship between over bark DBH (DBHOB) and height and tested whether thinning intensity affected allometric relationships between DBHOB and each of height, height DBHOB ratio (HDR) and crown width (CW).

2 Materials and methods

2.1 Study area

This study used data from a thinning trial at Inglehope (32° 45' S, 116° 11' E) which is located 12 km east of Dwellingup (Fig. 1). The forest was regenerated in 1924 and was thus 85 years old in 2010 when the last measurement was carried out. The forest overstorey is dominated by jarrah (99% of trees, with the remaining 1% being marri). The soil is yellow in colour and sandy ferruginous in nature with low fertility (Hingston et al., 1981). The area has a Mediterranean climate with an average annual rainfall of 1245 mm (measured in Dwellingup station from 1934 to 2010) concentrated in the winter months (BOM, 2019). Average annual rainfall at Inglehope is about 200 mm lower than at Dwellingup (Stoneman et al., 1996). Long term rainfall data show a declining trend for this area, consistent with a broader trend of decline across SWWA (Bates et al. 2008). The mean monthly maximum temperature of 29.7 °C occurs in January and the mean monthly minimum temperature of 5.5 °C occurs in July (BOM, 2019).

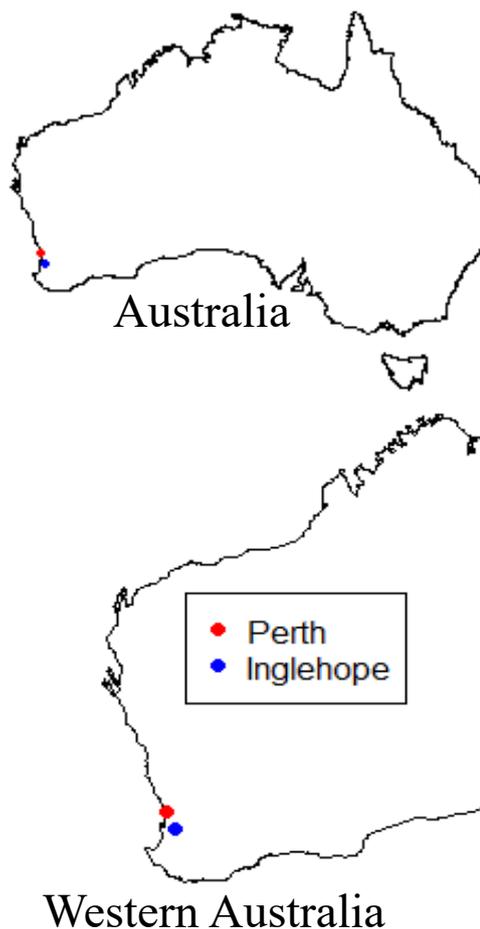


Fig. 1. Map of Australia showing study site

2.2 Treatments (thinning and fertilizer)

The Inglehope thinning trial consists of 30 plots (27 plots established in 1965 and three additional plots established in 1986) with six replicates of five different stand densities; initial thinning treatments implemented in 1965 were as follows: 7.0 (T1), 11.0 (T2), 15.4 (T3), 18.3 (T4) and 21.9 (T5) m² ha⁻¹ stand basal area under bark (BAUB). Stand density T5 represents unthinned

plots (control). Plot size for thinned treatments is 40×40 m (with an 8 m buffer on all sides) except for unthinned plots which are 20×20 m. Hereafter the period between 1965 and 1986 will be referred to as the first growth period. In 1986, a second thinning was carried out to the following stand BAUB: 5.5 (T1), 10.9 (T2), 16.4 (T3), 22.4 (T4) and 28.5 (T5) m² ha⁻¹. At this time, a fertilizer treatment (F0 unfertilized and F1 fertilized with 400 kg ha⁻¹ N and 229 kg ha⁻¹ P) was also applied to three of the six replicate plots in a completely randomized design. For the F1 plots, 200 kg ha⁻¹ N and 229 kg ha⁻¹ P were applied in autumn 1986 as 1145 kg ha⁻¹ of diammonium phosphate, and 200 kg ha⁻¹ N was applied in autumn 1987 as 588 kg ha⁻¹ of ammonium nitrate (Stoneman et al., 1996). The quantity of fertilizer applied was chosen to support optimum growth response (Stoneman et al., 1989). Hereafter the period between 1986 and 2010 will be referred to as the second growth period.

2.3 Measurement of individual trees within plots

Over the experimental period, measurements included DBHOB and bark thickness (in 1965, 1984, 1986, 2010), total height (in 1965, 1984, 2010), crown width (CW) (in 1985) and individual tree position (in 1985). Bark thickness of standing trees at breast height was measured using a bark gauge, and under bark DBH (DBHUB) was determined by subtracting twice the average bark thickness from the DBHOB. The CW was calculated as the average of two orthogonal crown measurements. In 1985, a theodolite was used to measure the location of centre and corners of each plot, and the position of each tree was mapped using direction and distance from the plot centre. Differential GPS was used to map plot centre and corners again in 2010. Field measured variables were used to calculate the slenderness coefficient (the ratio of the total height to the DBHOB of the individual tree: HDR) and height of dominant trees (H-DOM). H-DOM was calculated from the 100 tallest trees ha⁻¹ (16 tallest trees per plot for thinned treatment and four tallest trees per plot for unthinned treatment) (Štefančík et al., 2018).

2.4 Data analysis

2.4.1 Effect of treatment on individual tree and stand level variables

The effect of treatments (thinning and fertilizer as factors) on DBHUB, height, HDR, CW, stand BAUB and stem number per ha, was evaluated using one and two-way ANOVA (Table 1). Stand BAUB did not include the BAUB of the individual trees that were removed during thinning in 1965 and 1986. DBHUB, height and CW were evaluated at the individual tree level, while BAUB and stem number per ha were evaluated at the plot level. When analysing the effect of thinning treatment on individual tree and stand level variables, we assumed individual trees were distributed randomly within the plots but not within the thinning treatments, because they are clustered in plots. To account for this, we used thinning treatment as a fixed effect and plot as a random effect in mixed effect models, fitted using the maximum likelihood method. All data analysis was conducted in R (R Core Team 2019), and mixed-effects models were fitted using maximum likelihood with the ‘nlme’ package (Pinheiro et al. 2018)

2.4.2 Effect of treatment on individual tree and stand level growth

We evaluated the effect of treatment on growth of DBHUB and stand BAUB in both growth periods, hereafter referred to as Δ DBHUB and Δ BAUB. The growth of stand BAUB did not include the growth in the individual trees that were removed during thinning in 1965 and 1986. Only the thinning effect was evaluated in the first growth period; both thinning and fertilizer effects were evaluated in the second growth period. Furthermore, the effect of thinning on Δ height was evaluated for the whole period of 1965 to 2010 because height was not measured in the year when fertilizer was applied. Effect on Δ height was evaluated for two different groups: all trees together and just the dominant trees. One and two-way ANOVA were used to test the effect of treatments (thinning or thinning and fertilizer) on growth. Our data here includes clustering of trees within plots. Therefore, we used thinning treatment as a fixed effect and plot and individual tree as random effects.

2.4.3 Allometric relationship between DBHOB and height

As a scatter plot indicated a non-linear relationship between DBHOB and total height, 14 different non-linear allometric equations (Table S1) were fitted to the data. After a preliminary analysis of all equations, we selected only the four best equations for further analysis (Table 2). The parameters and fit statistics for each model were estimated in R (R Core Team, 2019) using the `nls` and `nlsLM` function in the `minpack.lm` package, and evaluated using multiple criteria including significance of estimated parameters (at 95% confidence interval); coefficient of determination (R^2 ; higher values indicate 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 and Anderson, 2002). Distribution of residuals was also considered in selecting the best model.

2.4.4 Effect of treatment on allometric relationships

We also wanted to test whether treatment affected allometric relationships between DBHOB and each of height, HDR and CW. To do this for height, we fitted a linear model predicting height as a power function (Huxley and Teissier, 1936) of DBHOB that was allowed to vary with thinning treatment by including an interaction: $\log(\text{height}) \sim \log(\text{DBHOB}) * \text{ThTr}$, where ThTr was the thinning treatment as a factor. We then tested whether the effect of treatment was significant in the model. The same approach was used for HDR and CW. For the second growth period, the effects of both thinning and fertilizer were tested by adding a fertilizer term to the linear model: $\log(\text{height}) \sim \log(\text{DBHOB}) * \text{ThTr} * \text{Fert}$ where Fert is a binary factor representing whether or not fertilizer was applied.

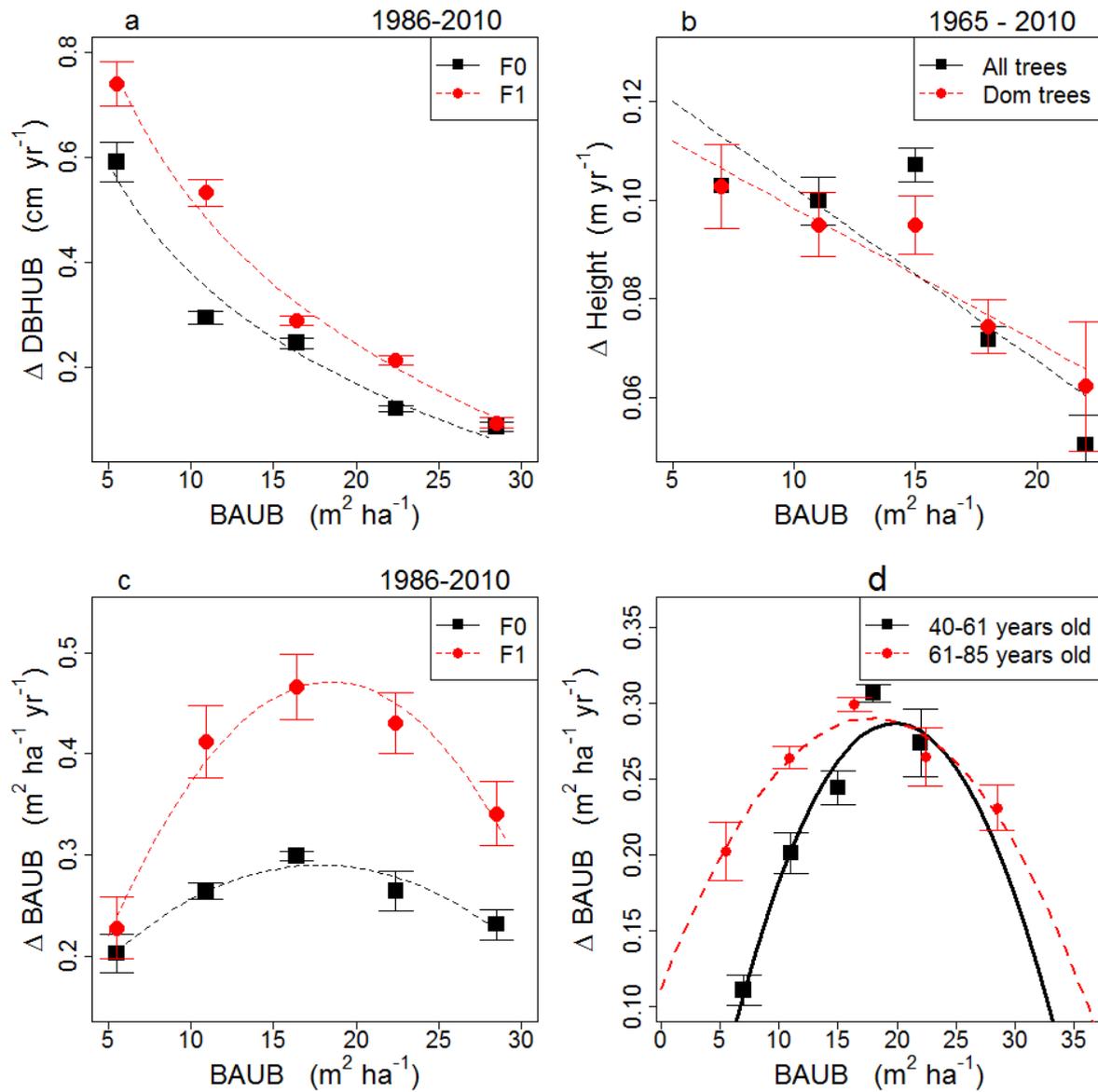


Fig. 2. Effect of stand density on growth; (a) DBHUB growth at second growth period, (b) height growth from 1965 to 2010, (c) stand BAUB growth at second growth period, (d) stand BAUB growth with respect to age. BAUB values represent the retained BAUB at the commencement of the growth period.

3 Results

3.1 Effect of treatment on individual tree and stand level variables

Table 1 shows arithmetic mean values of different variables at the individual tree and stand level for different treatments based on the latest data (Year = 2010). Thinning resulted in higher values

of DBHUB, height, H-DOM and CW, however, lower values of stand BAUB, HDR and stem number per ha (Table 1). Thinning had a significant effect on DBHUB, stand BAUB, HDR and stem number per ha in all three measurement times ($P < 0.001$), on height in 1965 ($P = 0.007$) and 2010 ($P < 0.001$), and on CW in 1985 ($P < 0.001$). Fertilizer had a significant effect on DBHUB ($P = 0.03$), HDR ($P = 0.001$) in 2010 but not on height, stand BAUB ($P = 0.82$) and stem number per ha. There was a significant interaction effect of fertilizer and thinning on DBHUB, height ($P = 0.005$) but not on stand BAUB ($P = 0.48$) and HDR ($P = 0.10$) (Table S2). We observed a low rate of self-thinning ($0.20\% \text{ yr}^{-1}$) in unthinned plots of jarrah.

Table 1 Data summary of individual tree and stand characteristics according to thinning and fertilizer treatments for the most recent measurement (2010) (values are arithmetic means) (T1, T2.....T5 are thinning treatments as described in method section, F0 is unfertilized, F1 is fertilized treatment (Note #data measured in 1985 only).

Variables	Treatments									
	T1F0	T1F1	T2F0	T2F1	T3F0	T3F1	T4F0	T4F1	T5F0	T5F1
DBHOB (cm)	53.65	54.51	37.01	44.84	37.74	34.21	26.52	28.38	20.83	20.79
DBHUB (cm)	49.94	52.32	33.86	42.49	34.59	31.23	23.62	26.70	18.51	18.85
Height (m)	27.38	27.60	24.83	26.91	26.80	25.12	24.45	24.56	23.41	21.97
HDR (m cm ⁻¹)	0.55	0.53	0.73	0.64	0.78	0.79	0.98	0.88	1.10	1.07
CW [#] (m)	5.68		4.59		4.03		2.97		2.51	
Stand BAUB (m ² ha ⁻¹)	9.94	9.81	16.89	19.36	22.85	25.18	27.95	32.96	34.22	34.38
Stem number ha ⁻¹	52	43	179	133	233	310	570	543	1050	1075

3.2 Effect of treatment on individual tree and stand level growth

Growth rate of DBHUB was higher in plots with lower stand density for both growth periods (Fig. 2a, S3a). Fertilizer increased the Δ DBHUB in all thinning treatments (Fig. 2a). Thinning enhanced growth of individual trees by up to seven-fold in heavily thinned plots compared to unthinned plots. The Δ DBHUB differed significantly with thinning ($P < 0.001$) in both growth periods and with fertilizer ($P < 0.001$) in the second growth period (Table S2). The Δ DBHUB increased as the DBHUB of the individual trees increased in all treatments over the first growth period (Fig. S3c). In the second growth period, Δ DBHUB increased with increasing DBHUB of trees in all treatments except in T1F0 where the Δ DBHUB decreased with increasing DBHUB (Fig. 3a). Fertilizer had a positive effect on Δ DBHUB (Fig. 3a). There were greater height increases in more heavily thinned plots: Δ height differed statistically ($P < 0.001$) with thinning in both all trees and dominant trees (Fig. 2b). The Δ height across the whole period decreased as the DBHUB of the individual trees increased, except in T4 and T5 (Fig. 3b).

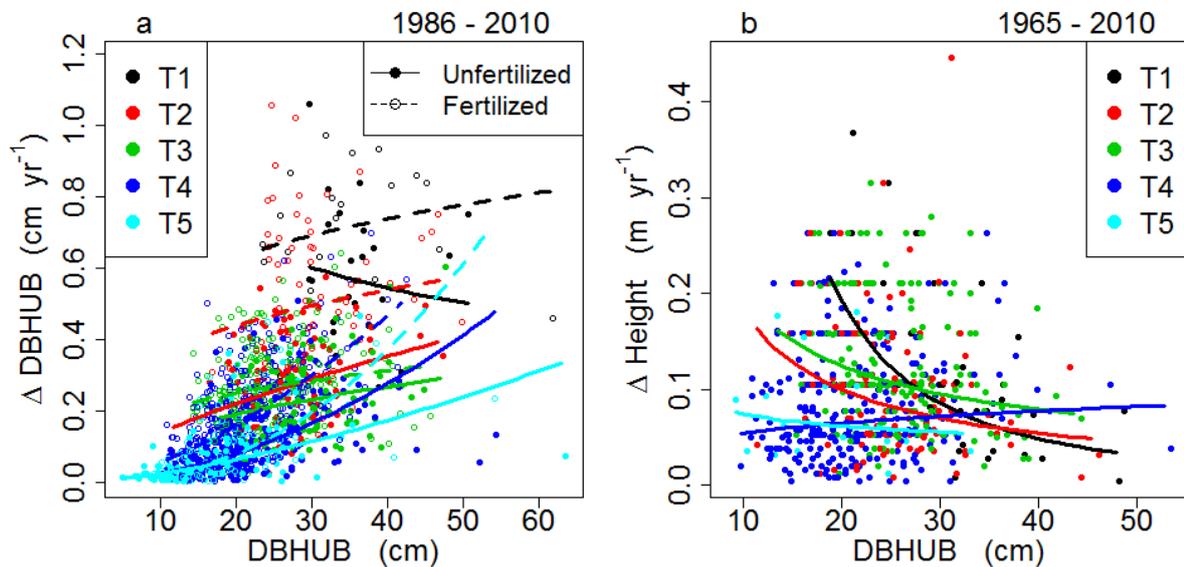


Fig. 3. Effect of treatment on growth with respect to size at the start of the growth period; (a) DBHUB at second growth period, (b) height of unfertilized treatment only from 1965 to 2010

Growth in stand BAUB increased with an increase in initial stand density in the first growth period (Fig. 2d, S3b). In the second growth period, growth in stand BAUB was also lowest at the lowest initial stand density but peaked at intermediate stand densities and then decreased with a further increase in initial stand density (Fig. 2c). This pattern was observed for both fertilized and unfertilized treatments (Fig. 2c, 2d). Fertilizer increased the stand BAUB in all thinning treatments. As the stand BAUB in unthinned treatment increased from 22 m²ha⁻¹ (in 1965) to 28 m²ha⁻¹ (in 1986) to 34 m²ha⁻¹ (in 2010), the stands were probably not at full stocking and not fully utilizing the resources of the site at the time of initial thinning.

3.3 Allometric relationship between DBHOB and height

All the parameters of all 14 allometric equations of DBHOB and height were highly significant ($p < 0.001$) (Table S1). Model M1 performed best, with the highest R^2 (0.8791), and the lowest RMSE (2.12 m) and AIC (15135), followed by M2, M3 and M4 (Table 2). However, the difference between the best four allometric equations was very small in terms of fit statistics and mean estimates (Table 2). As there were a few trees larger than 50 cm DBHOB, residual analysis showed a higher error for trees larger than 50 cm DBHOB (Fig. S3d). From the analysis of fit statistics and residual distribution, we chose M1 as the best model for the prediction of the height from the DBHOB (Table 2).

Table 2 Parameter values and fit statistics of different allometric equations for tree height and DBHOB (H=height in m, D=DBHOB in cm, b1, b2, b3 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	$H = 1.3 + \frac{D^2}{(b_1 + b_2 D + b_3 D^2)} + \varepsilon_{ij}$	Huang et al. (1992)	b ₁ =6.88 b ₂ =0.07 b ₃ =0.03	0.8791	2.12	15135
M2	$H = 1.3 + \exp^{(b_1 + b_2 D^{b_3})} + \varepsilon_{ij}$	Wang and Hann (1988)	b ₁ =3.45 b ₂ = -17.65 b ₃ = -1.15	0.8790	2.12	15135
M3	$H = 1.3 + b_1 \exp\left[\frac{b_2}{D}\right] + \varepsilon_{ij}$	Buford (1986)	b ₁ =34.25 b ₂ = -12.92	0.8789	2.13	15139
M4	$H = 1.3 + \frac{D^{b_1}}{(b_2 + b_3 D^{b_1})} + \varepsilon_{ij}$	Hossfeld (1822)	b ₁ =1.95 b ₂ =6.88 b ₃ =0.03	0.8787	2.13	15146

3.4 Effect of treatment on allometric relationships

Immediately after thinning (1965) there was no significant difference in DBHOB and height allometry ($P=0.22$) and DBHOB and HDR allometry ($P=0.28$) among thinning treatments (Fig. S3e, g). The DBHOB and height allometry in 1984 differed with thinning intensity ($P<0.001$) and in 2010 differed with thinning intensity ($P<0.001$) and fertilizer ($P=0.02$). Similarly, the DBHOB and HDR allometry in 1984 differed with thinning ($P<0.001$) and in 2010 differed with thinning ($P<0.001$) and fertilizer ($P=0.02$). Height and CW increased with an increase in DBHOB, however, HDR decreased (Fig. 4b, c, d). The DBHOB and CW allometry varied with thinning ($P<0.001$) in 1985.

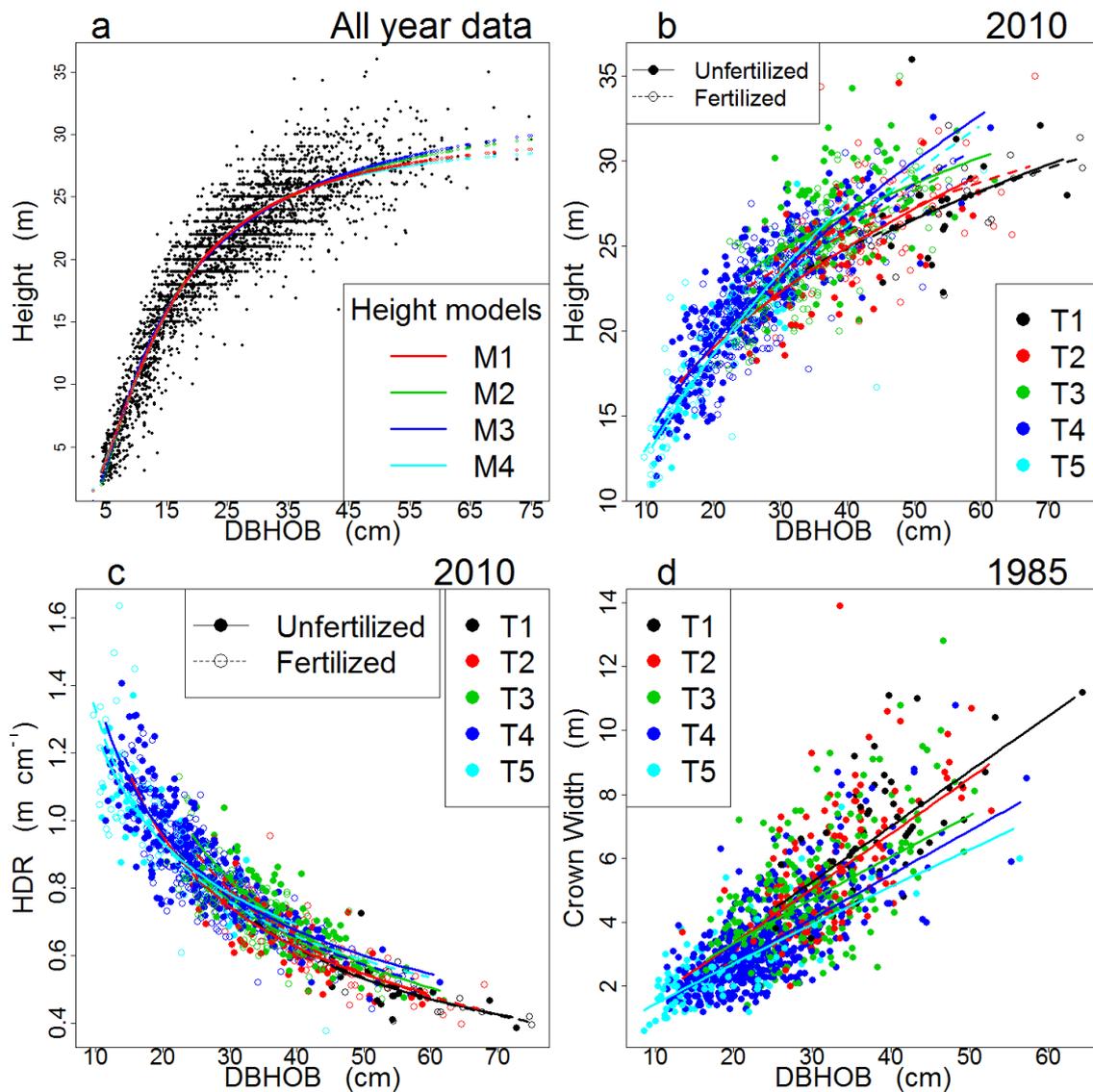


Fig. 4. Effect of treatment on allometry; (a) Curves of the different DBHOB height allometry models overlaid on the observed data, (b) height DBHOB allometry, (c) HDR DBHOB allometry, (d) CW DBHOB allometry.

4 Discussion

4.1 Effect of treatment on individual tree and stand level growth

Thinning not only decreases competition (for light or space or nutrients or water or for any combination of these), leaf area index and water loss during transpiration (Ruprecht and Stoneman, 1993; Stoneman et al., 1996; Reed et al., 2012) but also enhances access to water for retained trees (Stoneman et al., 1995; Stoneman et al., 1996; Hawthorne et al., 2013). The decrease in competition and increase in access to water contributes to higher growth of individual jarrah trees in thinned plots. Grigg and Grant (2009) found higher growth in average DBHUB in thinned plots of jarrah compared to unthinned plots in the Mediterranean climate in SWWA. They also found greater effect of fertilizer on DBHUB growth in thinned plots compared to unthinned plots. We also found that thinning increased the diameter growth and that fertilizer increased growth more in thinned plots than in unthinned plots. This result confirms the trend observed by Stoneman et al. (1996) on the same experimental site for the period between 1987 to 1991. The positive effect of thinning on jarrah growth (Stoneman et al., 1995; Koch and Ward, 2005) and other Eucalypts (Acuna et al., 2017; Volkova et al., 2017) has been reported in the literature.

Stand-level growth did not increase continuously with a decrease in stand density (Fig. 2c). Despite enhanced growth of individual trees, stand-level growth was constrained at low stand density because there were insufficient trees to fully occupy the site. Therefore, stand level growth first increased with an increase in stand density, reached a peak and then decreased with a further increase in stand density (Fig. 2c). This result is consistent with observations reported by Moller (1954), Grigg

and Grant (2009) and Bradshaw (2015a). The low rate of self-thinning of jarrah also contributes to low growth rates of individual trees in dense stands. At high stand densities, individual trees experience a high level of competition and thus each tree produces less assimilates; this could mean a higher proportion of assimilates is used for respiration and leaf formation so a lower proportion of assimilates is available for diameter growth than at the lower stand densities (as discussed in Stoneman et al., 1996). This general pattern of an intermediate level of thinning resulting in optimum stand growth is also observed in other forest species (Assmann, 1970; Smith, 1986). This pattern is the basis for designing optimum thinning management recommendations; however, the maximum basal growth and optimum stand density may vary according to site quality, as illustrated by Bradshaw (2015b) for *Eucalyptus diversicolor* in SWWA, with an earlier onset of competition effects on low quality-sites for stands having the same top height. Of course, ‘optimum’ thinning recommendations will depend on the management goal; the increased size of individual dominant trees resulting from heavier thinning might economically compensate for volume losses at the stand level.

The greater access to water by individual trees in thinned plots enabled a greater rate of photosynthesis than in unthinned plots (Stoneman et al., 1994a; 1995; 1996). Reduced shoot water stress due to thinning would have further increased diameter growth rates because plants favour allocation of more photosynthates to shoots than to roots (Begg and Turner, 1976; Gower et al., 1992). Thinning also results in increased light and nutrient availability to the remaining trees (Stoneman et al., 1995; Stoneman et al., 1996). The positive impact of thinning on individual growth is also associated with the thinning method (thinning from below). As thinning from below removes the small and slow-growing trees and the estimated growth is only of large-sized trees, this results in higher estimated growth rates than would be observed with other thinning methods. Low levels of thinning from below will reduce competition for water and nutrients for dominant trees but may not

reduce crown competition in the dominant layer. In this case, dominant trees will not be able to increase crown size and the effect on diameter growth of individual trees will be limited.

Most of the annual rainfall in the study site falls in winter (May to September) and infiltrates through the gravelly ground surface to the clays below (Churchward and Dimmock, 1989; BOM, 2019). Jarrah's major strategies for coping with dry summers are its extensive root system (sinker roots and fine roots), conservative development and slow growth rate (Abbott and Loneragan, 1983; Crombie et al., 1988; Crombie, 1997). The deeply descending sinker roots pass through cracks in the hard surface to moist clays up to 30 m below (Dell et al., 1983; Crombie et al., 1988; Churchward and Dimmock, 1989) and the extensively distributed fine roots in the surface soil absorb moisture during winter and even from the occasional summer rains (Stoneman et al., 1994b; Crombie, 1997). Fine roots (the most permeable portion of the root) and the root hairs present on them increase the absorptive surface area and improve the water uptake (McElrone et al., 2013). Thinning has potential to increase the length and biomass of fine roots (Asaye and Zewdie, 2013; Mosca et al., 2017). As fine roots are small, they can grow into smaller soil pores and make more root surface in contact with the soil and increase overall uptake of water (Macfall et al., 1991), and nutrients such as N (Sullivan et al., 2000) and P (Santner et al., 2012). Larger jarrah trees have more access to water stored deep within the soil profile via permanent root channels (Dell et al., 1983). Water uptake by roots and its delivery to leaves increases with an increase in size and age of the jarrah tree (Crombie, 1997). Greater water and nutrient uptake due to more fine roots and/or deep roots likely explains the observed increased growth of trees in thinned plants. In general, jarrah has a leafy crown that forms a shady canopy which inhibits the growth of new seedlings (Bradshaw, 2015a) which will have the indirect effect of controlling the forest density, keeping it in balance with the limited supply of water and minerals.

Heavy thinning may result in an increase in water yield and discharge from forest catchments (Stoneman, 1986; Stoneman and Schofield, 1989; Ruprecht and Stoneman, 1993; Bari and Ruprecht, 2003). Increased streamflow from thinned jarrah forest catchments has been demonstrated to persist for a decade or more following heavy thinning supplemented by effective control of coppice regrowth from stumps (Stoneman, 1993). Thinning of the jarrah forest of SWWA was shown to increase streamflow by 7.6%, groundwater level at mid-slope by 8 m and groundwater level in the valley by 4 m (Stoneman, 1993). An intensive jarrah thinning (crown cover reduced from 60% to 14%) in Hansen catchment in SWWA (annual rainfall 1200 mm) increased streamflow to ~20% of annual rainfall compared to ~6% of annual rainfall before thinning (Ruprecht and Schofield, 1991). The increased water yield from thinning operation usually returns to pre-thinning levels after a certain number of years, depending on the intensity of thinning, which must be considered when using thinning to manage water yields in the longer term. The larger trees resulted from thinning have greater value for timber products because larger logs yield higher recovery of sawn material. Gross bole volume will be higher in unthinned stands but most of this volume will be on small trees and therefore will only find markets in residue product of low commercial values.

Thinning from below retains larger trees that have likely been subject to more disturbance events (natural or anthropogenic), which increases the chances of hollow formation. Hollow development in jarrah is a slow process and assumed to occur in trees having a minimum age of 120-150 years (Whitford et al., 2015). As the trees in this study area are about 94 years old, the availability of tree hollows would be expected to increase progressively over the next three to five decades, especially in the thinned plots. Older jarrah trees with larger canopies have a higher number of hollows and these hollows provide potential nesting sites for different arboreal animals and birds including threatened cockatoos (Whitford and Williams, 2002; Johnstone et al., 2013). Larger trees also produce a greater amount of fruits and seeds (Cargill et al., 2016), which make a major

contribution to the diet of the threatened cockatoos (Lee et al., 2013). Thinning has also been reported to increase drought resistance (Vernon et al., 2018) and promote regeneration (Peacock, 2008) and may under some circumstances reduce fire hazard (Volkova et al., 2017).

4.2 Effect of treatment on allometric relationships

When the initial thinning operation was executed in 1965 the allometry was same in all treatments, as would be expected. Stand growth from 1965 to 2010, with different stand densities as a result of thinning in 1965 and 1986 and natural mortality, mainly in higher stand densities, introduced differences in DBHOB-height and DBHOB-HDR allometry in 1984 and 2010, and in DBHOB-CW allometry in 1985. The significant effect of thinning on DBHOB and height allometry is consistent with the results reported by Zhang et al. (1997) and Deng et al. (2019). In the open stands, trees prioritise diameter growth over height growth to withstand external forces such as wind and weight of the crown. In open stands, light competition is reduced, and the trees thus have less need to growth taller and compete for light. In general height growth is relatively less sensitive to stand density, whereas diameter growth is more sensitive to stand density and subsequently results in lower HDR for trees growing in lower stand densities. The mechanism of tree growth in dense and open stands is described by Metzger (Metzger, 1893). Individual trees having lower HDR are more resistant to external damage than trees with higher HDR (Wonn and O'Hara, 2001). The implication of this finding is that if the aim of the management is to produce longer and more cylindrical stems, the forest should be managed in denser stands, whereas, if the aim of the management is to produce shorter but stronger stems, the forest should be managed in less dense stands (Chaturvedi and Khanna, 2011).

Jarrah has a reputation for very limited self-thinning, and our data confirm low mortality rates (0.20% yr⁻¹). The rate of self-thinning (0.12%yr⁻¹) reported by Burrows et al. (2010) is even lower

than this study. Similar to results reported by other studies (Koch and Ward, 2005; Grigg and Grant, 2009), this study also found a slow rate of growth especially in unthinned plots of jarrah. Both self-thinning and growth results indicate low natural turnover: it takes a long time for a sapling to become a canopy tree, so only very few of them die each year. Thinning provides evidence that slow growth (in DBHUB, height and stand BAUB) is partly caused by competition, as trees grow faster when partly released from the competition.

5 Conclusions

The long-term datasets (45 years) used in this study showed that jarrah has a low degree of self-thinning and a low growth rate. Thinning reduced competition and adding fertilizer promoted the growth of individual jarrah trees. Heavy thinning increased DBHUB growth while intermediate levels of thinning increased stand basal area. Fertilizer had a positive effect on growth of DBHUB and stand BAUB for each thinning treatment. We also observed that thinning had a different effect on DBHUB and height growth of individual jarrah trees, which in turn had a significant effect on allometry between DBHOB and each of height, HDR and CW. Thinning potentially may shorten the rotation of jarrah for timber production and increase the water yield or streamflow from the forest catchment. Large sized trees resulting from thinning and fertilizer application are likely to provide a greater volume of timber, forage and habitat for arboreal fauna and birds including threatened cockatoos, and more visually appealing forests. Thinning is an effective management tool to promote the growth and development of jarrah stands comprised of larger trees and can be applied at operational scales provided that viable markets exist for small diameter logs and residue products generated by thinning.

Conflict of Interest: The authors declare that they have no conflict of interest.

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Supplementary materials: S1

Table S1: Parameter values and fit statistics of different height DBHOB allometric equations (H=height in m, D=DBHOB 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	R ²	RMSE	AIC
M1	$H = 1.3 + \frac{D^2}{(b_1 + b_2D + b_3D^2)} + \varepsilon_{ij}$	Huang et al. (1992)	b ₁ =5.02	0.8791	2.12	15135
			b ₂ =0.14			
			b ₃ =0.03			
M2	$H = 1.3 + \exp^{(b_1+b_2D^{b_3})} + \varepsilon_{ij}$	Wang and Hann (1988)	b ₁ =3.52	0.8790	2.12	15135
			b ₂ = -13.35			
			b ₃ = -1.05			
M3	$H = 1.3 + b_1 \exp\left[\frac{b_2}{D}\right] + \varepsilon_{ij}$	Buford (1986)	b ₁ =35.03	0.8789	2.13	15139
			b ₂ = -11.89			
M4	$H = 1.3 + \frac{D^{b_1}}{(b_2 + b_3 D^{b_1})} + \varepsilon_{ij}$	Hossfeld (1822)	b ₁ =1.81	0.8787	2.13	15146
			b ₂ =4.08			
			b ₃ =0.03			
M5	$H = 1.3 + b_1 + \frac{b_2}{D} + \frac{b_3}{D^2} + \varepsilon_{ij}$	Curtis (1967)	b ₁ =32.70	0.8768	2.14	15207
			b ₂ =-299.67			
			b ₃ =765.01			
M6	$H = 1.3 + b_1[1 - \exp(-b_2D)]^{b_3} + \varepsilon_{ij}$	Richards (1959), Chapman (1961)	b ₁ =27.51	0.8764	2.15	15217
			b ₂ =0.08			

			b ₃ =1.75			
M7	$H = 1.3 + b_1 \exp[-b_2 \exp(-b_3 D)] + \varepsilon_{ij}$	Winsor (1932)	b ₁ =26.68	0.8722	2.18	15355
			b ₂ =2.91			
			b ₃ =0.11			
M8	$H = 1.3 + \frac{b_1 D^2}{(D + b_2)^2} + \varepsilon_{ij}$	Hossfeld (1822)	b ₁ =38.93	0.8701	2.20	15388
			b ₂ =8.64			
M9	$H = 1.3 + b_1 [1 - \exp(-b_2 D)]^3 + \varepsilon_{ij}$	Bertalanffy (1949)	b ₁ =25.80	0.8649	2.25	15525
			b ₂ =0.1242			
M10	$H = 1.3 + b_1 D^{(b_2 + b_3 D)} + \varepsilon_{ij}$	Sharma (2009)	b ₁ =1.13	0.8645	2.25	15538
			b ₂ =1.02			
			b ₃ =-0.004			
M11	$H = 1.3 + \frac{b_1}{1 + b_2 \exp(-b_3 D)} + \varepsilon_{ij}$	Pearl and Reed (1920)	b ₁ =25.99	0.8627	2.26	15583
			b ₂ =12.96			
			b ₃ =6.65			
M12	$H = 1.3 + \frac{D}{(b_1 + b_2 D)} + \varepsilon_{ij}$	Prodan (1965)	b ₁ =0.62	0.8514	2.36	15856
			b ₂ =0.02			
M13	$H = 1.3 + \frac{b_1 D}{b_2 + D} + \varepsilon_{ij}$		b ₁ =44.80	0.8514	2.36	15856
			b ₂ =27.78			
M14	$H = 1.3 + b_1 + b_2 D + b_3 D^2 + \varepsilon_{ij}$	Staebler (1954)	b ₁ =1.15	0.8479	2.38	15941
			b ₂ =1.08			
			b ₃ =-0.01			

Table S2: Effect of thinning and fertilizer on growth of jarrah at different time periods (Note: * significant at 95%; **significant at 99%; *** significant at 99.9%, ^{ns}not significant, Thin=Thinning, Fert=Fertilizer)

Year	variables	Treatments										Significance on growth			Significance on retained tree		
		T1		T2		T3		T4		T5		Thin			Thin		
1965	DBHOB (cm)	24.98		22.14		22.33		19.29		16.16					***		
	DBHUB (cm)	22.45		19.16		19.26		16.26		14.21					***		
	Height (m)	21.78		21.04		21.77		21.82		20.08					**		
	BAUB (m ² ha-1)	6.99		11.04		15.40		18.33		21.94					***		
1986	DBHOB (cm)	39.09		31.36		29.37		24.09		19.01		***			***		
	DBHUB (cm)	35.44		28.31		26.45		21.43		16.73		***			***		
	BAUB (m ² ha-1)	5.5		10.9		16.4		22.4		28.5		***			***		
		T1F0	T1F1	T2F0	T2F1	T3F0	T3F1	T4F0	T4F1	T5F0	T5F1	Thin	Fert	Thin*Fert	Thin	Fert	Thin*Fert
1986	DBHOB (cm)	39.61	38.50	30.03	33.19	31.93	27.44	23.71	24.50	19.43	18.80				***	ns	***
	DBHUB (cm)	36.10	34.94	27.12	29.93	28.90	24.60	21.06	21.81	17.19	16.50				***	ns	***
	BAUB (m ² ha-1)	5.5	5.5	10.9	10.9	16.4	16.4	22.4	22.4	28.5	28.5				***	ns	ns
2010	DBHOB (cm)	53.65	54.51	37.01	44.84	37.74	34.21	26.52	28.38	20.83	20.79	***	***	***	***	*	***
	DBHUB (cm)	49.94	52.32	33.86	42.49	34.59	31.23	23.62	26.70	18.51	18.85	***	***	***	***	*	***
	Height (m)	27.38	27.60	24.83	26.91	26.80	25.12	24.45	24.56	23.41	21.97	*** (1965-2010)			***	ns	***
	BAUB (m ² ha-1)	9.94	9.81	16.89	19.36	22.85	25.18	27.95	32.96	34.22	34.38	*	*	ns	***	ns	ns
	Stem number ha ⁻¹	52	43	179	133	233	310	570	543	1050	1075	*	ns	ns	***	ns	ns

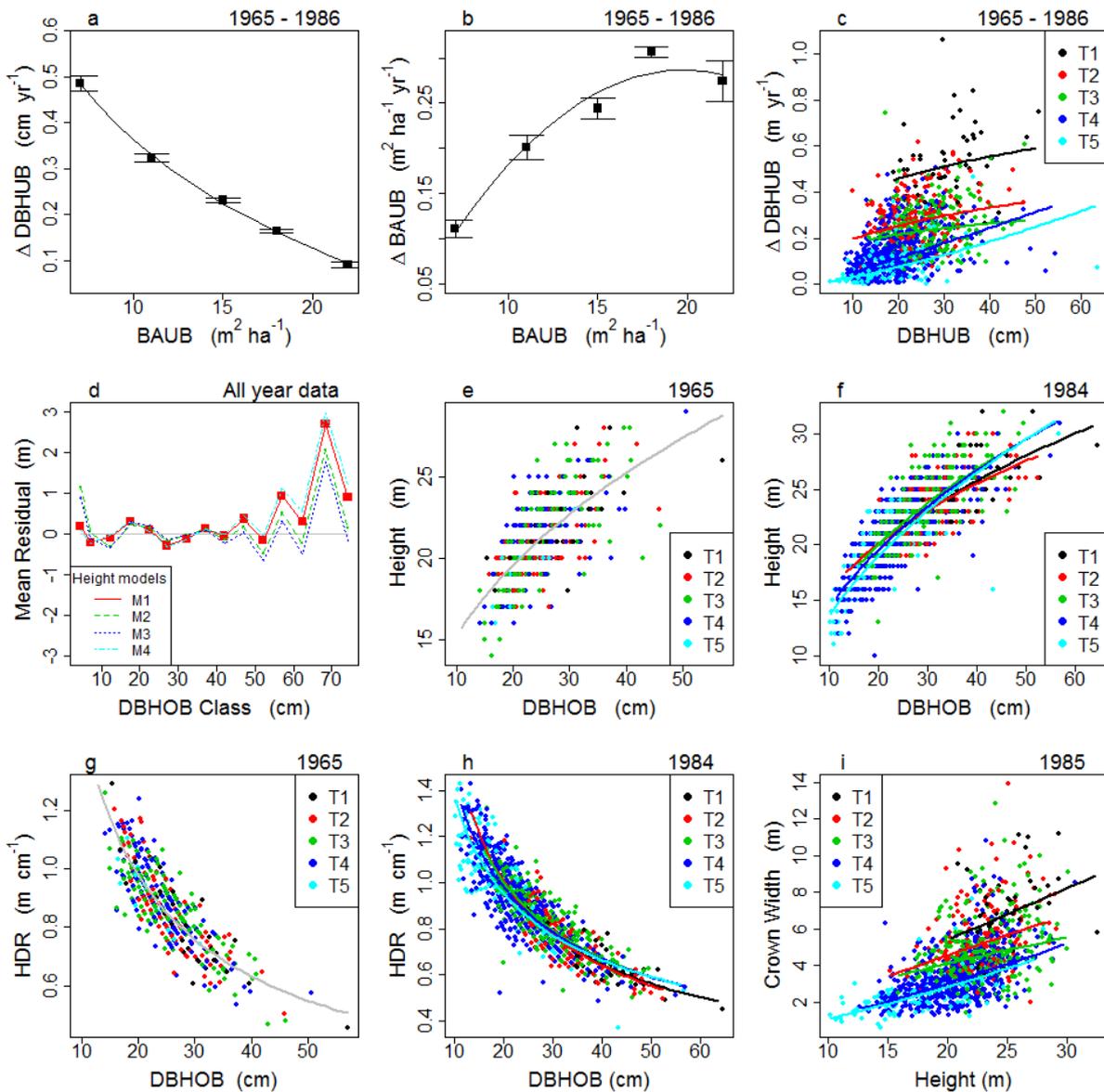


Fig. S3. (a) DBHUB growth at first growth period with respect to initial stand density, (b) stand BAUB growth at first growth period with respect to initial stand density, (c) DBHUB growth at first growth period with respect to initial DBHUB, (d) mean residuals, by DBHOB class, of predicted height in four height-DBHOB allometric models (for models see Table 2), (e) height-DBHOB allometry (1965; line fitted using simple power function), (f) height-DBHOB allometry (1984), (g) HDR-DBHOB allometry (1965), (h) HDR-DBHOB allometry (1984), (i) CW-height allometry (1985).

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CHAPTER 3

Effect of thinning on growth and allometry of *Eucalyptus diversicolor*

PREAMBLE

This chapter presents the long-term effect of thinning on individual tree and stand level growth and allometry between diameter at breast height (DBH) and each of height, crown width and height diameter ratio of *Eucalyptus diversicolor*.

It is presented as the manuscript submitted to and currently under review at *Forest Ecosystems*.

Formatting is that specified by the journal with the exception of page numbering. Supplementary material S2 is the materials for online publication with the submitted manuscript.

Effect of thinning on growth and allometry of *Eucalyptus diversicolor*

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Abstract

Background Karri (*Eucalyptus diversicolor*) forest is an endemic forest type of southwest Western Australia (SWWA), noted for being the tallest trees in the region, and providing commercial, ecological and conservation values. To inform management aimed at optimizing these values, a thinning trial was commenced in 1992. The aim of this study was to evaluate the effect of thinning on individual tree growth, stand level growth and allometry of even-aged karri. Mixed effects model was used to compare the effect of different levels of thinning on individual tree growth and stand level growth of karri. We developed allometric equations modelling the relationship between diameter at breast height (DBH) and height, and tested whether thinning affected this allometric relationship.

Results Thinning enhanced DBH, height and crown width (CW) growth of individual trees by up to 149%, 56% and 108% respectively in heavily thinned stands, with stand basal area growth optimised at retained basal areas of 13 m² ha⁻¹. Thinning had a significant effect on allometry of DBH with height, height-DBH ratio (HDR) and CW.

Conclusion Reduction in stand density through thinning from below increases diameter growth of individual trees. Stand level basal area growth is optimized at intermediate level of thinning. Thinning can be a good management tool for even-aged karri forest because it may promote the diameter and basal area growth, good health of individual trees, and possibly other ecological benefits.

Key words: Allometry, growth, karri, stand density, thinning.

1 Background

Karri (*Eucalyptus diversicolor* F. Muell.) forest is a unique, endemic forest type of southwest Western Australia (SWWA), noted for being the tallest in the region. It is an evergreen broadleaved tree of a large size (up to 80 m height and 3.5 m over bark diameter at breast height (DBH)) (Bradshaw 2015a). Karri forest occurs in the higher rainfall areas of the SWWA. Out of total karri forest, nearly 35% occurs as pure karri forests and the remainder occurs in mixture with marri (*Corymbia calophylla* (R. Br. ex Lindl.) K.D. Hill & L.A.S. Johnson) and to a lesser extent with jarrah (*Eucalyptus marginata* Donn ex. Smith) (Bradshaw 2015a). Of 0.19 million ha of karri forest in SWWA, two thirds are reserved for conservation and one third is managed for multiple use including timber production (CCWA 2013).

Karri has environmental, conservation, economic and cultural values. From environmental and conservation points of view, it occurs within one of the 35 global biodiversity hotspots recognised by Conservation International (FPC 2018). Karri trees are also used as nesting sites by arboreal fauna including cockatoos (*Calyptorhynchus baudinii*, *Calyptorhynchus latirostris* and *Calyptorhynchus banksia*) (Saunders 1979; Johnstone and Kirkby 1999; Chapman 2008; Johnstone and Kirkby 2008; Burrows et al. 2013). Karri forest is also valued due to its roles in protecting catchments (Borg 1988), providing wildlife habitat (24 mammal, 88 bird, 24 reptile, 16 amphibian and 8 fish species), amenity and recreation, tourism, honey production and carbon storage (CCWA 2013; Bradshaw 2015a; FPC

2018). Its economic values include timber for furniture and flooring, drinking water, food and medicine (CCWA 2013).

Karri is a moderately fast-growing tree and attains a mature structural stage at an age of about 100 years; the potential longevity of the species is about 350 years of age (CCWA 2013). Growth and development of karri is affected by site quality (Rayner 1991), topography, soil (Loneragan and Loneragan 1964; Hewett 1991; Breidahl and Hewett 1995), drought (Rayner 1992), fire (McCaw et al. 1994; McCaw and Smith 1997; McCaw et al. 1997; McCaw and Middleton 2015; Etchells et al. 2020), stand structure (Bradshaw 2015a), competition (Bradshaw 2015a) and rainfall.

As competition for light, nutrients, water and space increases with time after canopy closure, the growth of a forest stand decreases (Ryan et al. 1996; Pretzsch 2009; Forrester et al. 2013). Forest managers may seek to control these stages to optimize forest growth and other environmental benefits. Forest thinning is one of the potential and important options to maintain desired stand structure to optimise growth and vigour (Nogueira et al. 2015). Thinning increases the diameter growth of the retained stand (Stoneman et al. 1996) by reducing competition from neighbours, creating space for horizontal expansion and providing access to nutrients and light (Stoneman et al. 1996, Forrester et al. 2013). For karri specifically, thinning and fertilizer have been shown to increase the DBH, volume and basal area (Breidahl and Hewett 1995; Grove 1988). Tree growth varies with thinning intensity (Galloway et al. 2001). Response to thinning varies with stages of tree life, with thinning at sapling and pole stage rapidly increasing diameter growth. Tree quality, timber quality and timber yield vary with the selection of trees for thinning, thinning practices, including thinning intensity, as well as site, age, species and climate (MacDonald and Hubert 2002). Free crown thinning has a positive effect on tree quality (physically observed) (Stefancik and Bosela 2014) but effects of thinning from below are also highly site dependent (Skovsgaard 2009).

Stem diameter and height have been used commonly in forest inventories and growth and yield models (Curtis et al. 1967; Burkhardt et al. 1972; Wykoff et al. 1982). Because of lower cost, faster assessment and higher accuracy, the measurement of DBH is preferred to height (Colbert et al. 2002). Therefore, predicting height from DBH is one of the best options where direct height data are unavailable. Thinning affects DBH and height growth of individual trees in different ways (Deng et al. 2019): it has a positive impact on DBH growth (Zhang et al. 1997; Juodvalkis et al. 2005; Zhang et al. 2006; Kang et al. 2014), but not always on height growth (Harrington and Reukema 1983; Ginn et al. 1991; Oliver 1997). Diameter growth is highly dependent on the stand density (Hébert et al. 2016) whereas height growth reflects site quality (Zhang et al. 1997). As the effects of thinning on DBH and height growth differ, it is interesting to evaluate the effect of thinning on DBH-height allometry which is a determining factor in tree volume estimation.

In 1992 a thinning experiment was established in an even-aged stand of karri regenerated from seed trees following timber harvesting in 1969 (White 1974). The aim of the experiment was to evaluate the response of karri to different intensities of thinning from below. The experiment has been measured on five occasions (1992, 1997, 2002, 2010 and 2018) with preliminary results made available in reference material compiled for karri forest silviculture by Bradshaw (2015a). The experimental design included examples of stands dominated by karri and stands dominated by marri with a secondary component of karri. The overall aim of this paper is to examine the effects of thinning treatment on growth (both individual tree and stand level) and allometry of karri in the karri-dominated stands. We hypothesize that thinning would increase diameter growth and that thinning would decrease height diameter ratio. To achieve the aim of this study we first examined the effect of thinning treatment on individual trees and stand level variables, then investigated the effect of thinning treatment on individual trees and stand level growth. Then we fitted and compared 13

different allometric relationships between DBH and height. Finally, we tested whether thinning affected allometric relationships between DBH and each of height, height-DBH ratio (HDR) and crown width (CW).

2 Methods

2.1 Study area

The study area is located in karri forest in the Sutton block of SWWA (34° 28' S, and 116° 20' E) 38 km south-east of Manjimup, SWWA (Fig. 1). The forest is a regrowth forest regenerated from seed trees following timber harvesting in 1969 (White 1971) and consists of three species: karri (86% of trees), *Corymbia calophylla* (13%) and *E. marginata* (1%). The area has a Mediterranean climate with an average annual rainfall of 987 mm (measured in Manjimup station from 1915 to 2019). The monthly maximum and minimum temperature are 27.2°C in January and 6.4°C in July (BOM 2019). The soils of the study site are mainly yellow duplex and gravelly duplex, formed on weathered mottled and pallid zone material (McArthur 2004).

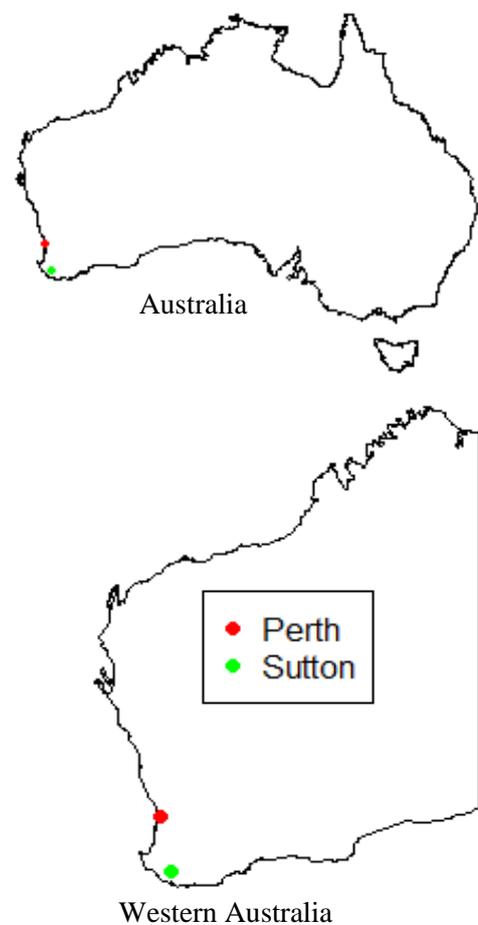


Fig. 1 Map of Australia showing study site

2.2 Treatment (thinning)

The Sutton thinning trial consists of 27 plots (size 30 m × 30 m plus an outer 10 m buffer on all sides to minimize the edge effect). The outer 10 m buffer also received the same intensity of

thinning as inside the plot, but measurements were only carried out in the inner 30 m × 30 m. Plots were selected to represent karri forest where the over-bark basal area (BA) of karri was >75% of the total over-bark basal area of the stand and top height was ≥20 m and to represent *C. calophylla* forest if the BA of *C. calophylla* was >60% of the total over-bark basal area of the stand and top height was ≥18 m. This gave a total of 19 plots for karri and 8 plots for *C. calophylla*. Due to the rareness of *E. marginata* trees, separate plots were not established for *E. marginata*. In this study, we only analysed the data from the 19 plots which were dominated by karri; the marri data are analysed in the next chapter. These karri plots were managed at six different stand densities, which were established in 1992 (age 23-years) as follows: 34.41 (T1), 20.06 (T2), 16.01 (T3), 13.05 (T4), 10.10 (T5) and 6.93 (T6) m² ha⁻¹ BA. T1 is unthinned (control) and T2, T3, T4, T5 and T6 represent an increasing order of thinning intensity. The number of replicate plots for T1, T2, T3, T4, T5 and T6 was 2, 2, 5, 3, 5, 2 respectively.

2.3 Sampling and measurement

In 1992, a Global Positioning System (GPS) was used to measure the location of the centre of each plot, and the position of each tree was mapped using azimuth and distance from the plot centre. The DBH of each tree and the total height and crown radius (CR) of a subsample of trees of each plot were measured in 1992, 1997, 2002, 2010 and 2018. At least 10 trees located at or near the centre of each plot were selected for measurement of height and CR. 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 all four directions (north, east, south and west). The field-measured variables were used to calculate height-diameter ratio (HDR=height/DBH, also called slenderness coefficient) and crown width (CW=2 × mean CR). To calculate the mean DBH and average height of the dominant trees of each plot (D-DOM and H-DOM), dominant trees were defined as trees whose crowns extend above the general

canopy level and thus receive full light from above and some light from the sides and have the largest and fullest crowns in the stand (Smith 1962; Helms 1998; Ashton and Kelty 2018).

2.4 Data analysis

2.4.1 Effect of thinning on individual tree and stand level variables

The effect of thinning treatment on DBH, 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 BA 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 in some treatments, and thus the assumption of equal variance among groups is difficult to test.

2.4.2 Effect of thinning on individual tree and stand level growth

The effect of thinning treatment on growth of DBH, height, and CW of individual trees for the period of 1992 to 2018 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). Growth of DBH, height and CW of individual trees were evaluated for two different groups: all trees together and the cohort of dominant trees only. Thinning treatment was included as a factor and a fixed effect. A random effect for plot and individual tree was also included, to account for possible correlation among trees in the same plot and repeated measurement of same tree at different measurement times. The effect of thinning treatment on growth of stand BA 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 in some treatments, and thus the assumption of equal variance among groups is difficult to test. We also tested whether the DBH 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.

2.4.3 Allometric relationship between DBH and height

As a scatter plot indicated a non-linear relationship between DBH and total height, 13 different non-linear allometric equations (Table S1) were fitted to the data to model this relationship. After a preliminary analysis of all equations, the five 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 (R Core Team 2019), and models were evaluated and compared using different criteria including significance of estimated parameters (at 95% confidence interval); 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 and Anderson 2002). The distribution of residuals was also considered in selecting the best model.

2.4.4 Effect of thinning on allometric relationships

We used the method of Bhandari et al. (2021) or chapter 2 of this thesis to test whether thinning treatment affected allometric relationships between DBH and each of height, HDR and CW, by fitting a model predicting height as a power function (Huxley and Teissier 1936) of DBH using a linear model including an interaction: $\log(\text{height}) \sim \log(\text{DBH}) * T$, where T was the thinning treatment as a factor. We then tested whether the effect of thinning treatment (T) was significant in the model. The same approach was used for HDR and CW.

Table 1 Mean±standard error values of individual tree and stand characteristics according to thinning treatment for the most recent measurement (2018) (values are arithmetic means). For each variable, the degrees of freedom (numerator/denominator), f-value and p-value from the mixed effect model is also shown.

Variables	Thinning treatments (BA in 1992 after thinning)						df	F-value	p-value
	T1(34.41)	T2(20.06)	T3(16.01)	T4(13.05)	T5(10.10)	T6(6.93)			
DBH (cm)	25.9±0.7	27.6±0.9	27.2±0.5	32.0±0.9	35.2±0.6	38.7±1.1	5/13	10.62	<0.001
Height (m)	28.4±1.2	29.1±0.7	28.7±0.6	32.9±0.8	32.6±0.4	33.1±0.7	5/13	5.59	0.005
HDR (m cm ⁻¹)	1.07±0.04	1.10±0.03	1.08±0.02	1.07±0.03	0.90±0.02	0.81±0.02	5/13	7.00	<0.002
CW (m)	4.5±0.5	4.5±0.3	4.8±0.3	5.4±0.4	6.4±0.2	7.7±0.3	5/13	7.47	<0.001
BA (m ² ha ⁻¹)	49.1±6.9	39.3±0.3	36.6±0.7	34.5±1.9	29.2±1.3	23.8±0.5	5/13	13.721	<0.001
Stem number per hectare (ha ⁻¹)	1016±183	638±27	571±30	403±87	295±11	200±22	5/13	19.43	<0.001

3 Results

3.1 Effect of thinning on individual tree and stand level variables

Table 1 shows the arithmetic mean values of different variables at individual tree and stand level for different thinning treatment at the end of the growth period (2018). Thinning produced larger trees in terms of DBH, height and CW with stronger effects at higher thinning intensity, but stand level BA and stem number per ha decreased with increasing thinning intensity. Thinning had a significant effect on DBH, height, CW, stand level BA and stem number per ha of retained trees at all five measurement times ($P < 0.05$), except the CW in 1992 ($P > 0.05$) (Table S2). The observed rate of self-thinning in unthinned plots of karri was $1.99\% \text{ yr}^{-1}$.

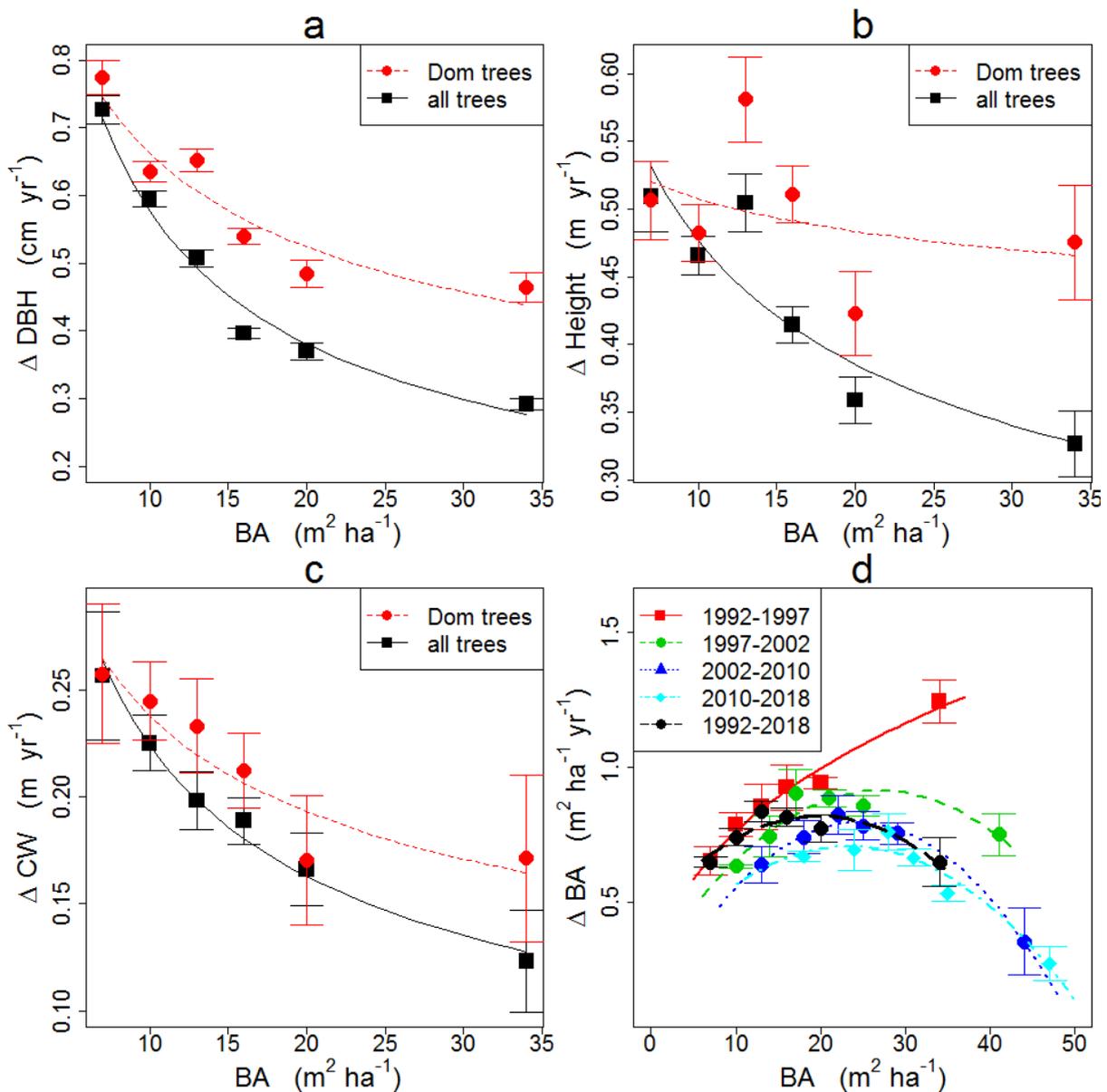


Fig. 2 Effect of stand density on growth (1992 to 2018) of; (a) DBH, (b) height, (c) CW, (d) stand BA. The error bars represent standard error. Δ denotes annual growth. BA values on the x-axis represent the retained BA at the start of the growth period.

3.2 Effect of thinning on individual tree and stand level growth

Growth of individuals' DBH, height and CW increased with a decrease in stand density for both all trees and dominant trees; however, the increment was higher for dominant trees compared to all trees (Fig. 2a, b, c, S3). The DBH, height and CW growth of all trees in lowest density (heavily

thinned) plots were 149%, 56%, 108% higher than the growth in highest density (unthinned) plots respectively. At the individual tree level, growth of DBH and growth of height increased with an increase in DBH across all thinning treatments (Fig. 3a, b). Growth of CW decreased with an increase in DBH for trees growing in low stand density (T5-T6) and grew at a relatively constant growth rate at intermediate density (T2-T4). At the highest stand density (T1), growth of CW increased significantly ($P < 0.05$) with an increase in DBH (Fig. 3c). Growth of DBH, stand basal area and stem number per ha differed significantly ($P < 0.05$) with thinning treatments at all growth periods (Table S2). Growth of height differed significantly ($P < 0.05$) with thinning treatments only during 2010 to 2018. Growth of CW differed significantly with thinning treatments only during 1992 to 1997 ($P < 0.05$) (Table S2). Growth of DBH and stand BA was higher and significantly different in the first growth period (1992-1997) compared to others and gradually decreased with increasing time from the second growth period (1997-2002) (Fig. 2d, 3d). In overall growth period (1992 to 2018) growth of stand BA peaked at intermediate stand densities ($13 \text{ m}^2 \text{ ha}^{-1}$) (Fig. 2d). This peak was not evident in the first growth period but was in all subsequent growth periods. Stand BA growth at an intermediate thinning treatment ($13 \text{ m}^2 \text{ ha}^{-1}$), was 28.7% higher than the growth in lowest stand density (heavily thinned plots) and 29.0% higher than the growth in highest stand density (unthinned plots). Overall, the growth rate of karri is moderately fast when compared to jarrah and marri. Thinning operation increased the variability in size (DBH) of individual trees. In thinned plots, the standard deviation of DBH was 4.08 cm in 1992 and 8.45 cm in 2018 (net increase of 4.36 cm in 26 years) whereas in unthinned stand, the standard deviation of DBH was 6.32 cm in 1992 and 7.87 cm in 2018 (net increase of 1.54 in 26 years) (Fig. 4f).

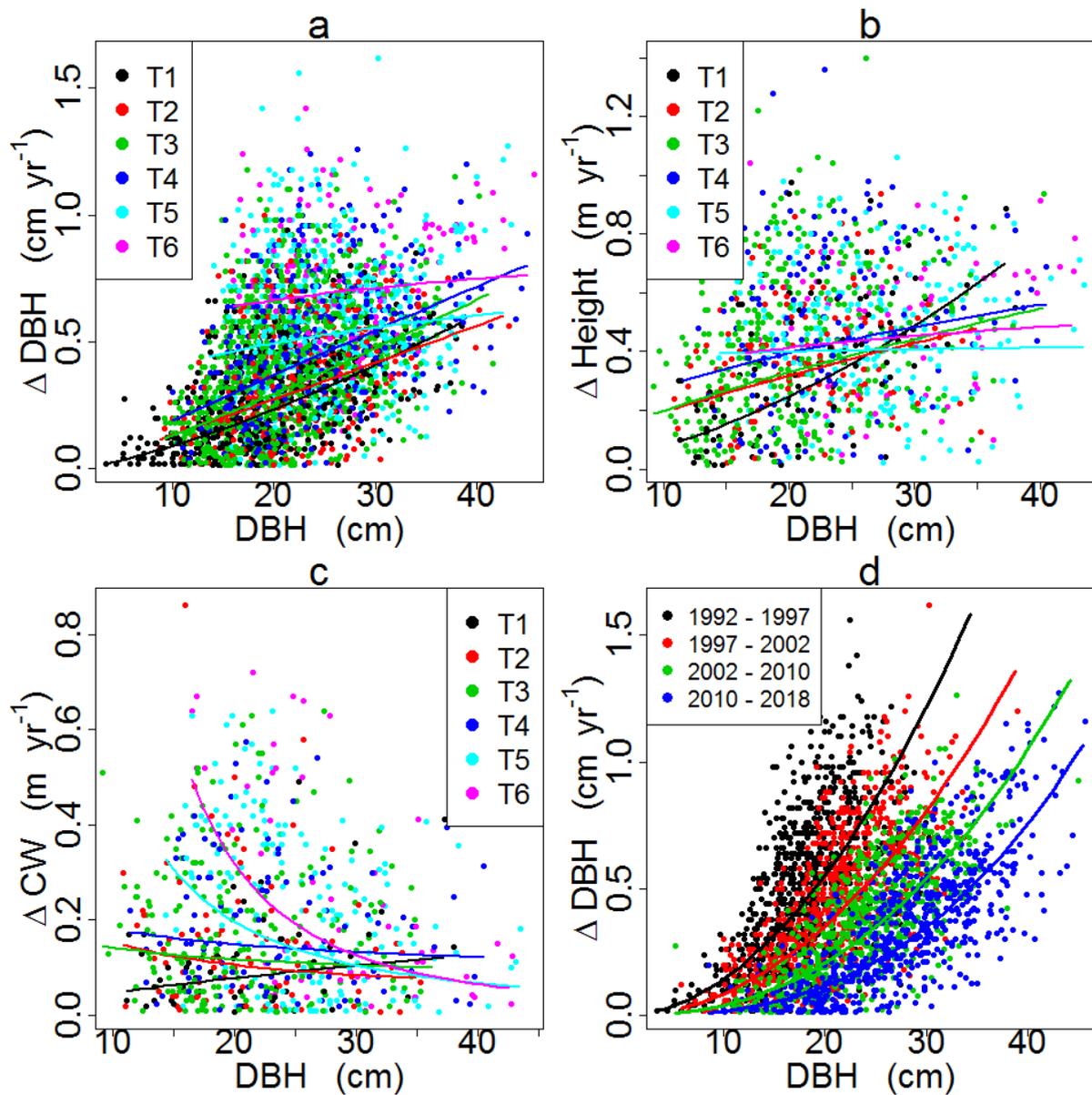


Fig. 3 Effect of stand density on growth (1992 to 2018) with respect to DBH; (a) DBH, (b) height, (c) CW, (d) Effect of time-period on DBH growth. Δ denotes annual growth.

3.3 Allometric relationship between DBH and height

All the parameters of all 13 equations of DBH-height allometry were highly significant ($p < 0.001$) (Table S1). Model M1 performed best, with the highest R^2 (0.7630), and the lowest RMSE (2.66 m) and AIC (7191), followed by M2, M3, M4 and M5 (Table 2). However, the difference among these five allometric equations was very small in terms of visual fit (Fig. 4a) and fit statistics

and mean estimates (Table 2). We did not see any systematic deviation of residuals against explanatory variables, but the variance of residuals was larger for trees of $DBH > 40$ cm as there were very few trees > 40 cm DBH (Fig. 4a, b). From the analysis of fit statistics and residual distribution, we selected model M1 as the best model for predicting height from DBH (Table 2).

Table 2 Parameter values and fit statistics of different allometric equations for tree height and DBH (H=height in m, D=DBH in cm, b1, b2, b3 are parameters that was 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	$H = 1.3 + \frac{D^2}{(b_1 + b_2 D + b_3 D^2)} + \varepsilon_{ij}$	Huang et al. (1992)	b ₁ = -1.983 b ₂ =0.880 b ₃ =0.011	0.763	2.667	7191.28
M2	$H = 1.3 + b_1 \exp\left\{\frac{b_2}{D + b_3}\right\} + \varepsilon_{ij}$	Ratkowsky (1990)	b ₁ =77.175 b ₂ =-54.393 b ₃ =20.057	0.763	2.668	7191.42
M3	$H = 1.3 + b_1 + b_2 D + b_3 D^2 + \varepsilon_{ij}$	Staebler (1954)	b ₁ =4.409 b ₂ =0.873 b ₃ = -0.005	0.763	2.667	7191.33
M4	$H = 1.3 + b_1 D^{b_2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	b ₁ =2.769 b ₂ =0.657	0.762	2.667	7191.32
M5	$H = 1.3 + b_1 \exp[-b_2 \exp(-b_3 D)] + \varepsilon_{ij}$	Winsor (1932)	b ₁ =43.264 b ₂ =1.870 b ₃ =0.043	0.762	2.669	7193.17

3.4 Effect of thinning on allometric relationships

Thinning had a significant effect on allometry of DBH with height and HDR in all measurement times ($P < 0.001$) except in 1992 ($P > 0.05$) (Fig. S3). Thinning had a significant effect on allometry of DBH with CW in 1992 ($P < 0.001$), 1997 ($P < 0.001$) and 2002 ($P = 0.001$), however, not in 2010 ($P = 0.84$) and 2018 ($P = 0.68$). Height and CW increased with an increase in DBH, but HDR decreased (Fig. 4c, d, e).

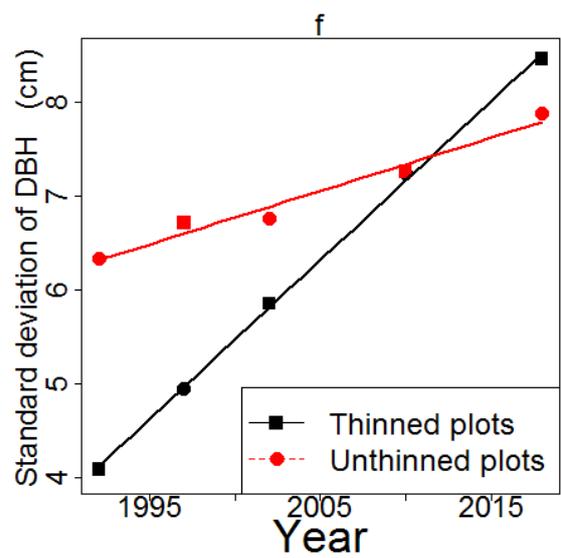
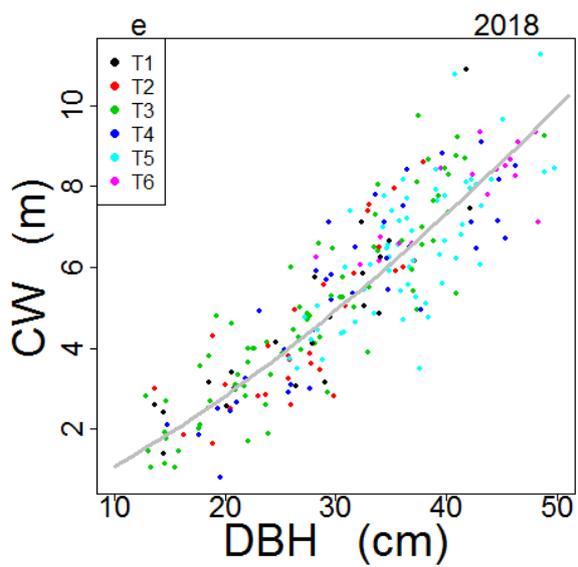
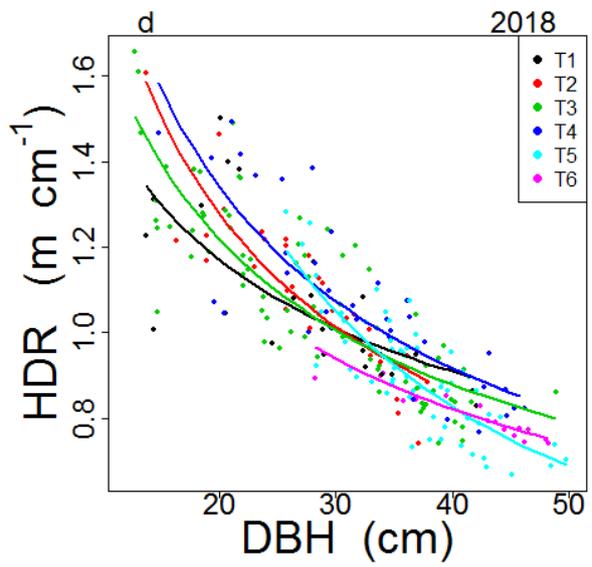
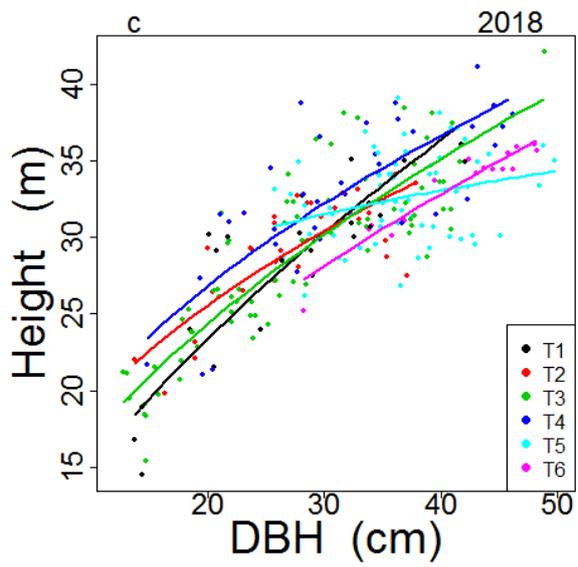
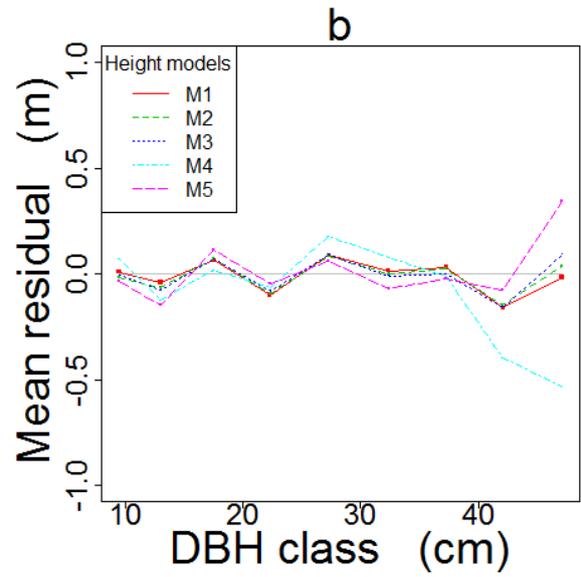
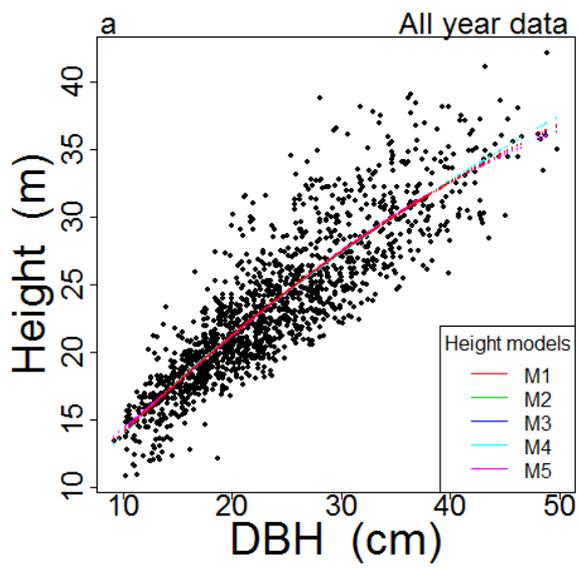


Fig. 4 (a) Curves of the five best DBH height allometry models overlaid on the observed data; (b) Mean residual from predicted height by DBH class of height DBH allometry models; (c) Effect of stand density on allometry of DBH with height; (d) Effect of stand density on allometry of DBH with HDR; (e) Effect of stand density on allometry of DBH with CW; (f) standard deviation of DBH in thinned and unthinned plots at different measurement periods.

4 Discussion

4.1 Effect of thinning on growth

This study showed higher growth of DBH and CW in plots with lower stand densities and confirms the trend reported by Bradshaw (2015a) for other even-aged regrowth stands of karri. Similar trends were found by Stoneman et al. (1996) in jarrah (*E. marginata*) and by Acuna et al. (2017) in *Eucalyptus globulus* in SWWA. Reductions in stand density not only decrease competition, leaf area index and water loss due to transpiration (Stoneman et al. 1989c; FPC 2018) but also increase access to light, nutrients and water by the retained trees (Stoneman et al. 1989c; Stoneman et al. 1996; Bradshaw 2010; DPAW 2012). The higher the access to light, nutrients and water of individual trees, the greater the rate of photosynthesis (Stoneman et al. 1996; Koch and Ward 2005). Reduced shoot water stress due to decreased stand density can further increase diameter growth rates because plants favour allocation of more photosynthates to shoots than roots (Begg and Turner 1976; Gower et al. 1992). The high growth of individual trees observed in low density plots is also associated with the thinning method (thinning from below). Thinning from below retains the largest and fastest-growing trees. This may have resulted in a higher growth rate than would be possible using other thinning methods. For example, thinning from above removes the taller trees from the stands which may result in lower growth rates than thinning from below.

We found that height growth was related inversely to stand density (Fig. 2b). This result is consistent with Koch and Ward (2005) and Bhandari et al. (2021) or chapter 2 of this thesis, who also found greater height growth of jarrah in plots with low stand density. Nineteen percent more height growth was reported in a thinned stand of *Eucalyptus globulus* in SWWA when compared to an unthinned stand (Acuna et al. 2017) which is lower than 56% observed in this study. Overall, thinning had a smaller positive effect on height growth than on DBH growth, which was increased by 149% compared to unthinned stand (Fig. 2a). Moreover, height growth of dominant trees was not significantly affected by thinning (Fig. 2b), in contrast to DBH growth. This suggests that thinning has little effect on height growth of dominant trees compared to DBH growth (Bhandari et al. 2021 or chapter 2). Other studies have shown that while thinning may increase height, such increases may be small and insignificant (Fedorova et al. 2016; Medeiros et al. 2017). Height growth of dominant trees is more influenced by site quality than thinning or other management interventions (Assmann 1970).

Growth in DBH and stand BA was highest in the first growth period (1992-1997) after thinning and then it decreased gradually in other growth periods (Fig. 2d, 3d). Two reasons may explain the decreasing trend of growth in consecutive growth periods after thinning. 1) the thinned plots have increased in basal area, with a corresponding increase in the level of inter-tree competition, so DBH and stand BA increment of individual trees has slowed. 2) a decreasing rainfall trend at the study site. The average annual rainfall 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 2019). The small difference in mean rainfall for the first three growth periods suggest that a decrease in rainfall is unlikely to be the principal factor explaining decreasing growth rate, however, the lower annual rainfall in the fourth growth period could have been a contributing factor. Increasing stand density with time likely affected growth most (Fig. 2d, 3d).

We observed a different pattern of BA growth at the stand-level for karri forest compared to the individual tree level. Over the whole period, stand BA growth was highest at intermediate thinning intensities (Fig. 2d). This suggests that intermediate levels of thinning are likely to optimize growth at the stand level, which is consistent with observations reported by Moller (1954), Assmann (1970), Grigg and Grant (2009), Pretzsch (2009) and Bradshaw (2015a, 2015b). Assmann (1961 and 1970) described how volume or stand basal area growth increases with a reduction in stand density up to a certain optimum, and then decreases with a further reduction in stand density. The reason why this pattern occurs is because, at low stand density, inter-tree competition is reduced, and individual trees have ready access to light, moisture, and nutrients. This results in higher diameter growth of individual trees; however, stand level growth is not at full potential because the number of trees is insufficient to fully occupy the site. At higher stand densities, reduced stand BA growth is thought to be due to greater competition, resulting in a higher proportion of assimilates being used for respiration and leaf formation so a lower proportion of assimilates is available for diameter growth (Stoneman et al. 1996). Understanding this pattern of growth is critical for designing optimal thinning management strategies.

Thinning of even-aged regrowth forest has potential to produce forests with enhanced structural complexity as illustrated by the higher degree of variation in size of individual trees in thinned plots compared to unthinned plots (Fig. 4f). Variation in tree size and growth is a result of variation in post-thinning growing space primarily in plots with the greatest reduction in stand density. This in turn provides a greater variety of niches and habitats for a wider range of wild species than unthinned forests with low structural complexity (CCWA 2004; McElhinny et al. 2005; McElhinny et al. 2006). Up to 11 mammal, 17 bird and one reptile species are totally dependent on hollows in standing trees for successful breeding in the forests of SWWA (Abbott and Whitford 2002). Older trees having large and /or senescent crowns have a higher chance of bearing hollows

which may be used as nesting sites by these species (Whitford 2002; Whitford and Williams 2002; Whitford and Stoneman 2004; Whitford et al. 2015). The average age of the trees in this study is about 50 years and the availability of tree hollows would be expected to increase progressively over the next four to six decades. In addition, large karri trees growing in low density stands have the potential to produce greater quantities of fruits and seeds which form a major part of the diet of arboreal animals (Bradshaw 2015a).

The trees produced as a result of thinning have a greater market value for timber because the larger logs yield higher recovery of sawn materials. Gross volume is likely to be higher in unthinned stands but most of this volume will be in small trees and therefore will only find markets for residue products of low commercial values. Besides improvement in growth and habitat of arboreal fauna, thinning has also been reported to increase water discharge in forest catchment (Borg et al. 1987; Stoneman et al. 1989; Bari et al. 1996; Bari and Ruprecht 2003; Hawthorne et al., 2013), increase drought resistance through minimizing moisture stress (Bradshaw 2015a) and promote regeneration to achieve the goal of sustainable forest management (Wang et al. 2019).

4.2 Effect of thinning on allometric relationships

No significant differences amongst treatments for DBH-height and DBH-HDR allometry were observed in 1992, reflecting the fact that retained trees had not yet responded to thinning. It is also observed that the thinning operation didn't introduce an allometric bias. Stand growth from 1992 to 2018, with different stand densities as a result of thinning in 1992 and natural mortality, introduced a different growth pattern or rate on DBH and height of individual trees. Because of different rate of growth on DBH and height because of thinning, we found a significant effect of thinning on allometry of DBH with each of height, HDR and CW in subsequent measurement times ($P < 0.001$) except in 2010 and 2018 for the DBH-CW allometry. Similar results for the effect of thinning on DBH-height

allometry were reported by Zhang et al. (1997), Deng et al. (2019) and Bhandari et al. (2021) or Chapter 2 of this thesis. Sumida (2015) and Trouvé et al. (2015) reported a higher radial growth and lower height growth in trees growing in open stand. Lines et al. (2012) and Forrester et al. (2017) found that competition played a determining role in the allometry of DBH and height. Variation in allometric relationships with a change in stand density suggested that those relationships were not static and represent the growth response of individual trees to thinning (Forrester et al. 2017).

In open stand there is no competition for light and therefore trees do not prioritise height growth. On the other hand, individual trees grown in open stand have larger crown and more leaf area. The larger amount of leaf area may induce hydraulic and mechanical constraint which may have prioritise radial growth in open stand (Trouvé et al. 2015). Individual trees growing in low-density stands prioritise diameter growth while individual trees growing in high stand density prioritise height growth (Metzger 1893; Kim et al. 2016; Forrester et al. 2017; Bhandari et al. 2021 or chapter 2). Because of the unidirectional nature of light, the height of individual trees plays an important role in light interception and thus, height may become a major determinant of growth of individual trees in dense stands (Weiner and Fishman 1994). Plastic response of height growth of individual trees is mainly caused by light competition and the height growth is restricted when the intensity of light competition becomes very strong (Xiao et al. 2006). Height growth is less sensitive to reduction in stand density while DBH growth is more sensitive. Our study showed the same trend with a higher rate of DBH growth resulting in lower HDR for trees growing at a low stand density. Individual trees having lower HDR are stronger and more stable than trees having higher HDR (Wilson and Oliver, 2000; Wonn and O'Hara 2001; Pretzsch 2009). Understanding different patterns of growth in DBH and height due to thinning may help guide forest management decisions. For example, the forest could be managed in denser stands to produce longer and more cylindrical stems. Alternatively, the forest

could be managed in less dense stands to produce shorter but stronger stems (Chaturvedi and Khanna 2011).

5 Conclusions

Results from this study spanning 26 years revealed that karri is a moderately fast-growing tree species. Thinning has shown evidence that the growth rate of karri is partly controlled by competition, as trees grow faster when partly released from the competition. DBH growth of trees growing at the lowest stand density was 1.49 times more than the trees growing in highest stand density, however, stand level basal area growth was maximum at intermediate levels of stand density. As the effect of stand density on DBH and height growth was different, we observed a significant effect of stand density on allometry between DBH and each of height, HDR and CW. Large-sized trees resulting from thinning may be healthier and are likely to provide a greater volume of timber, and possibly other ecological benefits such as habitat for wildlife, and thinning may also provide incidental benefits such as firewood. Thus, thinning may be a useful tool in the sustainable management of even-aged regrowth karri forest delivering large sized trees.

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Supplementary materials: S2

Table S1 Parameter values and fit statistics of different height DBHOB allometric equations of karri (H=height in m, D=DBHOB in cm, b_1 , b_2 , b_3 are parameters to be estimated). A constant value 1.3 is the height of the stem above the ground level at which DBH was measured and this constant value was added in the equation to avoid prediction of zero height when DBH approaches zero.

Model	Equation	References	Parameter value	R ²	RMSE	AIC
M1	$H = 1.3 + \frac{D^2}{(b_1 + b_2 D + b_3 D^2)} + \varepsilon_{ij}$	Huang et al. (1992)	b ₁ = -1.983	0.763	2.667	7191.28
b ₂ =0.880						
b ₃ =0.011						
M2	$H = 1.3 + b_1 \exp\left\{\frac{b_2}{D + b_3}\right\} + \varepsilon_{ij}$	Ratkowsky (1990)	b ₁ =77.175	0.763	2.668	7191.42
b ₂ =-54.393						
b ₃ =20.057						
M3	$H = 1.3 + b_1 + b_2 D + b_3 D^2 + \varepsilon_{ij}$	Staebler (1954)	b ₁ =4.409	0.763	2.667	7191.33
b ₂ =0.873						
b ₃ = -0.005						
M4	$H = 1.3 + b_1 D^{b_2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	b ₁ =2.769	0.762	2.667	7191.32
b ₂ =0.657						
M5	$H = 1.3 + b_1 \exp[-b_2 \exp(-b_3 D)] + \varepsilon_{ij}$	Winsor (1932)	b ₁ =43.264	0.762	2.669	7193.17
b ₂ =1.870						

			b ₃ =0.043			
M6	$H = 1.3 + \frac{b_1}{1 + b_2 \exp(-b_3 D)} + \varepsilon_{ij}$	Pearl and Reed (1920)	b ₁ =38.56 b ₂ =19.34 b ₃ =14.30	0.762	2.673	7197.19
M7	$H = 1.3 + b_1\{1 - \exp(-b_2 D)\} + \varepsilon_{ij}$	Meyer (1940)	b ₁ =43.70 b ₂ =0.03	0.759	2.684	7208.99
M8	$H = 1.3 + \left\{ \frac{D}{b_1 + b_2 D} \right\}^3 + \varepsilon_{ij}$	Naslund (1936)	b ₁ =0.91 b ₂ =0.004	0.759	2.686	7210.84
M9	$H = 1.3 + b_1 \left\{ \frac{D}{(D + 1)} \right\} + b_2 D + \varepsilon_{ij}$	Watts (1983)	b ₁ =8.26 b ₂ =0.59	0.759	2.689	7214.11
M10	$H = 1.3 + \frac{b_1 D^2}{(D + b_2)^2} + \varepsilon_{ij}$	Hossfeld (1822)	b ₁ =50.90 b ₂ =11.78	0.753	2.717	7245.46
M11	$H = 1.3 + \exp\left\{b_1 + \frac{b_2}{(D + 1)}\right\} + \varepsilon_{ij}$	Wykoff et al. (1982)	b ₁ =3.80 b ₂ =-16.53	0.744	2.769	7302.35
M12	$H = 1.3 + b_1 \exp\left(\frac{b_2}{D}\right) + \varepsilon_{ij}$	Buford (1986)	b ₁ =43.41 b ₂ = -15.04	0.740	2.791	7325.95
M13	$H = 1.3 + b_1\{1 - \exp(-b_2 D)\}^3 + \varepsilon_{ij}$	Bertalanffy (1949)	b ₁ =30.13 b ₂ =0.10	0.702	2.990	7531.57

Table S2 Effect of stand density on growth and allometric variables of karri at different time periods (Note: * significant at 95%; **significant at 99%; *** significant at 99.9%, ^{ns}not significant). Sig (growth) means significance of growth of the variables between two consecutive growth periods. Sig (retained) means significance on the retained values the variables at the beginning of each growth period.

Year	variables	Thinning						sig. (growth)	sig. (retained)
		T1	T2	T3	T4	T5	T6		
1992	DBH	12.28	18.03	17.33	19.44	20.38	20.79		***
	Height	17.08	18.41	18.13	19.55	20.42	20.15		**
	CW	3.49	3.34	3.01	3.20	3.59	3.65		ns
	BA (m ² ha ⁻¹)	34.42	20.06	15.61	13.05	10.10	6.93		***
	Stem ha ⁻¹	2116	722	615	418	300	200		***
1997	DBH	14.85	20.16	19.78	22.41	24.12	25.27	***	***
	Height	18.84	20.26	20.44	22.28	22.80	22.87	ns	**
	CW	3.90	4.44	4.22	4.61	5.44	6.12	***	***
	BA (m ² ha ⁻¹)	40.64	24.77	20.64	17.32	14.03	10.19	***	***
	Stem ha ⁻¹	1872	722	608	418	300	200	**	***
2002	DBH (cm)	17.40	22.05	21.90	25.15	27.31	29.00	***	***
	Height (m)	20.47	22.36	22.50	24.88	24.99	25.62	ns	**
	CW (m)	4.00	4.73	4.41	4.91	5.79	6.37	ns	***
	BA (m ² ha ⁻¹)	44.38	29.06	25.06	21.84	17.74	13.36	***	***
	Stem ha ⁻¹	1650	716	606	418	297	200	**	***

2010	DBH (cm)	21.35	24.67	24.55	28.58	31.53	34.07	***	***
	Height (m)	23.85	25.19	25.19	27.77	28.22	28.01	ns	*
	CW (m)	4.07	4.63	4.43	5.12	6.11	7.22	ns	***
	BA (m ² ha ⁻¹)	46.95	35.10	31.32	28.44	23.67	18.48	***	***
	Stem ha ⁻¹	1294	688	600	418	297	200	**	***
2018	DBH (cm)	25.90	27.64	27.25	32.02	35.23	38.72	***	***
	Height (m)	28.47	29.15	28.77	32.95	32.68	33.12	**	**
	CW (m)	4.57	4.50	4.82	5.42	6.47	7.74	ns	**
	BA (m ² ha ⁻¹)	49.14	39.36	36.64	34.52	29.23	23.83	***	***
	Stem ha ⁻¹	1016	638	571	403	295	200	***	***

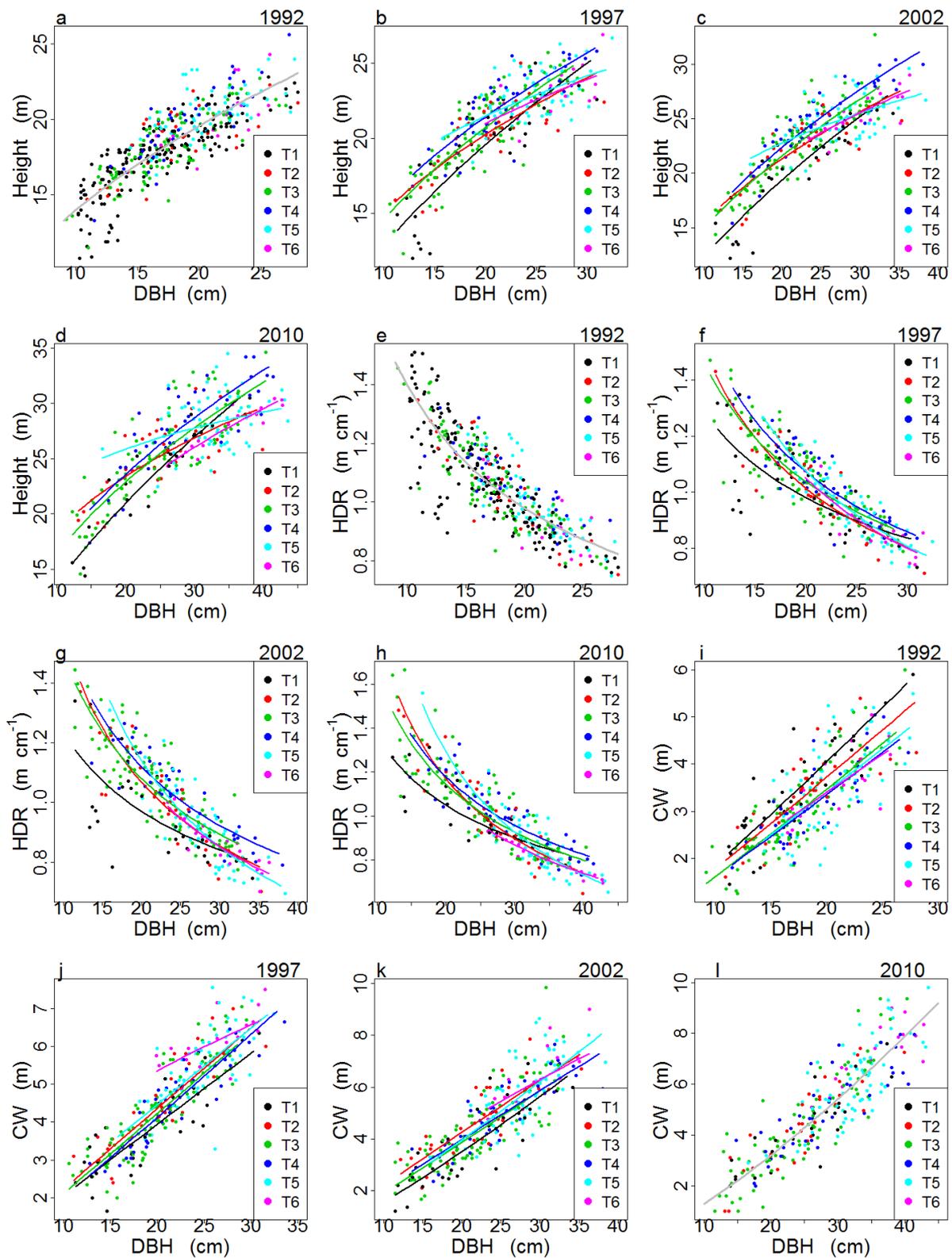


Fig. S3. Effect of stand density on allometry of DBH with (a) height in 1992, (b) height in 1997, (c) height in 2002, (d) height in 2010, (e) HDR in 1992, (f) HDR in 1997, (g) HDR in 2002, (h) HDR in 2010, (i) CW in 1992, (j) CW in 1997, (k) CW in 2002, (l) CW in 2010.

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CHAPTER 4

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

PREAMBLE

This chapter presents the long-term effect of thinning on individual tree and stand level growth and allometry between diameter at breast height (DBH) and each of height, crown width and height diameter ratio of *Corymbia calophylla*.

It is presented as the manuscript intended to submit at *Australian Forestry*. Formatting is that specified by the journal with the exception of page numbering. S3 is the supplementary materials for online submission with the manuscript.

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

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Abstract

Marri (*Corymbia calophylla*), an endemic and keystone tree species of South-west Western Australia (SWWA), provides significant environmental, conservation, economic and cultural values. This study aimed 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); however, DBHUB and CW were not significantly related. Height and CW increased with an increase in DBHUB but HDR decreased. Thinning has the potential to increase yields of timber and firewood.

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

1 Introduction

Marri (*Corymbia calophylla* (R. Br. ex Lindl.) K.D. Hill & L.A.S. Johnson), previously known as *Eucalyptus calophylla* (Hill and 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 (*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, furniture, flooring, 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 DBH 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 DBH growth (Zhang et al. 1997; Bhandari et al. 2021 or Chapter 2). In unthinned stands, greater competition for sunlight may lead to prioritization of vertical growth (Chaturvedi & Khanna, 2011; Kim et al., 2016). Because of the different nature of DBH and height growth, it is always important to analyse the effect of thinning on DBH-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, forest fire, drought and pathogens (Kimber 1981; Bradshaw 2012; Taylor et al. 2012; Paap et al. 2016, 2017, 2018;

Sapsford 2017) 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. In order 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. 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).

2 Materials and methods

2.1 Study area

The study was conducted at Sutton Forest block (34° 28' S, and 116° 20' E) 38 km south-east 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). Monthly maximum and minimum temperatures range from 30.7°C in February to 12.3°C in July (BOM 2019). The soils of the study site are mainly yellow and gravelly texture-contrast soils, formed on weathered mottled and pallid zone material (McArthur 2004).

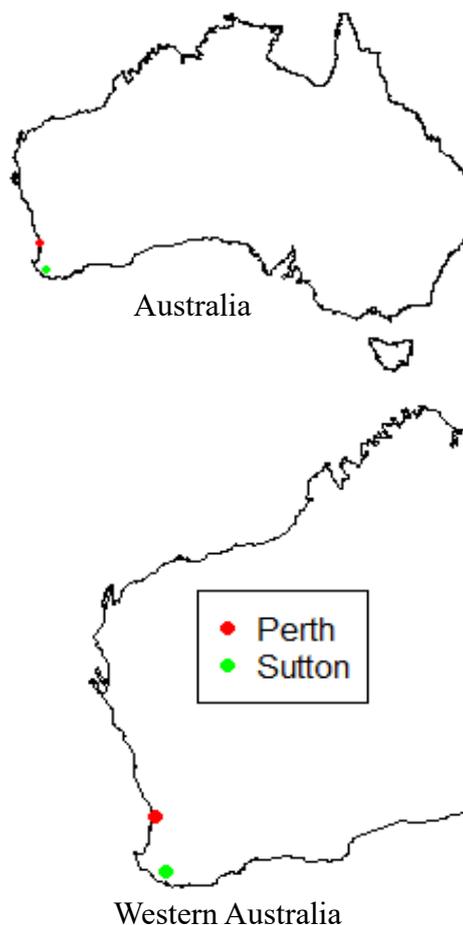


Figure 1. Map of Australia showing study site

2.2 Treatment (thinning / stand densities)

The thinning trial of 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 received the same intensity of thinning as the plot, but the tree measurements were carried out in the inner 30 m x 30 m. Thinning plots were established, and were assumed 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 the present paper, we analysed the 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 in Chapter 3 and chapter 6 of this thesis. 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) m² ha⁻¹ basal area under bark (BAUB, total for all species present). The BAUB of only marri trees in those treatment in 1992 was 15.2 (T1), 9.4 (T2), 8.1 (T3) and 5.3 (T4) m² ha⁻¹. T1 is the unthinned (control) and T2, T3 and T4 represent an increasing order of thinning intensity. These stands had very high stem density at the time of initial thinning but did not appear to be fully stocked in terms of basal area per ha.

2.3 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 at or near the centre of each plot were selected for measurement of height and CR. 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 all four directions. Under bark DBH (DBHUB), HDR and CW were calculated from the field measured variables. The DBHUB was calculated by subtracting twice the average bark thickness from the DBHOB. 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). The dominance was measured in 1992 when the trees were measured after establishment of the thinning trial.

2.4 Data analysis

2.4.1 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.

2.4.2 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.

2.4.3 Allometric relationship between DBH and height

Nine different linear and non-linear allometric equations (Table S1) 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.

2.4.4 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: $\log(\text{height}) \sim \log(\text{DBHUB}) * T$, 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.

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 is also shown. Note: all variables except BAUB (m² ha⁻¹) and Stem number per hectare (ha⁻¹) are presented for only marri trees. BAUB (m² 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 (21.62)	T2 (11.65)	T3 (9.91)	T4 (6.44)	df	F-value	p-value
DBHUB (cm)	15.7±0.5	21.8±0.5	27.78±0.8	30.2±1.2	3/4	44.53	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	15.68	0.007
Height (m)	20.4±0.6	21.1±0.6	23.7±0.7	25.8±1.1	3/4	5.07	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	13.33	0.010
Height-DBHUB ratio (m cm ⁻¹)	1.05±0.02	0.97±0.02	0.86±0.02	0.85±0.03	3/4	11.61	0.019
Crown width (m)	3.3±0.2	3.3±0.2	4.5±0.3	4.7±0.4	3/4	6.83	0.047
BAUB all species (m ² ha ⁻¹)	42.71±4.7	29.81±2.8	26.47±3.4	19.00±1.2	3/4	175.00	<0.001
Stem number per hectare all species (ha ⁻¹)	1905±383	655±67	361±28	238±39	3/4	14.66	0.012

3 Results

3.1 Effect of treatment on individual tree and stand level variables

Table 1 shows the arithmetic mean values and standard errors of different variables at the individual tree and stand levels for different stand densities at the end of the growth period (2018). Diameter and CW significantly increased ($P < 0.05$) with a decrease in stand density, but HDR, stand BAUB and number of trees per ha decreased significantly ($P < 0.05$). 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 S2) except the CW in 1992 and height in 1992, 1997, 2010 and 2018. Unthinned plots of marri had 32% fewer individual trees in 2018 than in 1992, a net change of $1.22\% \text{ yr}^{-1}$. We note that the number of replicate plots in each thinning treatment is low, meaning the power of the analysis is relatively low, and so significant results indicate that differences are quite clear.

Table 2. Parameter values and fit statistics of different allometric equations for tree height and DBHUB (H=height in m, D=DBHUB in cm, b1 and b2 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	$H = 1.3 + b_1 + b_2D + \varepsilon_{ij}$	Linear model	b ₁ =6.71 b ₂ =0.56	0.751	1.89	2252
M2	$H = 1.3 + b_1 \left\{ \frac{D}{(D + 1)} \right\} + b_2D + \varepsilon_{ij}$	Watts (1983)	b ₁ =7.47 b ₂ =0.54	0.751	1.89	2251
M3	$H = 1.3 + b_1D^{b_2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	b ₁ =2.78 b ₂ =0.62	0.752	1.89	2251

3.2 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 both all trees and 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. These differences in growth between thinned and unthinned treatment may be considered small in an absolute sense, but these are very slow-growing trees, so large absolute differences are not expected. They are still ecologically significant, and likely to be more significant in terms of competition. 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, 3b) 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).

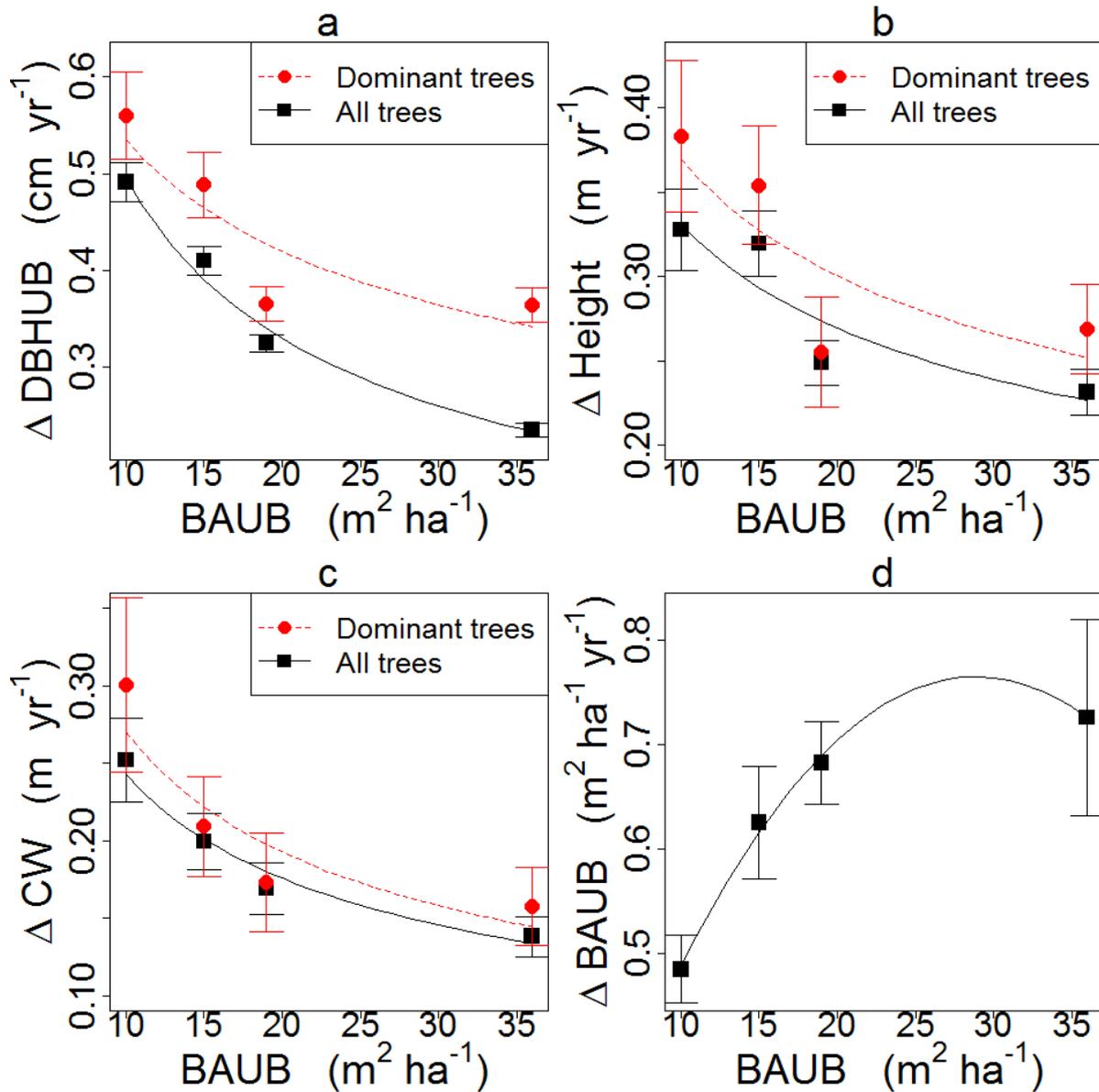


Figure 2. Effect of stand density on annual growth (1992-2018) of (a) DBHUB, (b) height, (c) CW, (d) stand BAUB. Δ denotes annual growth. Error bars denote standard error.

3.3 Allometric relationship between DBHUB and height

All parameters of all nine height-DBHUB allometric equations were highly significant ($p < 0.001$) (Table 2, Table S1) but equations M1, M2 and M3 produced higher R^2 , lower RMSE and AIC (Table 2, Table S1) 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.

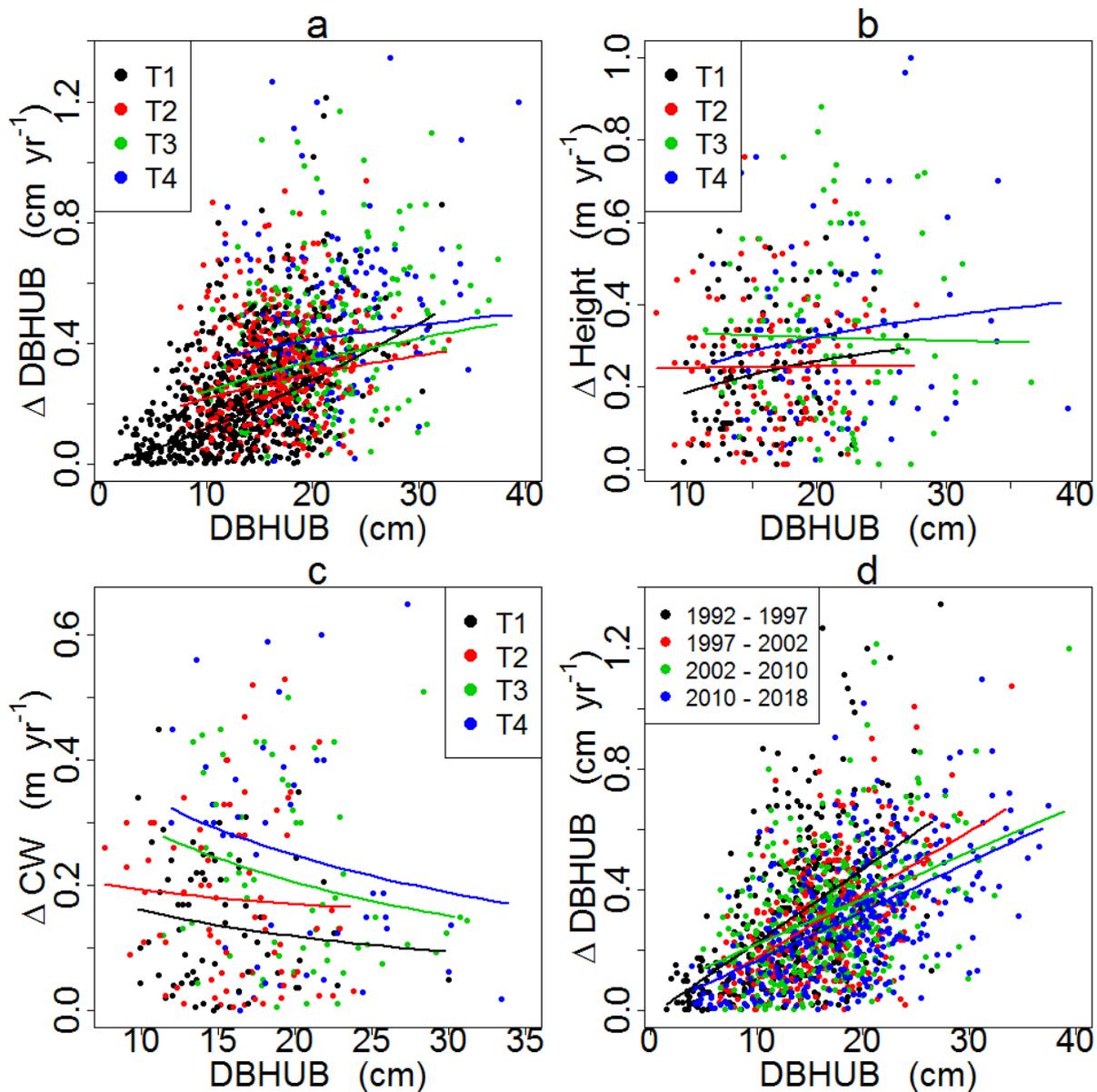


Figure 3. Effect of stand density on annual growth (1992-2018) with respect to DBHUB; (a) DBHUB, (b) height, (c) CW, (d) Effect of time period on DBHUB growth. Δ denotes annual growth.

3.4 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 ($P=0.24$) (Fig 4c,

S3). The differences among thinning treatments were similar for 1992, 1997 and 2002. The allometric relationship between HDR and DBHUB differed significantly with stand density (or thinning treatment) in 1992 ($P=0.03$), 1997 ($P=0.003$), 2002 ($P=0.004$), but not in 2010 ($P=0.14$) and 2018 ($P=0.11$) (Fig 4d, S3). The allometric relationship between CW and DBHUB did not differ significantly with stand density (or thinning treatment) in any of the measurement years (Fig 4e, S3). Height and CW increased with an increase in DBHUB, however, HDR decreased (Fig. 4a, c, d, and e).

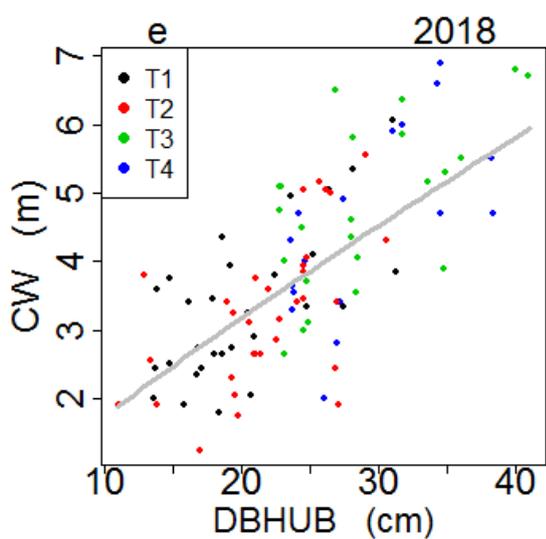
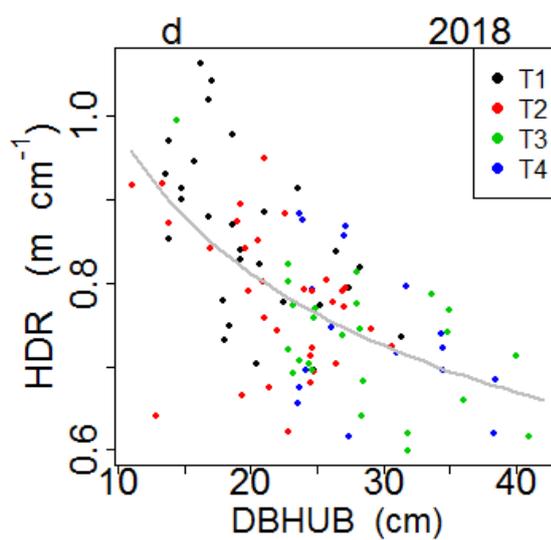
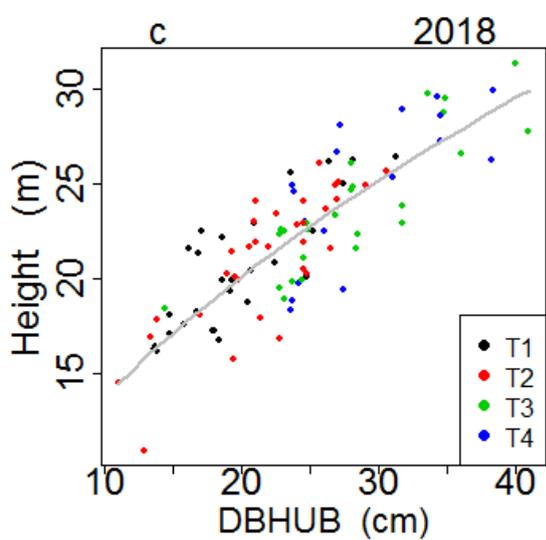
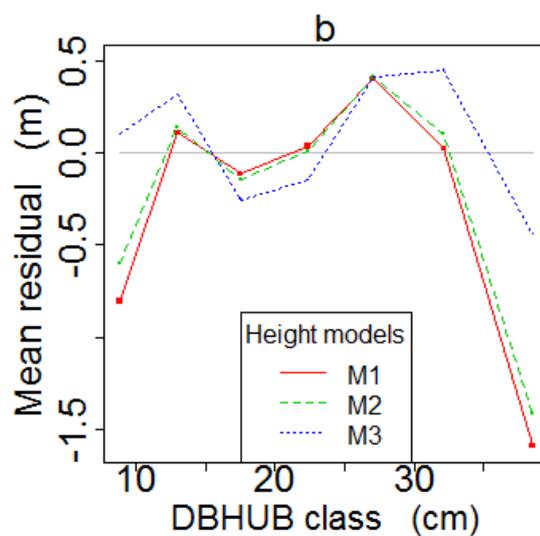
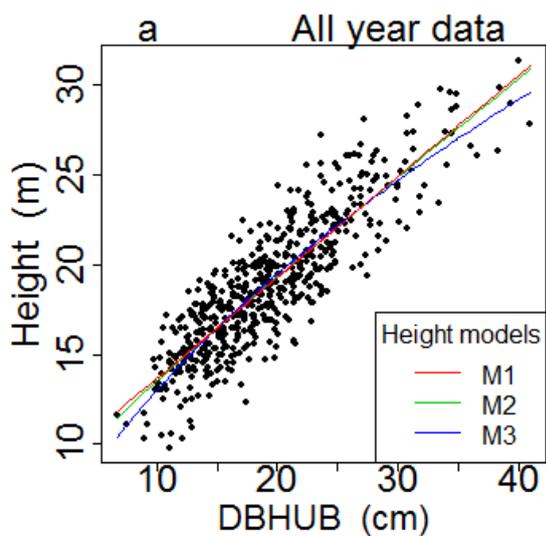


Figure 4. (a) Curves of the different DBHUB height allometry models overlaid on the observed data, (b) Mean residual from predicted height by DBHUB class of height DBHUB allometry models, (c) Effect of stand density on allometry of DBHUB with height, (d) Effect of stand density on allometry of DBHUB with HDR, (e) Effect of stand density on allometry of DBHUB with CW. The grey lines in c,d, and e represent overall allometric relationships between variables for all thinning treatments.

4 Discussion

4.1 Effect of treatments on individual tree and stand level variables

Low stand densities resulting from heavier thinning led to higher values of mean DBHUB, height and CW at the end of the 26-year study period. In addition, 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. (2021) or Chapter 2. Chapter 3 of this thesis found similar results in the 26-year thinning experiment in karri plots at the same experimental site of this study.

4.2 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. 2021 or Chapter 2). 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. (2021) or Chapter 2 of this thesis found that DBH growth increased continuously with an increase in thinning intensity, but the same effect was not observed consistently for height growth. Similar results were reported for the karri forest of SWWA (Chapter 3). The inconsistent effect of thinning on height growth may be because height growth is relatively less sensitive to stand density or thinning, whereas diameter growth is more sensitive to stand density or thinning. In dense plots, the individual trees tend to invest relatively more in height growth than in diameter growth 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 unthinned plots (1.05) (Table 1). 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 (Chapter 5 and 6).

Consistent with other studies (Janik et al. 2018; Bhandari et al. 2021 or Chapter 2; Chapter 3), we also found that trees with larger DBHUB had higher DBHUB growth and higher height growth except for T2 and T3 (Fig. 3a, b). This suggests that the DBHUB growth and height growth of individual trees of marri are still increasing and have not reached their peak. It is to be expected that DBH growth and height 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 it decreased gradually in later growth periods (Fig. 3d). 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 2019). 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. Another possible reason may be that trees of equal size (DBHUB) have different social positions and thus show different productivity levels across the different time points.

The present study showed an increase in growth of stand BAUB with an increase in stand density (Fig. 2d). 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 high 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), Bradshaw (2015a, 2015b), Bhandari et al. (2021) or Chapter 2 and Chapter 3. These studies did find that 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 (unthinned) stand in our study may be that this regrowth forest of relatively young age had not yet reached the critical density of trees where competition and tree allometry reduce growth rates. This is likely because the stand might not have been at the full stocking level at the initial thinning time. This highlights the lack of stocking tools/metrics available to guide stand level silviculture (esp. thinning) in Australia,

in contrast to wide range available in Europe and North America. 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 (karri which is generally large in diameter and height compared to marri), 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 m² ha⁻¹ which was the basal area range where the other studies (Bhandari et al., 2021 or Chapter 2) found reduced tree growth and so the relationship between stand density and basal area increment in denser marri stands remains uncertain.

Thinned stands resulted in a higher proportion of large marri trees on average than in unthinned stands and more intensely thinned stands had larger trees on average than less intensely thinned stands. 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). 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 crowns 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 conclusion, conservation of marri trees is of high importance from a habitat conservation point of view.

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) and improve tree regeneration which is most important for sustainable forest management. Thinning may help control canker disease caused by *Quambalaria coyrecup*, a potential threat to the health of marri forest (Paap et al. 2008, Sapsford 2017). 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. Retaining large trees in thinning operations to improve habitat will reduce the positive effect of thinning on water yield and the growth rate of smaller trees. Further research is needed to identify the right balance of forest management, taking into consideration the various services provided by the forest, as well as its age and condition.

4.3 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 (after control), T2, and is driven by the presence of a cohort of thinner and especially shorter trees, suggesting that this low level of thinning may have preferentially retained such trees. 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, in

contrast 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. (2021) or Chapter 2 in *Eucalyptus marginata* in SWWA and Chapter 3 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. Marri trees growing in the study area are also affected by neighbouring karri trees. Karri trees are taller 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 (Chapter 3) 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 (Table 1, S2). 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 (Fig. 4a, c, d, Fig. S3). The HDR of unthinned stands was higher than that of thinned stands (Table 1). Diameter growth is highly sensitive to reduction to stand density and therefore diameter growth is higher in low stand density plots, but height growth is relatively less sensitive to reduction in stand density compared to diameter growth. Therefore, HDR becomes smaller in thinned or open stands than in unthinned 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 (Wilson and Oliver 2000; Wonn & O'Hara 2001; Bobinac et al. 2018).

5 Conclusions

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 unthinned plots but unthinned 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 large 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.

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Supplementary materials: S3

Table S1. 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	R ²	RMSE	AIC
M1	$H = 1.3 + b_1 + b_2D + \varepsilon_{ij}$	Linear model	$b_1=6.71$	0.751	1.89	2252
			$b_2=0.56$			
M2	$H = 1.3 + b_1 \left\{ \frac{D}{(D+1)} \right\} + b_2D + \varepsilon_{ij}$	Watts (1983)	$b_1=7.47$	0.751	1.89	2251
			$b_2=0.54$			
M3	$H = 1.3 + b_1D^{b_2} + \varepsilon_{ij}$	Huxley and Teissier (1936)	$b_1=2.78$	0.752	1.89	2251
			$b_2=0.62$			
M4	$H = 1.3 + b_1\{1 - \exp(-b_2D)\} + \varepsilon_{ij}$	Meyer (1940)	$b_1=45.44$	0.730	1.95	2312
			$b_2=0.02$			
M5	$H = 1.3 + \left\{ \frac{D}{b_1 + b_2D} \right\}^3 + \varepsilon_{ij}$	Naslund (1936)	$b_1=1.02$	0.730	1.95	2312
			$b_2=0.003$			

M6	$H = 1.3 + \frac{b_1 D^2}{(D + b_2)^2} + \varepsilon_{ij}$	Hossfeld (1822)	b ₁ =46.73	0.720	1.99	2332
			b ₂ =14.96			
M7	$H = 1.3 + \exp\left\{b_1 + \frac{b_2}{(D + 1)}\right\} + \varepsilon_{ij}$	Wykoff et al. (1982)	b ₁ =3.66	0.708	2.03	2355
			b ₂ =-19.53			
M8	$H = 1.3 + b_1 \exp\left(\frac{b_2}{D}\right) + \varepsilon_{ij}$	Buford (1986)	b ₁ =37.69	0.704	2.05	2362
			b ₂ = -17.89			
M9	$H = 1.3 + b_1\{1 - \exp(-b_2 D)\}^3 + \varepsilon_{ij}$	Bertalanffy (1949)	b ₁ =25.17	0.674	2.15	2415
			b ₂ =0.09			

Table S2. 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 is also shown. P-value (growth) means p-value generated in mixed model analysis on change of variables between two consecutive growth periods. P-value (retained) means p-value generated in mixed model analysis on the retained values of the variables at the beginning of each growth period.

Year	variables	Thinning					p-value (growth)	p-value (retained)
		T1	T2	T3	T4	df		
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 ² ha ⁻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 ² ha ⁻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 ² ha ⁻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 ² ha ⁻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 ² ha ⁻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

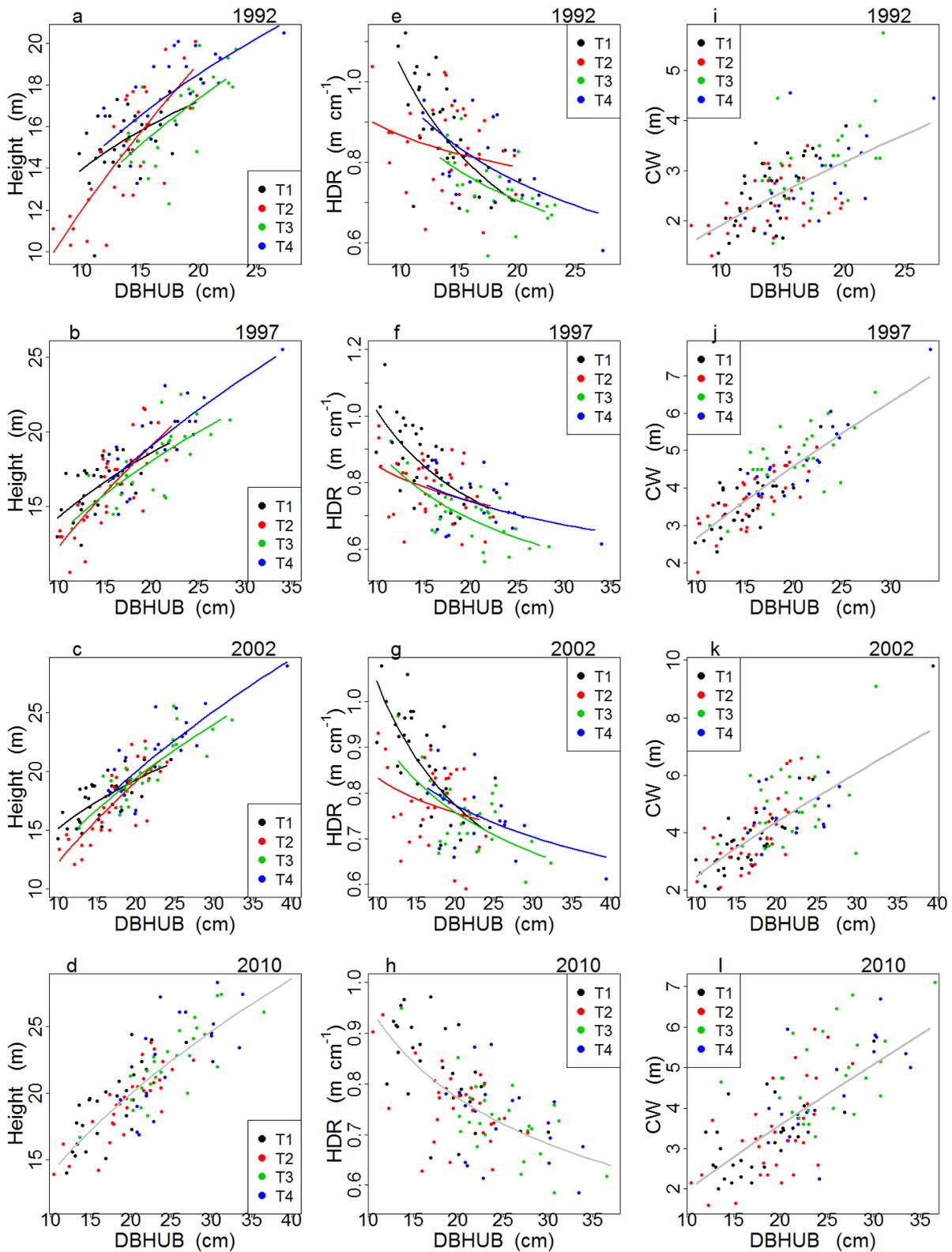


Figure S3. Effect of stand density on allometry of DBHUB with (a) height in 1992; (b) height in 1997; (c) height in 2002; (d) height in 2010; (e) HDR in 1992; (f) HDR in 1997; (g) HDR in 2002; (h) HDR in 2010; (i) CW in 1992; (j) CW in 1997; (k) CW in 2002; (l) CW in 2010

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CHAPTER 5

Individual tree growth in jarrah (*Eucalyptus marginata*) forest is explained by size and distance of neighbouring trees in thinned and non-thinned plots

PREAMBLE

This chapter presents a new DBH and distance-based competition index; the first individual tree growth model; optimal number and distance of competitors that needs to be considered when accounting for competition; and the idea of neighbouring tree growth being a useful indication of competition in thinned and non-thinned plots of *Eucalyptus marginata*.

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Individual tree growth in jarrah (*Eucalyptus marginata*) forest is explained by size and distance of neighbouring trees in thinned and non-thinned plots

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Highlights

- We developed a new spatial competition index to explain individual tree growth.
- Growth models were improved by including competition.
- Including 12 competitors around the subject tree optimised growth models.
- Including competitors up to ~10m from the subject tree optimised growth models.
- Our methods may help in identifying trees for thinning operations.

Abstract

Growth of an individual tree in a forest depends on multiple factors amongst which size, age and stand density can be of particular importance. The ability to understand how these factors influence individual growth can help understand forest growth and dynamics more generally. The overall objective of this study was to analyse the growth of individual trees of jarrah (*Eucalyptus marginata*), a wide-spread species having ecological and economic importance in south west Western Australia (SWWA). More specifically, we investigated 1) how well individual tree growth could be explained by considering tree size at the start of the growth period; 2) whether this explanation could be improved by also accounting for competition from neighbouring trees in different ways, 3) how many neighbouring trees or what neighbourhood distance needed to be considered when accounting for competition; and 4) whether neighbouring tree growth could be a useful indication of competition. Tree size was significant in explaining growth. Explanation was improved when competition was included in the models, based on R^2 (which ranged from 0.31 to 0.68). A new spatial competition index (CI) developed in this study performed better than previously developed CIs. Explanation of diameter growth was optimized by accounting for competition from the 10 to 12 closest competitors or competitors within ~10 m from the base of the subject tree. As competition from neighbours had a significant negative effect on growth, we recommend including neighbourhood competition when explaining/predicting growth and considering thinning treatments to minimize the effect of competition on growth. The modelling approaches developed in this study are likely to be useful tools for understanding and managing individual tree growth of any species in the world where competition among trees restricts individual growth. Novelties include the first model explaining individual jarrah growth; an effective new competition index; an approach to testing how many neighbouring trees or what neighbourhood distance needs to be considered when accounting for competition; and the idea of neighbouring tree growth being a useful indication of competition.

Key words: Competition; Growth; Jarrah; Model; Thinning

1 Introduction

Individual trees in a forest grow at different rates depending on a variety of factors, with tree size, age and stand density known to exert strong influence (Gyawali et al., 2015; Zhang et al., 2017). Many ecologists and foresters are trying to understand what factors influence this growth variation, as it has a critical role in explaining forest productivity and forest dynamics (Canham et al., 2006).

Tree size (stem diameter, height, crown width) is a widely used variable for explaining individual tree growth (Coomes and Allen, 2007; Gyawali et al., 2015; Zhang et al., 2017). In even-aged stands, individual trees grow rapidly during the seedling and sapling stage, reach a peak during middle age (pre-mature stage) and then growth decreases during the mature stages (Gove et al., 2019). However, the rate of growth, and the stage when this growth stabilises depends on species.

Competition is another important variable that affects individual tree growth (Opie, 1968; Contreras et al., 2011; Ford et al., 2017). Competition from neighbouring trees negatively affects tree growth with larger and nearer competitors better able to acquire resources and thus imposing higher competitive stress than smaller and more distant competitors (Opie, 1968; Pretzsch, 1997; Vettenranta, 1999; D'Amato and Puettmann, 2004; Stoll and Newbery, 2005; Weiner et al., 2009; Vanclay et al., 2013). As trees increase in age and size, they compete for light, space, nutrients and moisture. This competition commonly limits growth (Corona and Ferrara, 1989; Contreras et al., 2011) and can thus be quantified by comparing the growth of an individual tree with similar trees grown in open conditions. The magnitude of competition imposed on individual trees can be estimated using competition indices (CIs). Commonly used CIs have been categorized as either spatial or non-spatial. Non-spatial CIs are those CIs which do not consider the spatial location or distance of individual competitors relative to the tree for which the growth is explained (Schröder and Gadaw, 1999). Non-spatial CIs thus assume that the species and size of trees are uniformly distributed

throughout the stand (Weiskittel et al., 2011) and therefore best apply to even aged and homogeneous forests. Non-spatial CIs may be less useful for uneven-aged and mixed forests with more complex and heterogeneous species composition, size distributions and stand structure. Bridging models between non-spatial and spatial CIs have also been developed to simulate the growth of mixed forests in which non-spatial CIs perform poorly, but these have several limitations (see details in Perot et al., 2010).

Spatial CIs consider both tree size and spatial location of competitors in estimating the competition exerted by neighbouring trees, and are thus applicable to a broad range of circumstances irrespective of stand structure and species composition (Pretzsch, 1997; Vettenranta, 1999). Furthermore, spatial CIs can capture local interactions, individual variability, adaptive behaviour and heterogeneous distributions of resources (Grimm, 1999). Therefore, spatial CIs are more capable of explaining growth than non-spatial CIs (Contreras et al., 2011; Maleki et al., 2015), although non-spatial CIs have performed as strongly as spatial CIs in certain conditions (Martin and Ek, 1984; Corona and Ferrara, 1989). The explanative capacity of the CI also depends on age, size, stand density and light requirement of the species (Das, 2012; Kunstler et al., 2012, 2016; Vanclay et al. (2013); Zhang et al., 2017). Spatial CIs require more data than non-spatial CIs, so may be less useful for operational forest management. However, they may be useful for better understanding the dynamics of a forest under certain conditions.

Individual-based modelling (IBM) is one of the most comprehensive and detailed approaches to predict the growth of individual trees and has been applied in simulating future forest management scenarios (Vospernik, 2017), predicting/explaining wood quality (Sterba et al., 2006), predicting habitat quality (Vospernik and Reimoser, 2008) and planning forest management activities (Weiskittel et al., 2016). The IBM approach can capture the variation that exists amongst individual

trees in a forest or stand and assumes that those individual trees interact locally, and adapt differently, to their diverse local environments (Berger et al., 2008; DeAngelis and Grimm, 2014); it thus allows individual trees and their interactions to be represented in more detail than would be possible in more aggregated modelling approaches, such as stand-level modelling (Zhang and Lei, 2010; DeAngelis and Grimm, 2014). Even more detailed and complex modelling approaches exist, such as functional-structural plant models that describe the development of the three-dimensional architecture and structure of plants at the scale of individual tree organs (Guo et al., 2011; Xu et al., 2011), but these may be overly complex for representing the growth and interactions between large numbers of trees.

The overall objective of this study was to investigate the factors affecting the growth in diameter of a dominant species at the individual tree level. Jarrah (*Eucalyptus marginata* Donn ex. Smith), an important forest types in south-west Western Australia (SWWA), was chosen as the ‘model species’ for this study because of its high environmental and economic value, and the availability of relevant long-term data on jarrah forest managed under different thinning regimes in a predominantly even-aged stand of 100-year-old regrowth forest in SWWA. More specifically, we aimed to investigate 1) how well individual tree growth could be explained by considering tree size at the start of the growth period; 2) whether this explanation of growth could be improved by also accounting for competition from neighbouring trees in different ways; 3) how many neighbouring trees or what neighbourhood distance needed to be considered when accounting for competition; and 4) whether neighbouring tree growth could be a useful indication of competition.

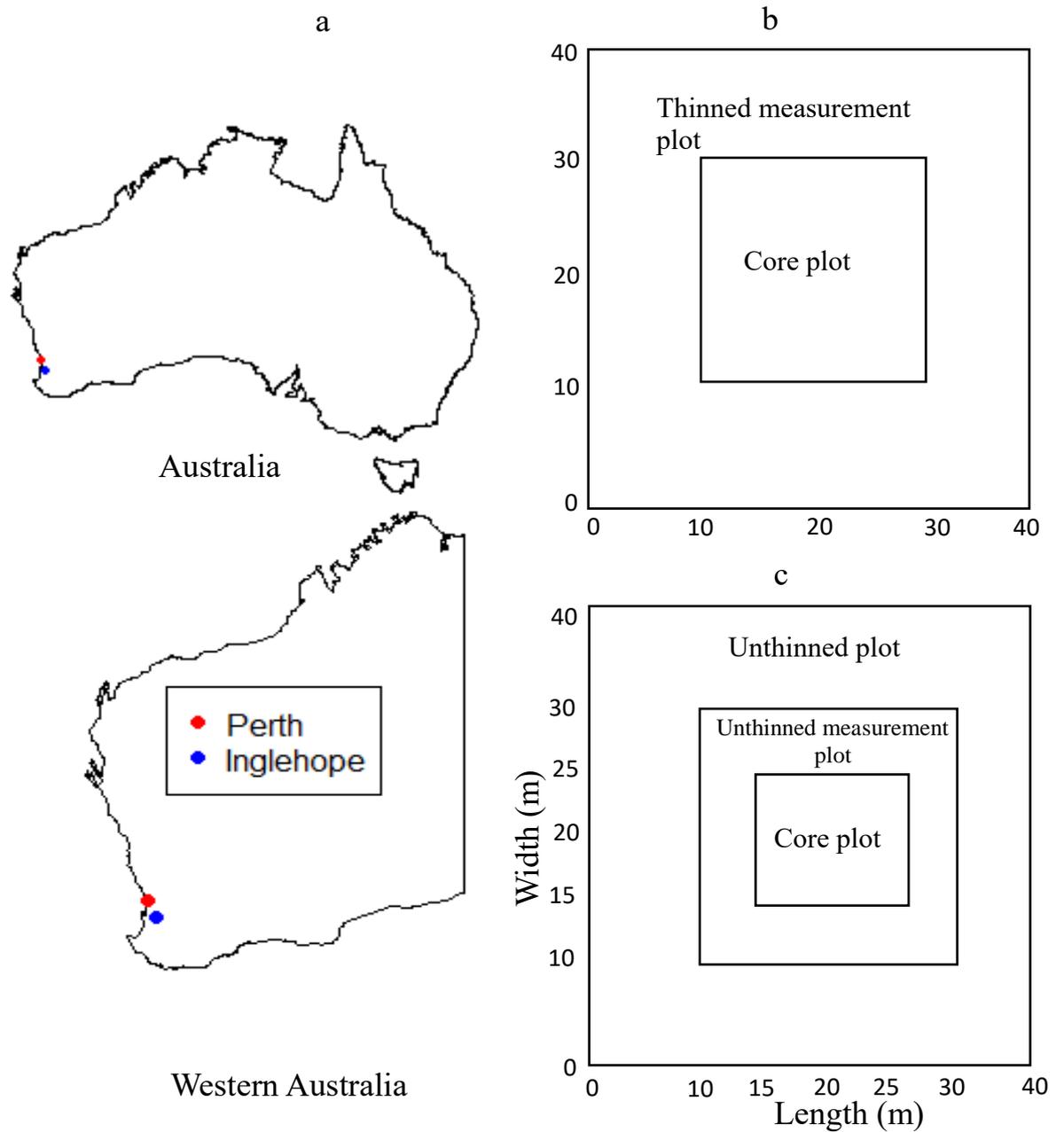


Fig. 1. Map of Australia and Western Australia showing study site (a); size and shape of thinned plot (40 m × 40 m) and core plot used for modelling (20 m × 20 m) (b); size and shape of unthinned plot (40 m × 40 m), unthinned measurement plot (20 m × 20 m) and unthinned core plot used for modelling (10 m × 10 m) (c)

2 Materials and methods

2.1 Study species and site

Jarrah forest, one of the native and widespread forest types of SWWA, provides a range of values including timber, firewood, wildlife habitat, water, honey, conservation and greenery (CCWA, 2013; Bradshaw, 2015). Jarrah forests are, however, susceptible to threats, including fire (Burrows et al., 2010; McCaw, 2013; Hollis et al., 2019), drought (Qiu et al., 2013; Standish et al., 2015) and competition (Bhandari et al., 2021). Jarrah forests have also been cleared for mining followed by rehabilitation (Grigg, 2017). Exploitation for timber has traditionally retained important legacy elements of the original forest including standing trees, ground logs and the seed and genetic resources of the site (Koch and Ward, 2005). Other potential threats in jarrah forests also include disease, introduction of exotic plant and/or animal species (e.g. *Vulpes vulpes*) (Davison, 2014). Empirical studies have also attempted to investigate the likely effect of global warming and climate change on jarrah forests growth, development and sustainable management (Standish et al., 2015; Matusick et al., 2016). To date there are no published models for explaining jarrah forest growth that represent differences between individual trees, although some studies have focused on stand level growth analysis of jarrah (Abbott and Loneragan 1983a; Abbott and Loneragan 1983b; Stoneman et al., 1996; Bhandari et al., 2021).

The study site is located in a jarrah dominated forest at Inglehope (32° 45' S, 116° 11' E) 12 km east of Dwellingup, SWWA (Fig. 1a). The forest overstorey consists of two species: jarrah (99% of trees) and marri (*Corymbia calophylla*) (1% of trees). The soil colour of the study site is yellow and sandy ferruginous in nature with low fertility (Hingston et al., 1981). The site has a Mediterranean climate with annual rainfall of around 1000 mm concentrated in winter months (BOM, 2019). It is estimated to be about 200 mm lower than the historical average annual rainfall of 1245 mm at the nearest weather station (measured in Dwellingup station from 1934 to 2010) (Stoneman et al., 1996).

Long term rainfall data shows a declining trend in this region (Bates et al., 2008). The mean monthly maximum temperature of 29.7 °C occurs in January and the mean monthly minimum temperature of 5.5 °C occurs in July (BOM, 2019).

2.2 Treatments (thinning and fertilisation)

The Inglehope thinning trial consists of 30 plots (27 plots established in 1965 and an additional three unthinned plots established in 1986). The trial used a complete randomized design with six replicates of five different thinning treatments (T1-T5), with each treatment being a different stand density; these densities were established in 1965 as 8.6 (T1), 14.4 (T2), 20.3 (T3), 25.1 (T4) and 27.9 (T5) m² ha⁻¹ basal area over bark (BAOB) equating to 7.0 (T1), 11.0 (T2), 15.4 (T3), 18.3 (T4) and 21.9 (T5) m² ha⁻¹ basal area under bark (BAUB). Treatment T5 represents unthinned plots (control). The plots were first thinned in 1965 (at the age of 40 years) and were last measured in 2010. Plot size was 40 m × 40 m with an 8 m experimental buffer on all sides that received the same thinning as the plots. For the unthinned control plots, only trees within an inner 20 m×20 m subplot were measured, because of the very large number of trees on these plots, while all trees were measured in the thinned plots (Fig. 1b, c). In 1986, a second thinning was carried out as follows: 6.8 (T1), 13.6 (T2), 20.4 (T3), 28.0 (T4) and 35.3 (T5) m² ha⁻¹ BAOB, equating to 5.5 (T1), 11.0 (T2), 16.5 (T3), 22.4 (T4) and 28.5 (T5) m² ha⁻¹ basal area under bark (BAUB) (Fig. 2d). At this time, a fertilizer treatment (F0 unfertilized and F1 fertilized with 400 kg ha⁻¹ N and 229 kg ha⁻¹ P) was also applied to 15 of the 30 replicate plots in a completely randomized design. The quantity of fertilizer applied was chosen to optimise growth response (Stoneman et al., 1989).

Table 1 Mean±standard deviation (range) values of individual tree and stand characteristics of thinned and unthinned plots for different years. DBH is diameter at breast height, BAUB is stand basal under bark. The data presented under ‘thinned plots’ represent all thinning intensities.

Plots	Variables	Mean±Std.(range)		
		1965	1984	2010
Thinned	DBH (cm)	18.2±6.0(5.9-48.8)	21.8±7.6(7.9-53.4)	29.9±10.3(9.9-72.5)
	Height (m)	19.1±3.5(7.7-32.0)	21.2±3.8(9.0-34.0)	23.6±3.7(11.5-36.0)
	BAUB (m ² ha ⁻¹)	13.2±4.3(6.5-19.3)	19.1±4.7(11.1-25.6)	21.1±8.2(7.6-34.4)
	Stem number (ha ⁻¹)	460±249(125-881)	454±242(125-868)	266±200(25-700)
Unthinned	DBH (cm)	14.2±5.7(8.1-49.6)	15.6±6.5(7.8-54.3)	18.2±7.9(8.8-59.4)
	Height (m)	16.6±3.5(11.1-29.1)	17.9±3.9(7.0-30.0)	18.5±4.3(3.1-29.5)
	BAUB (m ² ha ⁻¹)	21.9±1.8(20.1-23.8)	26.7±1.8(24.7-28.3)	32.8±3.3(29.7-36.3)
	Stem number (ha ⁻¹)	1192±52(1150-1250)	1183±57(1150-1250)	1067±87(975-1150)

2.3 Sampling and measurements

Over bark diameter at breast height (DBHOB), bark thickness of all the trees and height of sample trees was measured in 1965, 1984 and 2010. Bark thickness of standing trees at breast height was measured using a bark gauge, and under bark diameter at breast height (DBH, hereafter DBH denotes the under-bark diameter at breast height) was determined by subtracting twice the average bark thickness from the DBHOB. Hereafter the period between 1965 and 1984 will be referred to as the first growth period and the period between 1984 and 2010 will be referred to as the second growth period. In 1985, a theodolite was used to measure the location of the centre and corners of each plot. The position of each tree was mapped using direction and distance from the plot centre, and the distance among trees was calculated. Differential GPS was used to map plot centres and corners again in 2010. We used field measured height for those trees which were measured in the field and predicted height using the model of Bhandari et al. (2021) following a mixed effect modelling approach using a plot level random effect (Eq. 1) for those trees which were not measured in the field.

$$height_{ij} = 1.3 + \frac{dbh_{ij}^2}{\alpha_0 + \alpha_1 dbh_{ij} + \alpha_2 dbh_{ij}^2} + u_j + \varepsilon_{ij} \quad (Eq\ 1)$$

In this equation, $height_{ij}$ is the height of the i th tree on the j th plot, dbh_{ij} is the under-bark diameter at breast height of the i th tree on the j th plot, α_0 , α_1 and α_2 are fixed effect parameters, u_j is the random effect for the j th plot and ε_{ij} is the unexplained residual errors for the i th tree on the j th plot. The parameters of the model were estimated using the maximum likelihood method in the nlme package in R (Pinheiro et al., 2018; R Core Team, 2019). A summary of the data used in the modelling is presented in Table 1.

Periodic annual increment was estimated as the change in DBH over the time period, divided by the number of years, hereafter referred to as Δ DBH. For modelling purposes, we defined a core inner plot of 20 m \times 20 m for thinned plots (Fig. 1b) and 10 m \times 10 m for unthinned plots (Fig. 1c).

Only trees within the core plots were included in the analysis as ‘subject trees’, that is, trees for which growth was modelled, while all trees within the plots were included as possible competitors for the subject trees. This ensured sufficient detail was available for all competitors for all subject trees, as models required full details on all competitor trees within 10 m of every subject tree in the thinned plots, and within 5 m of every subject tree in the unthinned plots. The number of subject trees available to fit the model was 441 (thinned plots) and 33 (unthinned plots) in the first growth period and 259 (thinned plots) and 31 (unthinned plots) in the second growth period. We developed separate models for the two different time periods i.e., one for 1965 to 1984 and another for 1984 to 2010. Similarly, in each time period, we developed separate models for thinned and unthinned plots; this was necessary because of the different sizes of the core plots for the thinned vs unthinned plots.

2.4 Explaining growth based on size (Aim 1)

We used linear mixed-effect models, with Δ DBH of the individual trees as the response variable. Potential fixed effect explanatory variables considered included initial DBH, square of initial DBH, initial height, square of initial height, slenderness coefficient (ratio between height and DBH), whether fertilizer was applied. We included plot level random effects to account for possible correlation among trees within plots and avoid potential pseudo-replication. We used natural logarithmic transformation of dependent and independent variables, except for fertilizer; this improved adherence to model assumptions of normality of residuals, homogeneity of variance and linearity (Wykoff, 1990). To minimize the problem of multicollinearity, we used orthogonal polynomials for DBH and height. Variance inflation factor (VIF) was used to evaluate multicollinearity in independent variables, with a threshold of $VIF > 5$ considered to indicate problematic multicollinearity (Sileshi, 2014). Initially, we fitted a model with all available independent variables (except competition) and then selected the model with only significant explanatory variables that did not show multicollinearity. We found the model with DBH and/or

height as the explanatory variables performed better than with other variables. All models were evaluated using three fit statistics: coefficient of determination (R^2), root mean squared error (RMSE) (Montgomery et al., 2001) and AIC (Akaike, 1972). Fitted values for calculating fit statistics were estimated at the population level, i.e., without random (plot) effects.

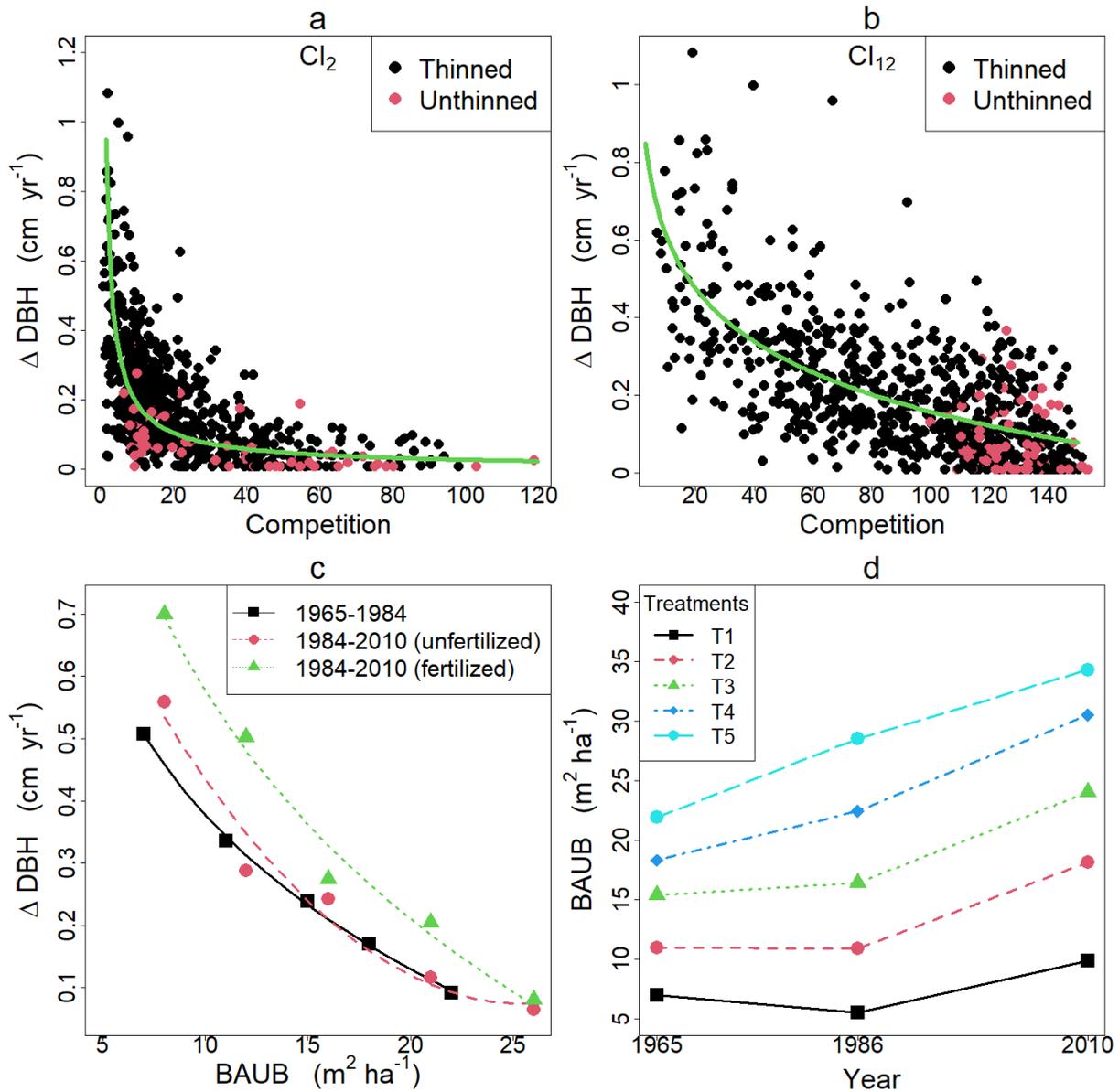


Fig. 2. Growth in DBH with respect to (a) a non-spatial CI (CI_2); (b) a spatial CI (CI_{12}) with thinned and unthinned plots distinguished; (c) Δ DBH at different levels of thinning intensity (measured by retained BAUB) for two different growth periods; and (d) Stand BAUB development at different levels of thinning intensity.

2.5 Adding competition to the models (Aim 2)

We considered twelve different competition indices (CIs) (five non-spatial and seven spatial) to quantify the level of competition experienced by each subject tree (Table 2). Eleven indices (all five non-spatial and six spatial) were selected from the scientific literature (Lorimer, 1983; Dale et al., 1985; Contreras et al., 2011; Maleki et al., 2015), and a twelfth index (CI_{12}) was developed during this study. CI_{12} uses the DBH of each competing tree and the distance between the subject tree and each competing tree (Table 2).

For this CI_{12} index, we assumed that the competitive effect of each neighbouring tree depends linearly on the diameter of the tree and declines exponentially with distance, and that the total competitive effect on a subject tree is the sum of the competitive effects of all other individual trees. The rate of this exponential decline is determined by a parameter k , and the numerical value of k was estimated by finding the power value that gave the best model fit for all data across all plots (based on model Akaike Information Criteria (AIC), where lower AIC indicates better model fit). A Pearson correlation matrix was used to evaluate the relationship of the 12 competition indices with each other and with periodic annual increment (PAI) of DBH and categorized as very high (>0.9), high (0.7-0.9), moderate (0.5-0.7), low (0.3-0.5) and negligible (0-0.3) (Mukaka, 2012). Since our new CI_{12} index had the best correlation with PAI, we used this index for the rest of our analysis.

We then added competition to the models without competition previously obtained in Aim 1, in order to evaluate to what extent this would improve explanation of individual tree growth. We also developed models using DBH and competition, but without height, for cases where height data were not available or for potential use in cases where height measures may not be available. In further analyses, we tried including additional stand level variables as explanatory variables separately, as

proxies of non-spatial CIs, to observe whether these variables further improved the model fit. These included initial stem number per ha, initial stand basal area per ha, and thinning intensity.

Table 2 Different spatial and non-spatial competition indices used in this study. Note: dbh_i =DBH of i^{th} subject tree, dbh_j = DBH of j^{th} competitor, $dist_{ij}$ = distance between i^{th} subject tree and j^{th} competitor tree, k =power, $height_i$ = height of i^{th} subject tree, $height_j$ =height of j^{th} competitor, g_j = basal area of competitor trees ($\text{m}^2 \text{ha}^{-1}$), d_q =quadratic mean diameter (square root of the arithmetic mean of squared values of DBH of all the trees in the plot), S = area of plot, N = Number of stem per ha.

Indices	References	Equation	
Non-spatial competition indices	CI ₁	Hamilton (1986)	$\frac{dbh_i}{d_q}$
	CI ₂	Corona and Ferrara (1989)	$\sum_{j \neq i} \frac{dbh_j^2}{dbh_i^2}$
	CI ₃	Wykoff (1990)	$\sum_{j \neq i} (dbh_j^2) \times 0.00007854$
	CI ₄	Steneker and Jarvis (1963)	$\frac{\sum_{j \neq i} (g_j)}{S}$
	CI ₅	Reineke (1933)	$10^{(\log N + 1.605 \times \log d_q - 1.605)}$
	CI ₆	Hegy (1974)	$\sum_{j \neq i} \frac{dbh_j}{dbh_i \times dist_{ij}}$
Spatial competition indices	CI ₇	Braathe (1980)	$\sum_{j \neq i} \frac{height_j}{height_i \times dist_{ij}}$
	CI ₈	Rouvinen and Kuuluvainen (1997)	$\sum_{j \neq i} \arctan\left(\frac{dbh_j}{dist_{ij}}\right)$
	CI ₉	Staebler (1951)	$\sum_{j \neq i} dist_{ij}$
	CI ₁₀	Rouvinen and Kuuluvainen (1997)	$\sum_{j \neq i} \arctan\left(\frac{height_j}{dist_{ij}}\right)$

CI ₁₁	Rouvinen and Kuuluvainen (1997)	$\sum_{j \neq i} \left(\frac{height_j}{height_i} \right) \times \arctan \left(\frac{height_j}{dist_{ij}} \right)$
CI ₁₂	This study	$\sum_{j \neq i} dbh_j \times \exp(-k \times dist_{ij})$

2.6 Testing the effect of number and distance of competitors (Aim 3)

For the previous analyses, we had assumed that all trees within 10 m (thinned plots) and 5 m (unthinned plots) of the subject tree had a competitive effect on the growth of the subject tree. We next wanted to test whether this assumption was reasonable in two ways. First, we considered whether using a different distance threshold would give better model explanations. To do this we limited our set of subject trees to only include those trees that were at least 12 m from the nearest plot boundary (i.e. reduced the size of the core plot to 16 m x 16 m. We then varied the distance threshold in increments of 1 m, from a minimum of 1 m up to maximum of 12 m (thinned plots), and for each threshold recalculated the CI₁₂ competition index including only those neighbour trees within the threshold distance, refitted the model and evaluated the model fit. Second, we tried a threshold based on number of trees rather than distance. To do this we limited our set of subject trees to only include those trees that had at least 12 neighbour trees closer than the nearest plot boundary. We then varied the number of competitors considered from one up to 12, and for each number we recalculated the CI₁₂ competition index, refitted the model and evaluated the model fit. We restricted this analysis to a maximum of 12 m and 12 trees to ensure enough subject trees remained in the subset analysed. When we allocated 12 competitors for each subject tree, we still had 399 subject trees for the thinned plots of the first growth period and 185 subject trees for the thinned plots of the second growth period to fit and evaluate the model. We did not consider distance and/or number thresholds for unthinned plots because competition was not a significant explanatory variable in unthinned plots.

2.7 Testing the effect of neighbouring tree growth on the model (Aim 4)

We hypothesised that the explanation of individual tree growth might be further improved by considering not just the size of neighbouring trees at the start of the growth period but also their growth during the period, since faster-growing neighbour trees are expected to capture greater amounts of resources such as water and nutrients. In reality, of course, this approach would not be practically useful for growth explanation since the amount of growth of neighbours during the period is not known at the start of the period and can only be calculated retrospectively. However, we were still interested in the theoretical question of whether individual tree growth was related to the growth of its neighbours over the same period. We therefore introduced another competition index (Eq. 2) to account for the growth of neighbouring trees.

$$CI = \sum_{j=1}^j \Delta dbh_j * \exp(-k * dist_{ij}) \quad Eq (2)$$

In this equation, Δdbh_j =DBH growth rate of j^{th} competitor tree, $dist_{ij}$ = distance between i^{th} subject tree and j^{th} competitor tree, and k is a constant power. All trees within a distance of 10 m (thinned plots) and 5 m (unthinned plots) of a subject tree were counted as competitors, so j is the number of individual trees within 10 m (thinned plots) and 5 m (unthinned plots) of the subject tree. The value of k was determined by finding the value that optimised model fit based on AIC. We tested both the ability of this competition index to explain Δ DBH of the subject tree by itself, and also whether it further improved the explanative ability of the previous best models.

3 Results

3.1 Comparing different competition indices

Pearson rank correlation coefficients between Δ DBH and CIs are presented in Table 3. The correlation among non-spatial indices ranged between -0.63 and +0.93 and among spatial indices ranged between -0.81 and +1.00. In general, the correlation coefficients of CIs within groups (spatial

CI vs spatial CI or non-spatial CI vs non-spatial CI) were higher than between groups (spatial CI vs non-spatial CI); however, we observed a high correlation between certain pairs of spatial and non-spatial indices whose mathematical forms are quite different. Competition indices had a negative correlation with Δ DBH except for CI_1 and CI_9 . The highest negative correlations with Δ DBH occurred for CI_2 from the non-spatial group and CI_{11} , and CI_{12} from the spatial group.

Table 3 Pearson rank correlation matrix of competition indices and (non-spatial competition indices CI₁ to CI₅ and spatial competition indices CI₆ to CI₁₂) ΔDBH

CI ₁														
CI ₂	-0.63	CI ₂												
CI ₃	-0.06	0.42	CI ₃											
CI ₄	0.01	0.43	0.73	CI ₄										
CI ₅	0.02	0.47	0.58	0.93	CI ₅									
CI ₆	-0.50	0.90	0.45	0.58	0.64	CI ₆								
CI ₇	-0.33	0.80	0.47	0.65	0.71	0.96	CI ₇							
CI ₈	-0.07	0.61	0.61	0.74	0.75	0.80	0.89	CI ₈						
CI ₉	0.07	-0.50	-0.42	-0.56	-0.63	-0.68	-0.75	-0.81	CI ₉					
CI ₁₀	-0.06	0.61	0.58	0.72	0.75	0.81	0.89	1.00	-0.81	CI ₁₀				
CI ₁₁	-0.35	0.83	0.57	0.66	0.68	0.93	0.96	0.92	-0.75	0.92	CI ₁₁			
CI ₁₂	-0.10	0.61	0.74	0.82	0.80	0.81	0.88	0.96	-0.77	0.95	0.89	CI ₁₂		
ΔDBH	0.31	-0.57	-0.45	-0.56	-0.52	-0.65	-0.65	-0.62	0.41	-0.62	-0.66	-0.66	ΔDBH	

The relationship between the most strongly correlated competition indices from non-spatial and spatial categories and Δ DBH with clear negative growth response to increasing competition as measured by CI_2 , and CI_{12} is presented in Figure 2a, b. The performance of the non-spatial competition index CI_2 was relatively lower than the spatial indices CI_{11} and CI_{12} . The correlation coefficients of CI_{11} and CI_{12} with Δ DBH were equal, however, we selected CI_{12} for further use in growth modelling as the CI based on DBH (CI_{12}) is more easily, accurately and cost-effectively estimated than the CI based on height (CI_{11}). While all three competition indices indicate a strong decline of growth with increasing competition intensity, the spatial indices CI_{11} and CI_{12} , which take into account distances from competitors, differentiate better the effects of intermediate levels of competition.

3.2 DBH growth modelling with/without competition

3.2.1 Thinned plots 1965-1984

The model based on tree size (initial DBH ($P < 0.001$) and initial height ($P = 0.008$)) described more than 33% of the growth variation ($R^2 = 0.336$, $RMSE = 0.128$, $AIC = 1096$) (Eq. 3). When CI_{12} ($P < 0.001$) was included in the model, R^2 increased from 0.336 to 0.457, $RMSE$ decreased from 0.128 to 0.111 and AIC decreased from 1096 to 1009 (Eq. 4) (Table 4). The model with initial DBH and CI_{12} developed to be applicable in the absence of height data (Eq. 5) showed a decrease in R^2 from 0.457 to 0.440, increased $RMSE$ from 0.111 to 0.116 and increased AIC from 1009 to 1020 compared to the model that also includes height.

$$\log(\Delta dbh) = -8.4424 + 1.0825 \log(dbh) + 1.1617 \log(height) \quad Eq (3)$$

$$\log(\Delta dbh) = -6.9242 + 0.6665 \log(dbh) + 1.2959 \log(height) - 0.0258 (CI_{12}) \quad Eq(4)$$

$$\log(\Delta dbh) = -5.0902 + 1.3533 \log(dbh) - 0.0234 (CI_{12}) \quad Eq (5)$$

3.2.2 Thinned plots 1984-2010

The model based on tree size (initial DBH ($P < 0.001$), initial height ($P < 0.001$)) and fertilizer ($P < 0.001$) described more than 53% of the growth variation ($R^2 = 0.535$, $RMSE = 0.147$, $AIC = 541$) (Eq. 6). When the CI_{12} ($P < 0.001$) was included in the model, R^2 increased from 0.535 to 0.661, $RMSE$ decreased from 0.147 to 0.122 and AIC decreased from 541 to 469 (Eq. 7) (Table 4). The model with initial DBH, competition and fertilizer (Eq. 8) showed a decrease in R^2 from 0.661 to 0.619, increased $RMSE$ from 0.122 to 0.123 and increased AIC from 469 to 491 compared with the model that includes height.

$$\log(\Delta dbh) = -10.9905 + 0.5101 \log(dbh) + 2.4496 \log(height) + 0.5715 fert \quad Eq (6)$$

$$\log(\Delta dbh) = -9.4214 + 0.2402 \log(dbh) + 2.4115 \log(height) - 0.0143 (CI_{12}) + 0.5610 fert \quad Eq (7)$$

$$\log(\Delta dbh) = -4.8785 + 1.1840 \log(dbh) - 0.0119 (CI_{12}) + 0.5690 fert \quad Eq (8)$$

3.2.3 Unthinned plots 1965-1984

The model based on tree size (initial DBH ($P < 0.001$)) described more than 64% of the growth variation ($R^2 = 0.642$, $RMSE = 0.068$) (Eq. 9). Height was not a significant explanatory variable ($P = 0.62$) and was therefore excluded from the model. Including the competition index did not significantly improve the model ($P = 0.51$).

$$\log(\Delta dbh) = -9.6086 + 2.5393 \log(dbh) \quad (Eq 9)$$

3.2.4 Unthinned plots 1984-2010

The model based on tree size (initial DBH) described more than 61% of the growth variation ($R^2=0.619$, $RMSE=0.050$) (Eq. 10). Height was not a significant explanatory variable ($P=0.59$) when used with DBH, but it was significant ($P<0.001$) when used alone in place of DBH. Fertilizer was not a significant explanatory variable when used with DBH ($P=0.54$) nor when used alone ($P=0.31$). Including the competition index again did not significantly improve the model ($P = 0.84$).

$$\log(\Delta dbh) = -8.9300 + 2.1497 \log(dbh) \quad (Eq\ 10)$$

Table 4 Fit statistics for models with and without stand level variables included as explanatory variable (initial stem number per ha, initial stand basal area, thinning intensity). Note: ns means that adding the stand level explanatory variable did not significantly improve the model fit at a 95% confidence level; fit statistics are not shown in these cases. NA means not applicable (unthinned plots had no thinning intensity). # indicates models that include the CI; note that these were never significantly improved by the addition of stand level explanatory variables.

Plots	Growth period	Eqs.	Fit statistics	Model without stand- level variables	Model with stand level variables		
					Stem number per ha	Stand basal area	Thinning intensity
Thinned	1965-1984	Eq 3	R ²	0.336	0.412	0.447	0.446
			RMSE	0.128	0.114	0.111	0.111
			AIC	1096	1044	1017	1022
		Eq 4 [#]	R ²	0.457			
			RMSE	0.111	ns	ns	ns
			AIC	1009			
	1984-2010	Eq 5 [#]	R ²	0.440			
			RMSE	0.116	ns	ns	ns
			AIC	1020			
		Eq 6	R ²	0.535	0.651	0.647	0.644

			RMSE	0.147	0.127	0.136	0.129
			AIC	541	470	473	479
		Eq 7 [#]	R ²	0.661			
			RMSE	0.122	ns	ns	ns
			AIC	469			
		Eq 8 [#]	R ²	0.619	ns		
			RMSE	0.123		ns	ns
			AIC	491			
	1965-1984	Eq 9	R ²	0.642			
			RMSE	0.068	ns	ns	NA
	1984-2010	Eq 10	R ²	0.619	0.717	0.687	
			RMSE	0.050	0.046	0.049	NA

Unthinned

3.2.5 Adding stand level variables

The results from adding stand level variables (initial stem number per ha, initial stand basal area, thinning intensity) separately as explanatory variable to the basic models (model with tree size and/or CI_{12} and/or fertilizer) as proxies of non-spatial CIs are presented in Table 4. For the thinned plots, each of the three stand level variables significantly improved those models which did not include the competition index, but did not significantly improve those models which did include the competition index. For unthinned plots, where the competition index was excluded in the base models, adding initial stem number per ha or initial stand basal area significantly improved models for the second growth period, but not the first.

Models for ΔDBH were more accurate for thinned compared than for unthinned plots, and for the second growth period compared to the first growth period (Fig. 3). Residuals were distributed normally and did not show any systematic trend or bias when plotted against the initial DBH and predicted ΔDBH .

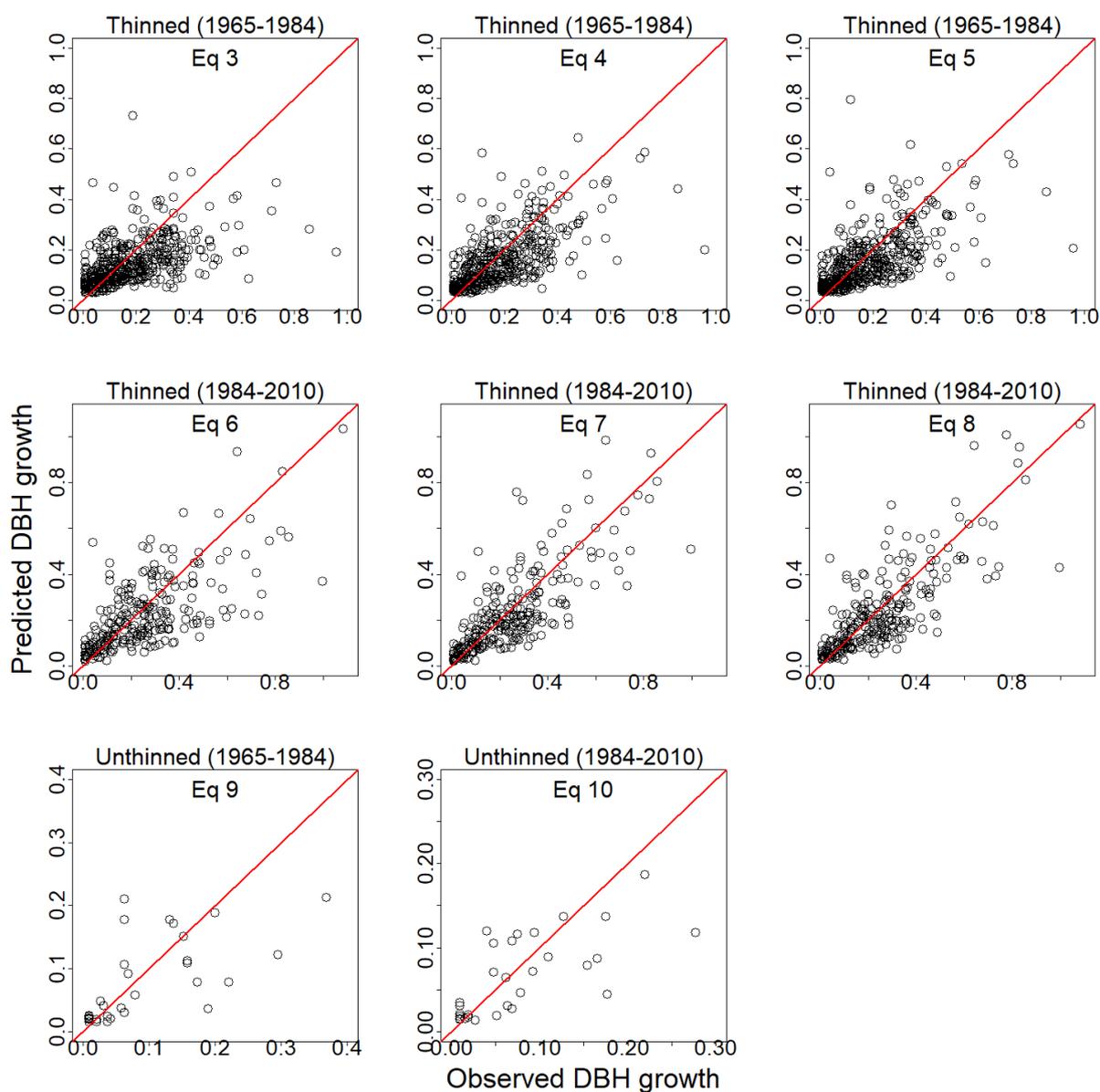


Fig. 3. Relationship between observed and predicted DBH growth. Eq. (3) (1965-1984), Eq. 6 (1984-2010), Eq. 9 (1965-1984) and Eq. 10 (1984-2010) are the model without competition. Eq. 4 (1965-1984), Eq. 5 (1965-1984), Eq. 7 (1984-2010) and Eq. 8 (1984-2010) are the model with competition (CI_{12}). The red line in each figure is the 1:1 reference line.

3.3 Testing the number and distance of competitors

Our analysis of distance and number thresholds for competitor effects showed that 10 to 12 competitors (number) and ~ 7 to 10 m (distance) from the base of the subject tree were sufficient in

explaining the subject trees' growth (Fig. 4). The sufficient number and sufficient distance of competitors were both greater in the second growth period.

3.4 Testing the effect of neighbouring tree growth

Trees near fast-growing neighbouring trees grew slower than trees near slow-growing neighbouring trees. The growth of neighbour trees (Eq. 2) was a significant explanatory variable ($P < 0.05$) in both growth periods in both thinned and unthinned plots, but the explanative capacity of neighbour tree growth was lower than that of tree size and competition index CI_{12} . When neighbour tree growth (Eq. 2) was added to models that already included the CI_{12} competition index (Eqs. 4, 5, 7, 8), neighbour tree growth did not significantly improve the explanations.

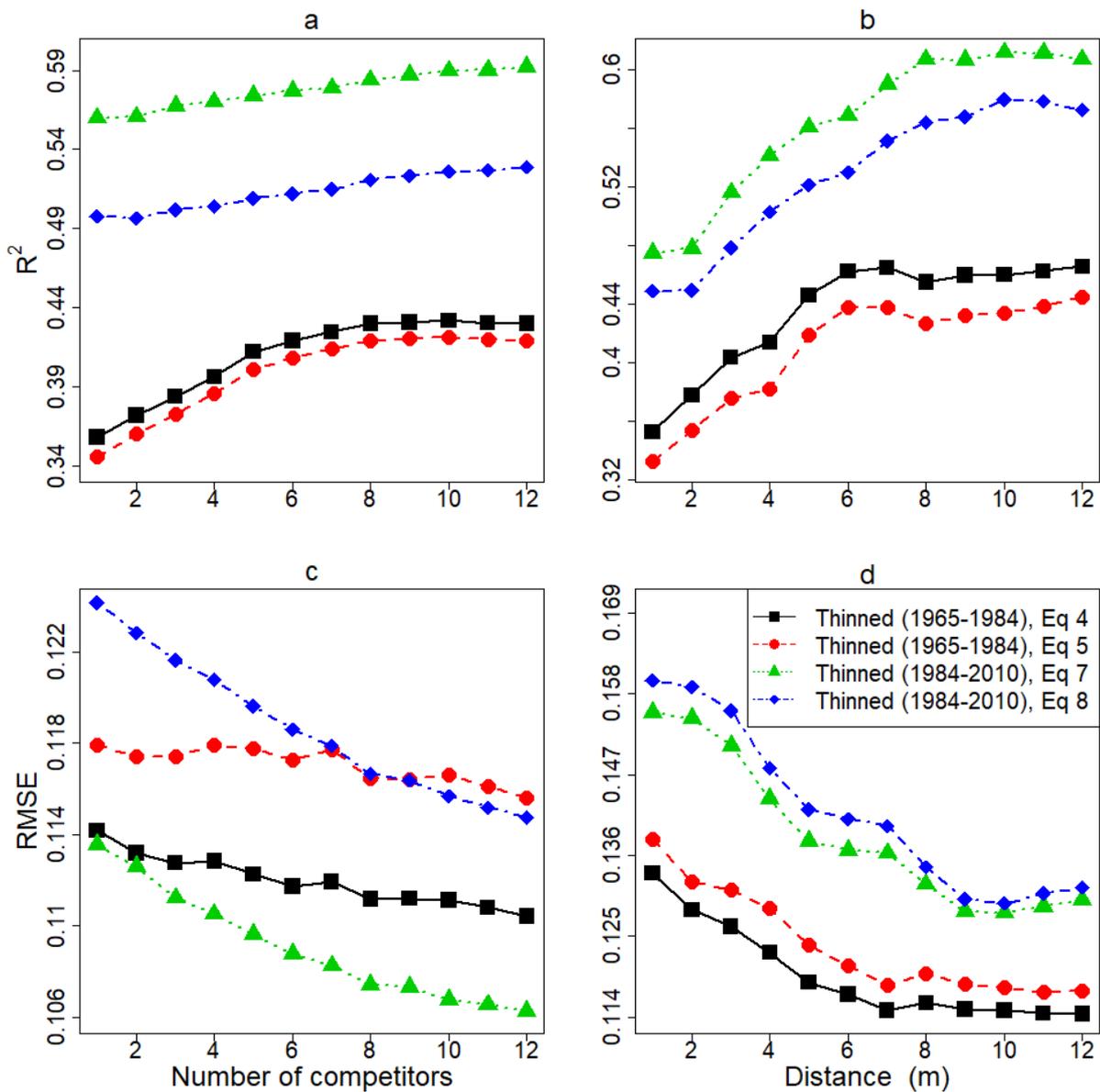


Fig. 4. Effect of number and distance of competitors on the amount of variance explained by the diameter growth model; (a) Variation in co-efficient of determination (R^2) with the number of competitor trees; (b) Variation in R^2 with the distance (m) of competitors; (c) Variation in root mean squared error (RMSE) with the number of competitor trees; (d) Variation in RMSE with the distance (m) of competitors. Note that the R^2 and RMSE show consistent (but inverted) patterns across distance and number of competitors within the same data set (i.e., growth period) as expected.

4 Discussion

This study developed the first individual tree level growth models for jarrah grown in the Mediterranean forest of SWWA, and found that accounting for local variation in competition is important in explaining individual growth of jarrah. Some key novel developments of this study include 1) a new spatial competition index (CI_{12}) which performed better than previously developed spatial and non-spatial competition indices; 2) a new approach for identifying the optimum number of competitors (10 to 12 for our data on jarrah) and optimum distance (10 m) that need to be considered while accounting for neighbourhood competition; and 3) the idea of neighbouring tree growth being a useful indication of competition.

4.1 Comparison of competition indices

As trees increase in age and size, they compete for light, space, nutrients and moisture. This competition, which commonly limits growth (Corona and Ferrara, 1989; Contreras et al., 2011), can be quantified as a function of the growth of an individual tree compared with another individual tree, grown in open conditions. Our study of 12 CIs found a negative correlation of CI with growth for 10 indices. The observed positive correlation of CI_1 and CI_9 with growth was expected based on their mathematical formulation.

Seven of the CIs we tested were spatial indices, and most of these indices were better than the non-spatial indices in explaining growth (Table 3). This is consistent with previous studies of CIs, some of which showed that spatial indices were better than non-spatial indices at quantifying competition (Contreras et al., 2011; Maleki et al., 2015). In some cases where the inter-tree distances are approximately constant (plantation) or very low, non-spatial CIs also perform as well as spatial CIs (Martin and Ek, 1984; Corona and Ferrara, 1989). In the present study, spatial indices CI_{11} and CI_{12} were best at quantifying competition. We chose CI_{12} for subsequent modelling because this index

uses DBH which is less time consuming and less costly to measure than tree height, which is required for CI₁₁.

4.2 DBH increment models

4.2.1 Effect of tree size

In the present study, tree size (DBH and/or height) was a significant explanatory variable of growth and described the largest proportion of variation in DBH growth. In subtropical Queensland Australia, DBH showed a quadratic relationship with DBH growth for some eucalypt species and a linear relationship for other eucalypt species (Ngugi et al. 2015). Our study showed a power law relationship between DBH growth and DBH of individual trees. In the Mediterranean climate of SWWA, age and tree size have been shown to be positively correlated with volume growth in *E. globulus* (Acuna et al., 2017). In Northern Brazil, DBH described up to 98% of growth variation in *Eucalyptus* (Martins et al., 2014).

Tree size plays a crucial role in access to resources (Pretzsch, 2009; Landsberg and Sands, 2011), so it is not unexpected that it also is an explanatory variable of growth. Two reasons behind the positive relationship between tree size and growth are 1. Larger trees can capture more resources than smaller trees (e.g., the light at the top of the canopy, water at greater depth); 2. Larger trees have more photosynthetic surface area than smaller trees (Herault et al., 2011; Rüger and Condit, 2012). In tropical forests, taller trees have been found to have faster growth than shorter trees (Boyden et al., 2005; Muller-Landau et al., 2006; Rüger et al., 2011). Our study also showed that taller and larger diameter trees had a higher growth rate than shorter and thinner diameter trees. This is consistent with both the work of King et al. (2006) who showed that the greater the height of the tree, the greater the mean crown illumination, and with the metabolic theory of ecology (Enquist, 2002; Zhang et al., 2017). Based on the assumption that trees have an efficient transport system, and that photosynthetic

surface area increases as the number of leaves on a tree increase, the metabolic theory of ecology states that DBH growth increases with tree size by an invariant power law (Zhang et al., 2017). Many studies have confirmed this theory (e.g., Herault et al., 2011; Rüger and Condit, 2012) although growth rate does not always increase with size or age. Growth rate increases during sapling and immature stages of growth, peaks once the tree is mature and then eventually declines with further increase in the tree age or size (Gove et al., 2019). Individual trees growing in our study area are still far from reaching their maximum size. In both growth periods, the diameter growth of individual trees is increasing with an increase in DBH.

4.2.2 Effect of competition

Our results showed that competition was a significant explanatory variable in the thinned plots. Other studies have also found competition to be a significant explanatory variable in growth models (Vettenranta, 1999; Contreras et al., 2011; Vanclay et al., 2013; Maleki et al., 2015), including a study of *E. obliqua* in Australia which found neighbourhood density is a significant explanatory variable of growth along with tree size (Bi and Turvey, 1996). As the thinned plots in our study consist of plots with different stand densities ranging from heavily thinned to lightly thinned, the inter-tree distances are highly variable, introducing variation in magnitude of competition and its effect on growth. Inter-tree distances are a good explanatory variable of individual tree growth in irregular stands (Lorimer, 1983). Variation in stand density is therefore likely to be a cause of the significant effect of spatial CIs in our growth models for the thinned plots. Consistent with the other studies (Pretzsch, 1997; Contreras et al., 2011; Das et al., 2011; Zhang et al., 2017; Yang et al., 2019), we found a negative impact of competition on growth (Fig. 2a, b, c). This is due to a higher degree of competition reducing available resources and decreasing the growth of individual trees.

For the thinned plots, proxies of non-spatial CIs (the stand level variables, basal area, stem number per ha and thinning intensity) improved the model as a significant explanatory variable of growth, however, not at the level of improvement provided by the spatial CI (CI_{12}). When the non-spatial proxies, CI_{12} and tree size were used in the model, these proxies were not significant. This suggests that the non-spatial proxies may be useful as proxies of competition when spatial CIs are not available but provide no additional benefit when spatial CIs are available. We recommend that stand basal area or stem number per ha be used as explanatory variables in the absence of spatial CIs because use of thinning intensity as a non-spatial proxy restricts the applicability of growth models to thinned plots. Several studies have used these proxies in growth models. In a study of the growth of naturally regenerated *Fagus sylvatica*, Diaconu et al. (2015) used stand basal area in addition to tree size, release intensity and size to explain individual tree growth; the model described 73% of the variation in individual tree basal area growth. In a study of the growth of *Quercus species* and *Pinus echinata*, Lhotka and Loewenstein (2011) used stand basal area and stem number per ha to explain individual tree growth; the model described 26% to 57% of the variation in individual tree diameter growth. In a study of *Pinus resinosa* plantations, Martin and Ek (1984) concluded that the relative size of the subject tree and some of the stand density measures (plot basal area) performed best in explaining individual tree diameter growth.

For the unthinned plots, two proxies of non-spatial CIs (the stand level variables, stand basal area and stem number per ha) were significant explanatory variables of growth only in the second growth period. In contrast to the thinned plots, competition (CI_{12}) was not a significant explanatory variable in the unthinned plots. Different levels of thinning of this 100-year-old natural regrowth stand created variation in competition and inter-tree distances across the plots, which facilitated the development of growth models incorporating spatial CIs. In unthinned plots tree spacing is less variable, and low self-thinning ($0.20\% \text{ yr}^{-1}$ for jarrah) (Bhandari et al., 2021) pushes these plots

towards full stocking. In this situation, there is less variation in spatial CIs (all trees experience high levels of local competition), and thus they are less likely to be significant explanatory variables. The residual variation in all models must be due to other stochastic factors such as spatial variations in seed fall density, seed bed quality and soil moisture affecting early establishment; pre-existing lignotubers providing rapid establishment of some advanced growth; and preferential root access to soil moisture via root channels promoting growth of some individuals. Above-ground competition is not very strong in thinned plots (canopy opening and plentiful light), but may have strongly affected the growth in unthinned plots. Belowground competition is also reduced in thinned plots, but may be less constrained to nearest neighbours, as lateral roots extend well beyond the aboveground projection of trees.

4.2.3 Testing the number and distance of competitors

Our study showed that as many as 12 neighbour trees, up to a distance of 10 m, may influence the growth of subject trees. The number of, and distance to, competitors that influenced the growth of subject trees was greater in second growth period. There are two possible reasons for this difference. 1. As a tree increases in age and size, it occupies more space and requires more resources (Opie, 1968; Martin and Ek, 1984) resulting in competition over a larger area. 2. Declining rainfall; it is well known that moisture is a limiting factor for tree growth in SWWA (Burrows et al., 2010). Records indicate that rainfall in SWWA has been decreasing since the 1970s (BOM, 2019). For example, average annual rainfall from 1965 to 1984 was 1233 mm and from 1984 to 2010 was 1138 mm (BOM, 2019). As rainfall decreases, competition between trees increases as their roots search for moisture over a larger area (Casper et al., 2003; Deng et al., 2006) as well as greater depth of soil.

In a study in Canada, Canham et al. (2004) found no competitive effect of neighbouring trees that were growing beyond 8 m for western hemlock and 13 m for western red cedar. In a study carried

out in Norway spruce, Ledermann and Stage (2001) found that the competitive effect of neighbour trees depends on the social position of subject tree and competitors. In another modelling study, Stage and Ledermann (2008) concluded that the distance to significant competitors varied according to whether the subject tree was dominant, codominant or intermediate. Dominant subject trees were affected by competitors from a longer distance (16 m to 20 m) than intermediate subject trees (11 m to 16 m). Dominance status has been shown to affect competitive interactions between trees, but we had insufficient information to test this as a variable in the models. In any case dominance status is reflected by DBH and height which provide more objective and quantitative measures.

Though the growth of a subject tree was affected by as many as 12 neighbour competitors in our study, only some of these were close enough to affect light availability. It seems more likely that their root systems overlap in search of moisture and nutrients. Change in DBH was used as a reasonable simple first attempt at a proxy for resource use. The fact that it did not add significantly to the model does not exclude the possibility that another proxy of resource use might perform better. We acknowledge that a proxy based on the estimated change in area/volume/biomass may perform better, and should be considered in future work. Analysing the directional effect of competitors may help to understand the extent to which individual trees in the jarrah forest compete for above- vs below-ground resources. In the southern hemisphere, competition for above ground resources (light) may be greatest with competitors growing north of a subject tree, however, we did not evaluate the effect of competitors from separate directions. Evaluating the effect of competitors from north vs south direction or east vs west direction on growth of subject tree is a potential field of future study.

5 Conclusions

Individual tree-level growth of jarrah varies with tree size but models explaining jarrah growth can be significantly improved by adding competition indices (CI). Spatial CIs performed better than

non-spatial CIs. The spatial CI was a significant explanatory variable only in thinned plots. Explanation of diameter growth can be optimized if 10 to 12 competitors (by number) or competitors within ~10 m (by distance) from the base of the subject tree are included in the model. As competition from neighbours was a significant explanatory variable with a negative effect on growth, we recommend including neighbourhood competition when explaining/predicting growth and when considering thinning treatments to minimize the effect of competition on growth. The optimized distance and number of competitors in this study may be helpful in identifying which trees should be removed in subsequent thinning operations to optimise growth of the retained stand, recognising that trees may be retained to meet objectives other than productive potential including as wildlife habitat and for cultural and aesthetic reasons. Further studies in evaluating the directional effect of competitors might provide insight into identifying the extent to which competition in the jarrah forest is above ground or below ground or both.

Conflict of Interest: The authors declare that they have no conflict of interest.

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CHAPTER 6

Investigating the effect of neighbour competition on individual tree growth in thinned and unthinned eucalypt forests

PREAMBLE

This chapter presents a new CW and distance-based CI; individual tree growth models; optimal number and distance of competitors that needs to be considered when accounting for competition; validation and sensitivity analysis of developed models in thinned and unthinned karri and marri forests.

It is presented as the manuscript published at *Forest Ecology and Management* (<https://doi.org/10.1016/j.foreco.2021.119637>). Formatting is that specified by the journal with the exception of minor editing and page numbering.

Investigating the effect of neighbour competition on individual tree growth in thinned and unthinned eucalypt forests

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Highlights

- A new crown-width and distance-based competition index was developed.
- Diameter and age are significant predictors of individual tree growth.
- Growth prediction is improved by including competition in the model.
- Including up to 14 competitors around the target tree improves growth predictions.
- Including competitors up to ~7 m from the target tree improves growth predictions.

Abstract

Competition from neighbouring trees generally has a negative effect on the growth of an individual tree; however, the magnitude of competition is expected to vary with size and proximity of the tree and its competitors. Eucalypt forests (natural/plantation) are widespread throughout the world, and have high economic, ecological and conservation importance. Recent work carried out in eucalypt forest of Western Australia showed that growth of individual trees could be explained by a flexible novel competition index that accounts for proximity and size of competitors. This study aimed to further test and extend those methods, by applying them to long-term time-series data on thinned and unthinned plots of two important new species (karri and marri) in a more productive environment. More specifically, we aimed to compare the usefulness of different competition indices (CIs) including a novel index using crown-width; develop models to understand and predict the growth of karri and marri individuals, using tree size and age; test whether including measures of neighbourhood competition would improve growth predictions for these species; validate the predictive ability of the models and analyse the sensitivity of their parameters; and investigate how many neighbouring trees or what neighbourhood distance needed to be considered when accounting for competition. Our new crown-width CI was useful, but not as useful as previous diameter-based CI. Diameter and age were significant predictors, and prediction was further improved by inter-tree competition. Leave-one-out cross-validation showed that our models are well validated, and sensitivity of karri model parameters was less than 13% while sensitivity of marri model parameters was a little higher (<20%). Including up to 14 competitors or competitors within ~7 m distance from the base of the target tree was optimal in predicting growth. Our new models and methods may help to identify trees to be removed during thinning and assist in determining the appropriate size of plots for studying the effect of competition on individual tree growth. New insights from this study include the individual tree growth models for karri and marri; validation and sensitivity analysis of these models; improved understanding of competition for two important new eucalypt species; a new crown and distance-based CI; and

evidence for the usefulness of our recently developed diameter and distance-based CI for two new species.

Key words: Neighbourhood competition, Tree size, Growth, Model, Thinning

1 Introduction

Competition generally has a negative effect on the growth of individual trees; however, the magnitude of competition varies with size and proximity of the competitors. Large and near competitors have higher competitive stress than small and distant competitors (Opie, 1968; D'Amato and Puettmann, 2004; Weiner et al., 2009; Forrester et al., 2011; Forrester et al., 2013; Bhandari et al., 2021a). Past studies had shown that competition in forest trees can be one-sided (asymmetric) (above-ground competition for light) and/or two-sided (symmetric) (below-ground competition for water and nutrients) (Kikuzawa and Umeki, 1996; Kohyama and Takada, 2009), or in reality, lie somewhere between these two extremes (Yokozawa & Hara, 1992). The degree of symmetry/asymmetry is likely to depend on a range of different factors (Forrester 2019). The magnitude of competition imposed on individual trees can be estimated using spatial and non-spatial competition indices (CIs). Spatial CIs have been reported to perform better than non-spatial CIs (Contreras et al., 2011; Maleki et al., 2015), but non-spatial CIs have performed as strongly as spatial CIs in plantations where inter-tree distance are similar (Martin and Ek, 1984; Corona and Ferrara, 1989).

Individual-based modelling (IBM), also called agent-based modelling, is one of the most appropriate modelling approaches to predict the growth of individual trees in heterogeneous and structurally complex forests (Grimm, 1999; Grimm and Railsback, 2005; DeAngelis and Grimm, 2014). This modelling approach is applicable in simulating future forest management scenarios

(Vospernik, 2017), predicting wood quality (Sterba et al., 2006), predicting habitat quality (Vospernik and Reimoser, 2008) and planning forest management activities (Weiskittel et al., 2016). Unlike population models described as “top down” models, IBM are “bottom up” models in which population level behaviour emerges from interactions among individual trees and their abiotic environment (DeAngelis and Grimm, 2014). The ability to include any number of individual-level mechanisms in IBM is one of the advantages of IBM. In IBM, individual tree interactions are represented in more detail than would be possible in more aggregated modelling approaches such as stand-level modelling approaches (Zhang and Lei, 2010; DeAngelis and Grimm, 2014). Individual-based models represent a relatively detailed and complex modelling approach because input information is provided at the individual tree level (DeAngelis and Grimm, 2014). Individual-based models are capable of describing the variation that exists in individual trees of a forest or stand, and assume that those individual trees interact locally, and adapt differently to their diverse local environments (Berger *et al.*, 2008; DeAngelis and Grimm, 2014). Whilst more complex and detailed modelling approaches have been developed and implemented, such as functional structural plant models that can describe the development of the three-dimensional architecture and structure of plants at the scale of individual tree organs (Xu *et al.*, 2011; Guo *et al.*, 2011; Wang et al., 2020), these modelling approaches are relatively complex for representing the growth and interaction between large numbers of trees growing in the forest. Across the various modelling approaches, different predictor variables have been used (diameter, height, age, crown width, basal area and density) (Zhang et al., 2016; Ford et al., 2017; Luo et al., 2019; Ou et al., 2019).

Diameter at breast height (DBH), height and age of individual trees have been commonly used as predictors in individual tree growth models, as these variables are measured routinely in forest inventories (Martins et al., 2014; Gyawali et al., 20015; Lhotka and Loewenstein, 2011; Lhotka, 2017). The use of DBH as a predictor variable is more common than height (Gyawali et al., 2015; Ou

et al., 2019) because it is cost effective, readily measured to a high level of accuracy and highly correlated to individual tree volume (Sileshi, 2014; Kuyah and Rosenstock, 2015). In general, an individual tree's relative growth rate is rapid during early age (seedling and sapling stage), stabilises during middle age (pre-mature stage) and then declines during the mature and senescent stages (Schongart et al., 2015; Chaturvedi and Khanna, 2011). Absolute growth rates, however, tend to increase with size. Larger trees have more access to light, space and nutrients, and thus have faster girth and height growth rates compared to smaller trees (Stephenson et al., 2014). Large sized trees generally have a greater photosynthetic area and therefore growth is mechanistically related to size by an invariant power law (Enquist, 2002). Other than tree size, competition is another important factor that influences individual tree growth (Coomes and Allen, 2007; Zhang et al., 2016; Ford et al., 2017; Tomlinson et al., 2018; Junior et al., 2019; Luo et al., 2019).

Karri (*Eucalyptus diversicolor* F. Muell.) forms tall open forests in high rainfall areas of south-west Western Australia (SWWA) (Bradshaw, 2015; Bhandari et al., 2021b). Approximately 65% of karri forest occurs as a mixed forest with marri (*Corymbia calophylla*; a eucalypt formerly known as *Eucalyptus calophylla*) and to a lesser extent with jarrah (*E. marginata*), red tingle (*E. jacksonii*), yellow tingle (*E. guilfoylei*) and Rate's tingle (*E. brevistylis*) (Bradshaw et al., 1997). Famous for its beauty (karri trees are one of the largest trees in the world), the karri forest is important for conservation, tourism, recreation, wild habitat, water regulation and timber production (Bradshaw, 2015). Karri forests are, however, susceptible to threats including fire and drought (McCaw et al., 2000; Robinson et al., 2003; McCaw and Middleton, 2015; Etchells et al., 2020). Thinning can be used to promote the growth of future crop trees and utilise wood from smaller trees that would otherwise be died due to competition-induced mortality. Thinning in some cases may also reduce fire intensity (Banerjee, 2020) and increase water availability to the retained trees (Ruprecht et al., 1991). As noted above, the karri and marri forests of SWWA have environmental and economic value, yet

global warming and climate change are likely, in the future, to affect their growth, development and sustainable management. Individual-based models which can predict future growth can be supportive tools in the sustainable management of these forest in the long term. An individual tree growth model has been recently developed by Bhandari et al. (2021a) for another south-west Western Australia eucalypt species, jarrah, for a lower rainfall location, but this was not validated, or sensitivity analysed. The optimal number and distance of competitors for explaining jarrah growth was also analysed in that study. However, similar models explaining and ideally predicting individual growth of karri and marri are lacking, as is understanding of the optimal number and distance of competitors for understanding and predicting growth of karri and marri.

The general aim of this study was to develop and test approaches for explaining and predicting growth in diameter of karri and marri at the individual tree level using long-term data on karri and marri forest managed under different thinning regimes in a predominantly even-aged stand of 49-year-old regrowth forest in SWWA. More specifically, we aimed to 1) compare the usefulness of a range of different CIs in predicting growth; 2) develop a growth model based on size and age and then test whether including competition in the model improves growth prediction; 3) validate the developed models and conduct a sensitivity analysis for their parameters; 4) determine how many neighbouring trees and what neighbourhood distance should be considered when accounting for competition. We hypothesized that including competition would improve growth predictions and that the predictive ability of the model would initially increase, then reach a peak and decrease as the number or distance of competitors from the base of target tree increased. We also hypothesized that the optimum number and distance of competitors required to predict the growth for karri is larger than that required for jarrah because the karri trees are bigger.

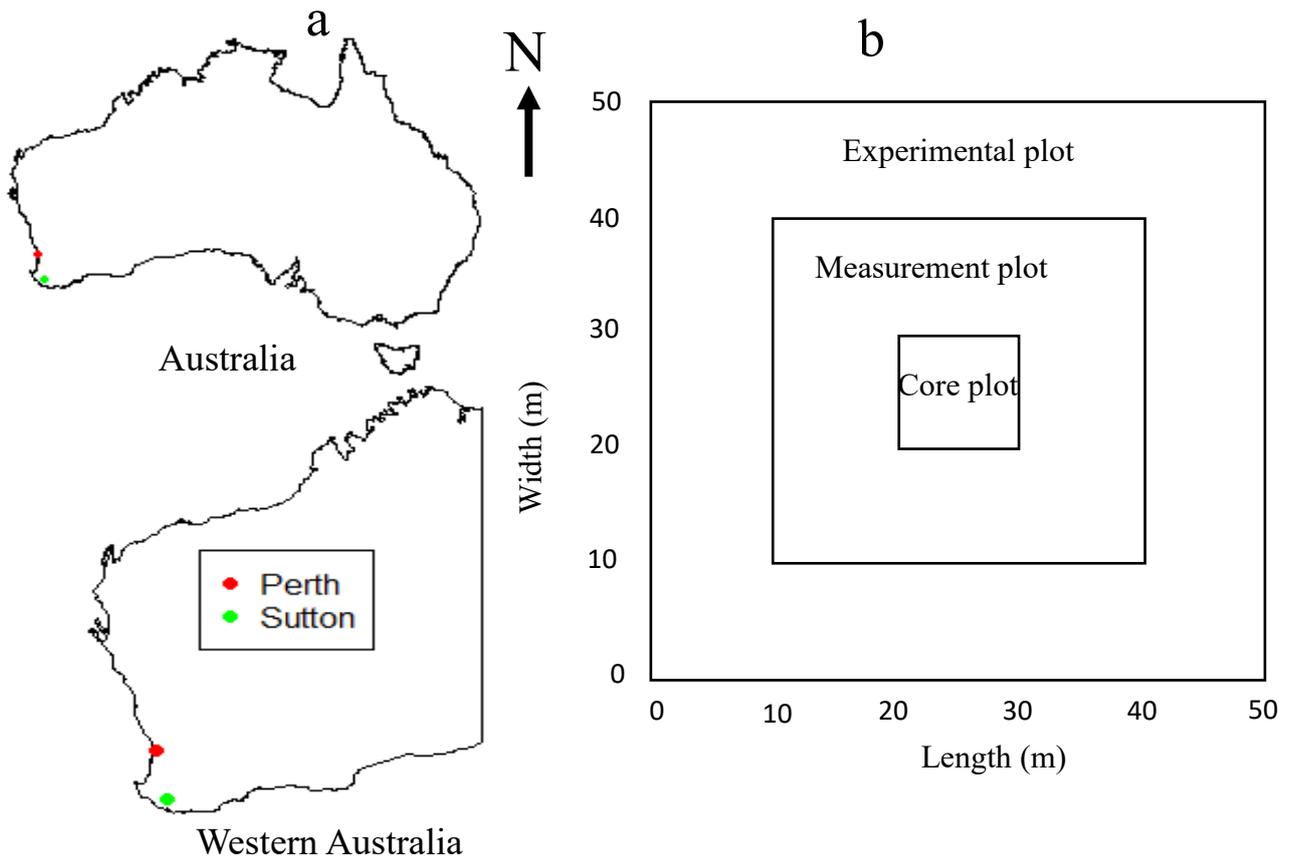


Fig. 1. Map of Australia and Western Australia showing study site (a); size and shape of experimental plot, measurement plot and core plot (b). N denotes north azimuth.

2 Materials and methods

2.1 Study area

The study area is located in karri-dominated forest in Sutton block, 40 km southeast of Manjimup, SWWA (Latitude $34^{\circ} 28'$ and longitude $116^{\circ} 20'$) (Fig. 1). The forest was clear-felled in 1969 with retention of seed trees, and was thus 49 years old in 2018 when the most recent tree measurements were carried out. Overstorey species composition was karri (86% of number of trees), marri (13%) and jarrah (1%). The site has a Mediterranean climate with an average annual rainfall of 980 mm (measured in Manjimup station from 1915 to 2019). The highest mean monthly maximum temperature is 27.20°C in January and the lowest mean monthly minimum temperature is 6.40°C in July (BOM, 2019).

2.2 Thinning treatment

The Sutton thinning trial consists of 27 plots (size 30 m × 30 m plus an outer 10 m experimental buffer on all sides that received the same thinning as the plots). Plots were denominated karri if the basal area over bark (BAOB) of karri was >75% and top height was ≥20 m and marri plots if the BAOB of marri was >60% and top height was ≥18 m. This gave a total of 19 plots for karri and 8 plots for marri. Due to the very small proportion of jarrah trees, separate plots were not established for jarrah. Karri plots were thinned non-commercially to six different thinning treatments (T1-T6), with each treatment being a different stand density, in 1992 (23 years after clear-felling) as follows: 34 (T1), 20 (T2), 16 (T3), 13 (T4), 10 (T5) and 7 (T6) m² ha⁻¹ basal area over bark (BAOB). Marri plots were also thinned to four different thinning treatments (T1-T4), with each treatment being a different stand density, in 1992 as follows: 37 (T1), 19 (T2), 15 (T3) and 10 (T4) m² ha⁻¹ BAOB. Treatment T1 represents unthinned (control) plots for both species.

2.3 Sampling and measurement

Diameter at breast height (DBH) of all the trees and height and crown radius (CR) of a subsample of trees was measured in 1992, 1997, 2002, 2010 and 2018. At least 10 trees located at or near the centre of each plot were selected for measurement of height and CR, ensuring that they were a representative sample. In 1992, the position of each tree was mapped using azimuth and distance from the plot centre. As the forest was clear felled in 1969 and then regenerated, the age of the forest at first thinning in 1992 was 23 years, then 28 in 1997, 33 in 2002, 41 in 2010 and 49 years in 2018 (the last inventory). For the models, we used field measured height for those trees which were measured in the field. Height prediction models were developed from the field measured data and used to predict the height for those trees whose height was not measured in the field using equations 1-3, following a mixed effect modelling approach with plot-level random effect. The parameters of

each model were estimated using the maximum likelihood method in the nlme package in R (Pinheiro et al., 2018; R Core Team, 2019). We fitted height prediction models for each measurement time separately and predicted the height of the individual trees which were not measured in the field.

$$height_{ij} = 1.3 + \frac{(dbh_{ij})^2}{\alpha_0 + \alpha_1 \times dbh_{ij} + \alpha_2 \times (dbh_{ij})^2} + u_j + \varepsilon_{ij} \quad Eq (1) \text{ karri}$$

$$height_{ij} = 1.3 + \alpha_0 + \alpha_1 \times dbh_{ij} + u_j + \varepsilon_{ij} \quad Eq (2) \text{ marri}$$

$$height_{ij} = 1.3 + \frac{\alpha_0 \times (dbh_{ij})^2}{(dbh_{ij} + \alpha_1)^2} + u_j + \varepsilon_{ij} \quad Eq (3) \text{ jarrah}$$

In these equations, $height_{ij}$ is the estimated height of the i^{th} tree on the j^{th} plot, dbh_{ij} is the diameter at breast height of the i^{th} tree on the j^{th} plot, α_0 , α_1 and α_2 are fixed effect parameters, u_j is the random effect for the j^{th} plot and ε_{ij} is the unexplained residual error for the i^{th} tree on the j^{th} plot. For the competition models, we used field measured crown width ($CW = 2 \times \text{mean CR}$) for those trees which were measured in the field. Crown width prediction models were developed from the field measured data and used to predict the CW for those trees whose CW was not measured in the field, using equation 4 following a mixed effect modelling approach using plot-level random effect. The model parameters were again estimated using the maximum likelihood method in the nlme package in R (Pinheiro et al., 2018; R Core Team, 2019). We fitted crown width prediction models for each measurement time separately and predicted the crown width of the individual trees which were not measured in the field. We estimated different species-specific coefficients for each measurement time to predict the crown width of the individual trees which were not measured in the field.

$$CW_{ij} = \alpha_0 \times dbh_{ij}^{\alpha_1} + \mu_j + \varepsilon_{ij} \quad Eq (4)$$

In this equation, cw_{ij} is the estimated crown width of the i^{th} tree on the j^{th} plot, dbh_{ij} is the diameter at breast height of the i^{th} tree on the j^{th} plot, α_0 and α_1 are fixed effect parameters, u_j is the random effect for the j^{th} plot and ε_{ij} is the unexplained residual error for the i^{th} tree on the j^{th} plot. The summary of the data used in the modelling is presented in Table 1.

Table 1 Descriptive statistics of the data used in this study. Diameter at breast height (DBH), height and crown width (CW) are individual tree level variables while basal area and stem number per ha are stand level variables.

Species	Variables	Mean±std.(range)		
		1992	2002	2018
Karri	DBH (cm)	16.6±5.8(1.9-34.8)	22.3±6.9(4.1-45.0)	29.8±8.7(10.1-55.1)
	Height (m)	18.3±3.0(2.3-25.6)	23.2±3.5(11.0-32.7)	30.7±5(14.5-42.1)
	CW (m)	3.3±0.9(1.3-6.0)	4.8±1.6(1.2-10.5)	5.5±2.2(0.8-11.3)
	Basal area (m ² ha ⁻¹)	15.4±7.7(6.8-36.8)	23.9±8.7(13.2-48.1)	34.6±7.5(23.3-55.7)
	Stem number ha ⁻¹	627±564(178-2378)	574±426(178-1833)	487±252(178-1200)
Marri	DBH (cm)	16.0±6.3(1.7-35.3)	19.9±7.7(3.4-47.4)	24.4±9.2(3.7-65.2)
	Height (m)	16.1±2.4(9.8-20.5)	18.9±3.2(10.0-29.0)	22.4±4.2(10.9-33.8)
	CW (m)	2.7±0.74(1.3-5.8)	4.3±1.4(1.5-9.8)	3.8±1.4(1.0-9.0)
	Basal area (m ² ha ⁻¹)	20.1±10.7(10.0-36.6)	29.5±11.6(17.3-47.7)	41.1±14.3(24.6-62.2)
	Stem number ha ⁻¹	1021±1152(233-3389)	921±958(244-2856)	790±738(200-2289)
Jarrah	DBH (cm)	8.6±3.3(2.0-24.0)	9.3±4.1(2.7-33.2)	11.3±5.3(4.5-42.9)
	Height (m)	11.6±2.9(8.6-16.7)	17.9±4.6(12.7-21.6)	22.1±8.9(15.8-28.5)
	CW (m)	1.8±0.5(1.5-3.2)	4.3±1.6(2.8-6.0)	4.4±4.3(1.4-7.5)
	Basal area (m ² ha ⁻¹)	2.3±2.5(0.3-6.3)	2.5±2.5(0.5-6.5)	2.7±2.4(0.7-6.2)
	Stem number ha ⁻¹	340±471(11-1133)	309±442(11-1067)	218±314(11-767)

Periodic annual increment (PAI) for each growth-period was calculated as the change in DBH over the growth-period divided by the number of years, hereafter referred to as Δ DBH. For modelling purposes, we defined a core inner plot of 10 m \times 10 m. The target trees for modelling purposes were selected only from the central core plot, to ensure sufficient detail was available for all competitors for all target trees; this ensured we had full details on all competitor trees within 10 m of every target tree. Δ DBH differed significantly between species ($P < 0.001$) (Fig. 2d). Therefore, separate growth models for the two species (karri and marri) were developed. We did not develop a model for jarrah, as the number of individual trees of jarrah was small, but individual jarrah trees were included as competitors wherever they were present.

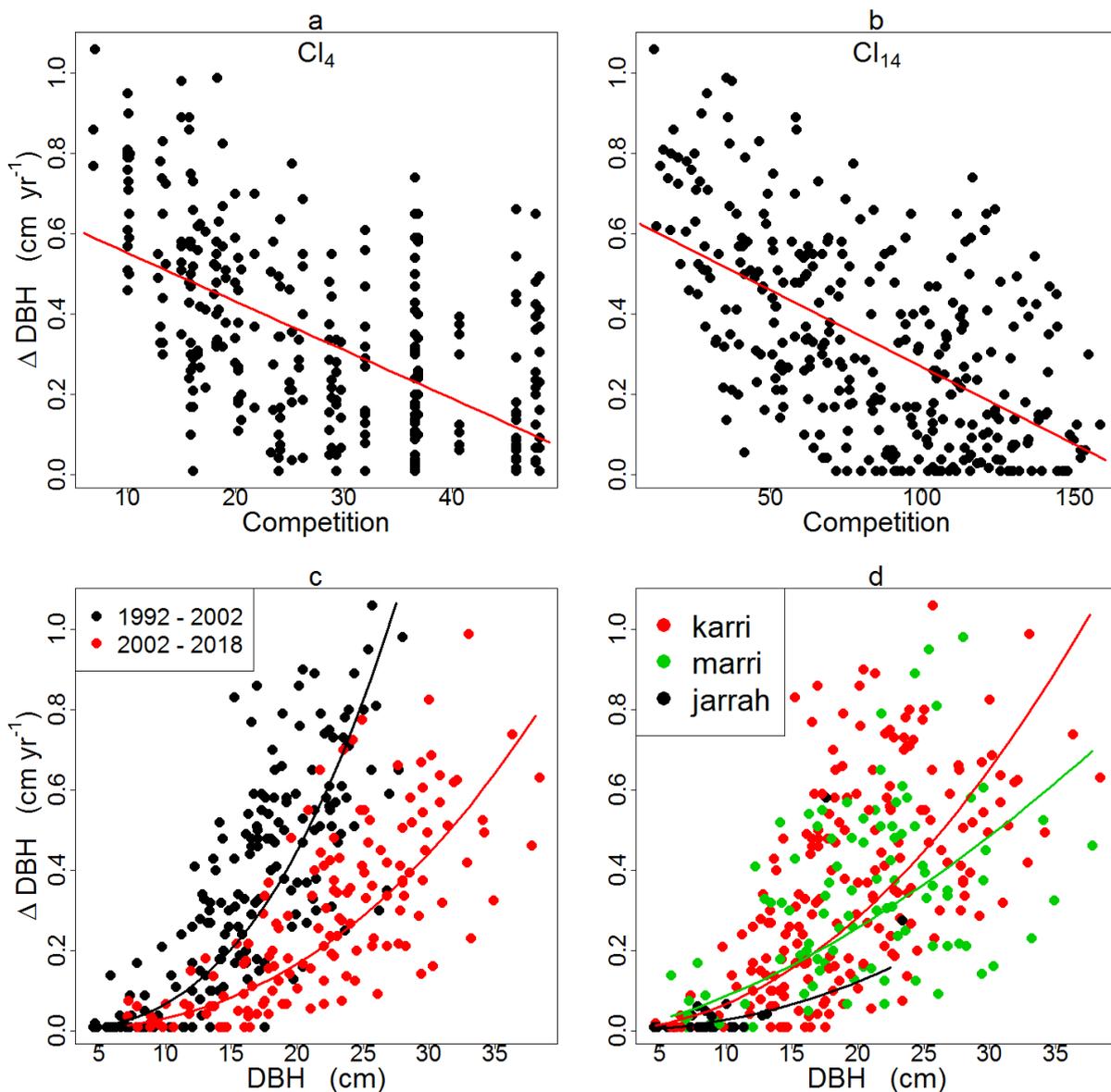


Fig. 2. Growth (Δ DBH) with respect to, (a) a non-spatial CI (CI_4); (b) a spatial CI (CI_{14}); and (c) DBH growth at two different growth periods; (d) DBH growth for three different tree species. The fitted equations are for (a) $\Delta dbh = 0.67 - 0.01(CI_4)$, $P < 0.001$; (b) $\Delta dbh = 0.65 - 0.003(CI_{14})$, $P < 0.001$; (c) 1992-2002: $\Delta dbh = -8.94 + 2.71 \log(dbh)$, $P < 0.001$; 2002-2018: $\Delta dbh = -8.95 + 2.39 \log(dbh)$, $P < 0.001$; (d) karri: $y = -7.42 + 2.05 \log(dbh)$, $P < 0.001$; marri: $y = -6.03 + 1.56 \log(dbh)$, $P < 0.001$; jarrah: $y = -8.43 + 2.11 \log(dbh)$, $P < 0.001$.

2.4 Compare the usefulness of a range of different CIs (Aim 1)

Fourteen different competition indices (CIs) (five non-spatial and nine spatial) were used to quantify the level of competition experienced by the target tree (target tree in this study is defined as the tree whose growth is being predicted) (Table 2). Thirteen indices (five non-spatial and eight spatial) were selected from the scientific literature (Lorimer, 1983; Dale et al., 1985; Contreras et al., 2011; Maleki et al., 2015; Bhandari et al., 2021a), by considering available tree variables. One new spatial index, CI_{13} , which uses the CW of each competitor and the distance between the target tree and each competitor, was developed during this study.

For CI_{13} we assumed that the competitive effect of each neighbouring tree depends linearly on the CW of the tree and declines exponentially with distance, and that the total competitive effect on a target tree is the sum of the competitive effects of all other individual trees. The rate of exponential decline is determined by a parameter k , and the numerical value of k was estimated by finding the value that gave the best model fit for all data across all plots (based on model AIC, where lower AIC indicates better model fit). A Pearson correlation matrix was used to evaluate the relationship of the 14 CIs with each other and with DBH growth. This new index CI_{13} is similar to the index we recently developed and tested for jarrah, CI_{14} , but CI_{14} uses DBH instead of CW.

Table 2 Different competition indices (non-spatial competition indices CI₁ to CI₅ and spatial competition indices CI₆ to CI₁₄) used in this study. Note: dbh_i=DBH of ith target tree, dbh_j= DBH of jth competitor, dist_{ij}= distance between ith target tree and jth competitor tree, k=power, height_i= height of ith target tree, height_j=height of jth competitor, g_j = basal area of competitor trees (m² ha⁻¹), mcr= Mean crown radius, b=mcr expansion factor (A value of 3.5 was assumed based on recommendations of previous studies), cw_j=Crown width of jth competitor, cw_i=Crown width of ith target tree, S= area of plot, d_q= quadratic mean diameter (square root of the arithmetic mean of squared values of DBH), N= Number of stems per ha.

Indices	References	Equations
CI ₁	Corona and Ferrara (1989)	$\sum_{j \neq i} \frac{dbh_j^2}{dbh_i^2}$
CI ₂	Wykoff (1990)	$\sum_{j \neq i} (dbh_j^2) \times 0.00007854$
CI ₃	Corona and Ferrara (1989)	$\sum_{j \neq i} \frac{cw_j}{cw_i}$
CI ₄	Steneker and Jarvis (1963)	$\frac{\sum_{j \neq i} (g_j)}{S}$
CI ₅	Reineke (1933)	$10^{(\log N + 1.605 \times \log d_q - 1.605)}$
CI ₆	Hegyí (1974)	$\sum_{j \neq i} \frac{dbh_j}{dbh_i \times dist_{ij}}$
CI ₇	Hegyí (1974)	$\sum_{j \neq i} \frac{cw_j}{cw_i \times dist_{ij}}$
CI ₈	Corona and Ferrara (1989)	$\sum_{j \neq i} \left(\frac{dbh_j}{dbh_i} \times \left(\frac{b \times mcr}{dist_{ij}} \right) \right)$
CI ₉	Lin (1974)	$2 \sum_{j \neq i} \arctan \left(\frac{dbh_j}{2 dist_{ij}} \right)$
CI ₁₀	Rouvinen and Kuuluvainen (1997)	$\sum_{j \neq i} \arctan \left(\frac{dbh_j}{dist_{ij}} \right)$
CI ₁₁	Rouvinen and Kuuluvainen (1997)	$\sum_{j \neq i} \left(\frac{height_j}{height_i} \right) \times \arctan \left(\frac{height_j}{dist_{ij}} \right)$

CI ₁₂	Braathe (1980)	$\sum_{j \neq i} \frac{height_j}{height_i \times dist_{ij}}$
CI ₁₃	This study	$\sum_{j \neq i} cw_j * \exp(k * dist_{ij}))$
CI ₁₄	Bhandari et al. (2021a)	$\sum_{j \neq i} dbh_j * \exp(k * dist_{ij}))$

2.5 Development of growth models based on size and age (with/without competition) (Aim 2)

Mixed effect modelling approach was used considering Δ DBH of individual tree as the response variable and tree size and age as the predictor variables. We used initial DBH, square of initial DBH, initial height, square of initial height, initial CW, square of initial CW, initial age and square of initial age as the fixed effect, plot ID as the plot-level random effect and individual tree ID as the individual tree-level random effect to account for possible correlations among trees within plots and correlations among repeated measurements at different times on the same tree. Multicollinearity among independent variables was evaluated using variance inflation factor (VIF) with a threshold of $VIF > 5$ considered to indicate problematic multicollinearity (Sileshi, 2014). In the beginning, we fitted a model with all available independent variables and then selected the model with only significant predictor variables that did not show multicollinearity. We found the model with initial DBH and initial age as the predictor variable performed better than with other variables. The non-independent predictive ability of the models was evaluated using three fit statistics (estimated at the population level, i.e., without random effects: R^2 , RMSE (Montgomery et al., 2001) and AIC (Akaike, 1972).

Inter-tree competition in the form of a spatial competition index (CI₁₄) was added to the models without competition developed in this study, in order to evaluate whether accounting for

competition would improve prediction of individual tree growth. In further analyses, stand level variables (initial stem number per ha and initial stand basal area) were included separately, to observe whether these variables further improved the model fit.

2.6 Validation and sensitivity analysis (Aim 3)

The ability of the models to predict independent data was validated using the leave-one-out cross-validation (LOOCV) method, in which all observations from one plot at a time were left out as independent validation data, the model refitted to the reduced data set, and then the refitted model used to predict the left out observations. This process was repeated until observations from each plot had been used as validation data, giving an independent prediction for each observation. We calculated R^2 and RMSE for these independent validation predictions in comparison to the real observations, and also plotted predicted DBH growth against the observed DBH growth. Predicted values for validation were estimated at the population level, i.e., without random effects, thus testing the ability of our model to predict for new plots. To measure the sensitivity of model parameters to the precise data included, we also recorded the fitted model parameter value each time we left out observations from one plot for validation, and finally calculated the coefficient of variance (CV) of all these recorded values for each predictor variable. We also repeated this sensitivity analysis leaving out one tree at a time, rather than one plot at a time.

2.7 Testing the effect of number and distance of competitors on the model (Aim 4)

We followed the methods of Bhandari et al. (2021a) to test the effect of number and distance of competitors on the predictive ability of the growth model, and determine the optimal number and distance of competitors. For this analysis, we divided the data sets into two growth periods (1992 to 2002 or first growth period and 2002 to 2018 or second growth period) to observe whether the optimal number and distance of competitor varies between first and second growth period.

3 Results

3.1 Comparing different competition indices

Correlation among CIs and between Δ DBH and each of the CIs is presented in Table 3. The correlation coefficients among spatial CIs (0.25 to 1) were greater than those among non-spatial CIs (-0.22 to 0.89). All the competition indices had a negative correlation with Δ DBH. Indices CI_1 and CI_4 from the group of non-spatial CIs, and CI_{11} and CI_{14} from the group of spatial CIs had the highest negative correlation with Δ DBH (Table 3). Correlations of spatial CIs with Δ DBH were generally stronger than correlations of non-spatial CIs with Δ DBH. The CI_{11} and CI_{14} were equally correlated with Δ DBH, however, we selected CI_{14} for further use in the modelling because DBH can be measured easily and more accurately than the height of the individual trees. Even though CI_4 performed nearly as well as these two spatial CIs, we wanted to use a spatial CI to allow us to account for differences in competition among trees within the same plot. Growth of target trees decreased with an increase in competition (Fig. 2a, b).

Table 3 Pearson rank correlation matrix of competition indices (non-spatial competition indices CI₁ to CI₅ and spatial competition indices CI₆ to CI₁₄) and Δ DBH. Correlation values are presented below the diagonal and p-value of correlation test is presented above the diagonal.

CI ₁	0.77	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.02	CI ₂	0.96	0.06	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	0.18	<0.01	0.42	<0.01	<0.01
0.87	-0.01	CI ₃	<0.01	<0.01	<0.01	<0.01	0.13	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.32	0.10	0.34	CI ₄	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.34	-0.22	0.35	0.89	CI ₅	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.68	-0.25	0.58	0.49	0.56	CI ₆	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.77	-0.25	0.80	0.43	0.50	0.91	CI ₇	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.25	0.14	0.08	0.58	0.51	0.69	0.45	CI ₈	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.44	0.25	0.48	0.81	0.69	0.51	0.45	0.63	CI ₉	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
0.43	0.23	0.47	0.78	0.68	0.49	0.43	0.60	1.00	CI ₁₀	<0.01	<0.01	<0.01	<0.01	<0.01
0.85	0.07	0.93	0.49	0.46	0.61	0.77	0.25	0.65	0.65	CI ₁₁	<0.01	<0.01	<0.01	<0.01
0.68	-0.28	0.68	0.51	0.59	0.96	0.97	0.61	0.52	0.50	0.71	CI ₁₂	<0.01	<0.01	<0.01
0.43	0.05	0.43	0.81	0.77	0.65	0.59	0.67	0.84	0.81	0.55	0.65	CI ₁₃	<0.01	<0.01
0.46	0.17	0.48	0.87	0.76	0.59	0.53	0.68	0.95	0.93	0.63	0.60	0.94	CI ₁₄	<0.01
-0.56	-0.16	-0.52	-0.56	-0.48	-0.52	-0.48	-0.37	-0.55	-0.54	-0.58	-0.48	-0.51	-0.58	Δ DBH

3.2 DBH growth modelling with / without competition

3.2.1 Karri

Initial DBH ($P < 0.001$) and age ($P < 0.001$) explained more than 56% of the variation ($R^2 = 0.5648$, $RMSE = 0.2025$, $AIC = 1072$) in log-transformed DBH growth of karri (Eq. 5). Inclusion of competition (CI_{14} , $P < 0.001$) along with initial DBH and age as predictor variables increased R^2 from 0.5648 to 0.6031, decreased RMSE from 0.2025 to 0.1947, and AIC from 1072 to 1038 (Eq. 6) (Table 4). In both models for both species, DBH has a positive correlation with growth and age has a negative correlation. Similarly, competition also has a negative correlation with the growth of individual trees.

$$\log(\Delta dbh) = 1.9911 + 2.6415 \log(dbh) - 3.3367 \log(age) \quad Eq (5)$$

$$\log(\Delta dbh) = 2.0755 + 2.7287 \log(dbh) - 3.4020 \log(age) - 0.0477 CI_{14} \quad Eq (6)$$

3.2.2 Marri

Initial DBH ($P < 0.001$) and age ($P < 0.001$) explained more than 39% variation ($R^2 = 0.3931$, $RMSE = 0.2142$, $AIC = 533$) in log-transformed DBH growth of marri (Eq. 7). Inclusion of competition (CI_{14} , $P = 0.002$) along with initial DBH and age as predictor variables increased R^2 from 0.3931 to 0.4219, decreased RMSE from 0.2142 to 0.2076 and AIC from 533 to 525 (Eq. 8) (Table 4).

$$\log(\Delta dbh) = 2.1560 + 1.6364 \log(dbh) - 2.5303 \log(age) \quad Eq (7)$$

$$\log(\Delta dbh) = 1.5624 + 1.5222 \log(dbh) - 2.0792 \log(age) - 0.0031 CI_{14} \quad Eq (8)$$

Table 4 Fit statistics for models with and without stand level variables. Note: ns means that adding the stand level predictor variable did not significantly improve the model fit at a 95% confidence level; fit statistics are not shown in these cases. * indicates models that include the CI.

Species	Eqs.	Fit statistics	Model without stand-level variables	Models with stand level variables	
				Stem number per ha	Stand basal area
Karri	Eq. 5	R ²	0.5648	ns	0.5739
		RMSE	0.2025		0.1969
		AIC	1072		1067
	Eq. 6*	R ²	0.6031		
		RMSE	0.1947	ns	ns
		AIC	1038		
Marri	Eq. 7	R ²	0.3931	ns	0.4027
		RMSE	0.2142		0.2119
		AIC	533		529
	Eq. 8*	R ²	0.4219		
		RMSE	0.2076	ns	ns
		AIC	525		

Table 4 presents results obtained when the stand level variables (initial stem number per ha, initial stand basal area) as predictor was added separately to the basic models (model with tree size, age and/or CI₁₄). Stand level variables were significant predictors and improved the models when the competition index (CI₁₄) was not used as predictor variable.

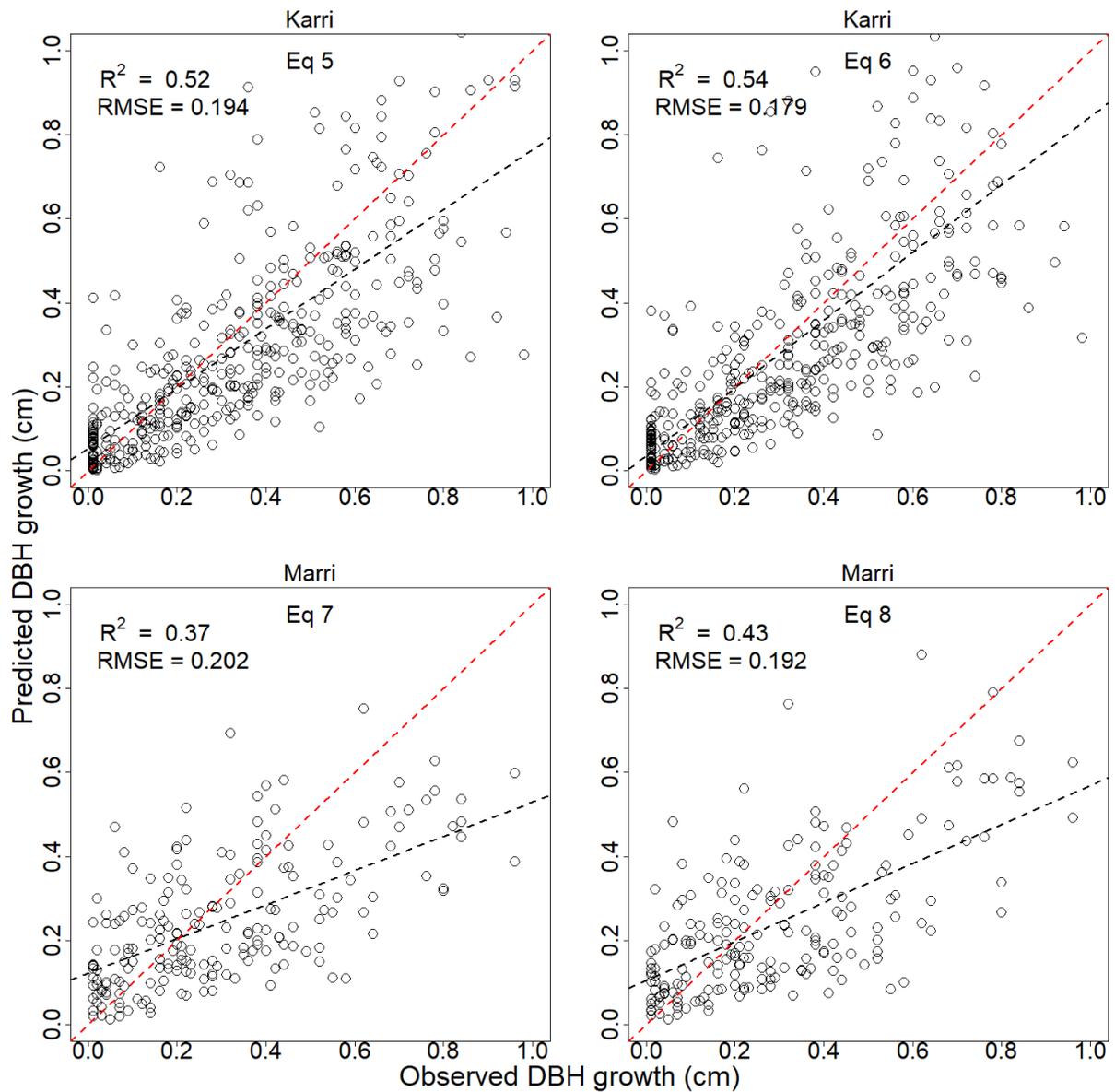


Fig. 3. Leave-one-plot-out cross-validation of models. Equation 5 and equation 7 are the models without competition. Equation 6 and equation 8 are the models with competition (CI_{14}). The red dotted line in each figure is the 1:1 reference line and the black dotted line is the best fit line. R^2 is coefficient of determination and RMSE is root mean squared error.

3.3 Validation and model parameter sensitivity analysis

Validation statistics (R^2 and RMSE) and plots showed that our models were useful predictors of karri growth, being able to predict about 56% of variation (Fig. 3). They were less useful for

predicting marri growth. There was some evidence of a systematic underestimation of higher growth values for both species.

For both karri growth models (with competition and without competition), the DBH parameter was less sensitive to dropping data observations (leave-one-tree-out or leave-one-plot-out) than the age parameter (Table 5). The parameters in the model without competition were less sensitive than the model with competition. For both marri growth models (with competition and without competition), the DBH parameter was more sensitive than the age parameter, and the parameters in the model without competition were less sensitive than the model with competition. Overall, the karri growth model parameters were less sensitive to dropping data observations (leave-one-tree-out or leave-one-plot-out) than the marri growth model parameters.

Table 5 Sensitivity analysis of the karri and marri growth models for different predictor variables (DBH, age, and competition). The values given in the table are coefficient of variation (CV) for leave-one-tree-out and for leave-one-plot-out for three variables (DBH, Age and competition) separately.

Species	Eqs.	Sensitivity of variables (measured by coefficient of variation in %)					
		Leave-one-tree-out			Leave-one-plot-out		
		DBH	Age	Competition	DBH	Age	Competition
Karri	5	0.52	0.54	NA	2.91	1.93	NA
	6	0.59	0.68	2.50	2.12	2.41	12.29
Marri	7	2.10	1.34	NA	8.09	3.65	NA
	8	2.87	1.81	7.40	12.34	4.33	19.95

3.4 Testing the number and distance of competitors

The results indicate that 11 to 14 competitors (number) and 5 m (distance from base of target tree) for karri and 10 competitors (number) and 7 m (distance) for marri respectively were best in predicting the target tree's growth (Fig. 4). The optimum number and distance of competitors required for the best predictions was greater in the second growth period for karri; however, it did not vary in case of marri (Fig. 4).

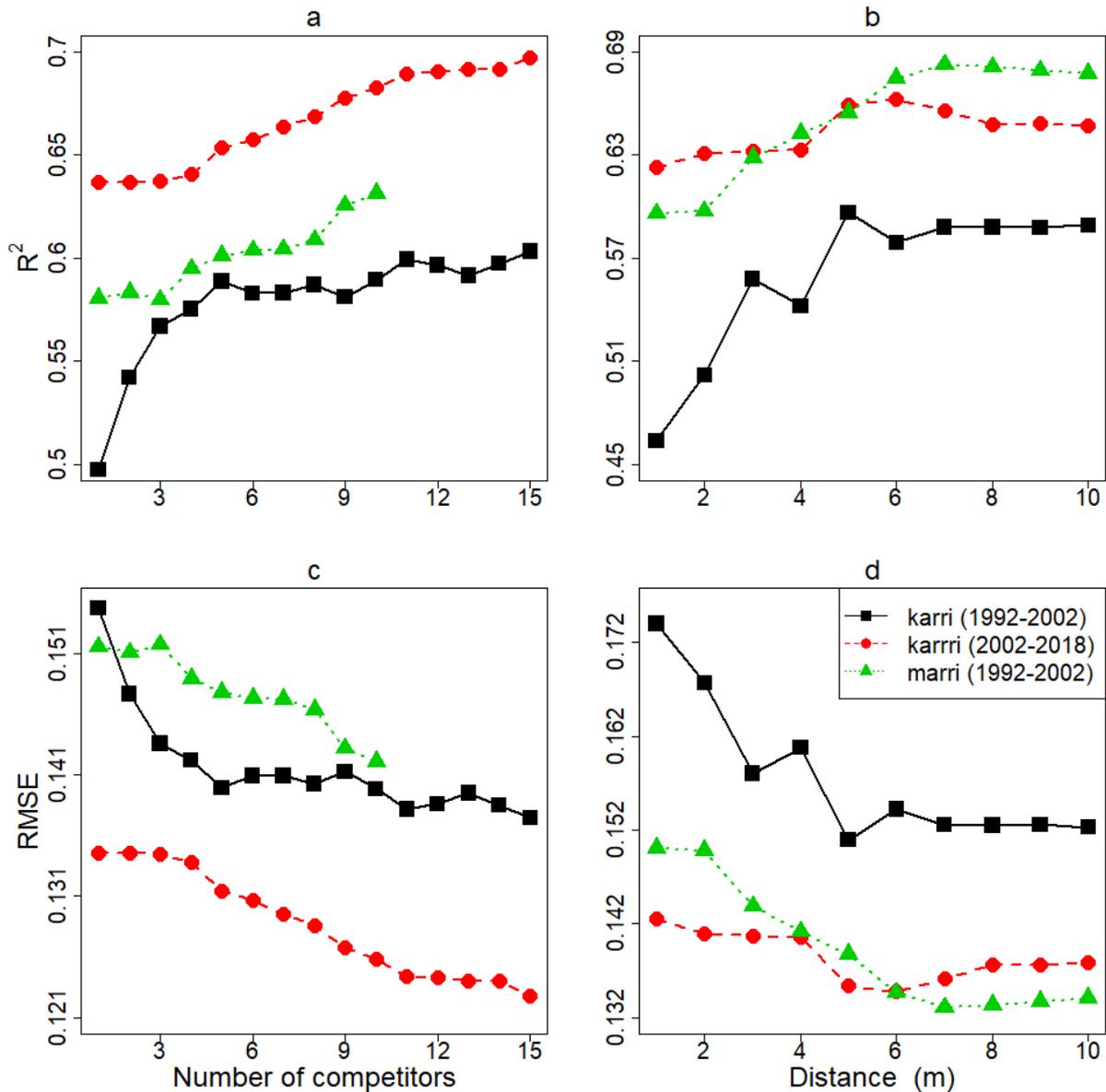


Fig. 4. Effect of number and distance of competitors on the predictive ability of the diameter growth model; (a) Variation in co-efficient of determination (R^2) with the number of competitor trees; (b)

Variation in R^2 with the distance (m) of competitors; (c) Variation in root mean squared error (RMSE) with the number of competitor trees; (d) Variation in RMSE with the distance (m) of competitors. Note that the R^2 and RMSE show consistent (but inverted) patterns across distance and number of competitors within the same data set (i.e., growth period) as expected. All the fitted models in this figure are based on $\Delta\text{DBH} \sim \text{DBH}$ only. We did not include the model for marri growth for 2002 to 2018 because competition was not a significant predictor variable in the model.

4 Discussion

The main findings from this study, in relation to each of our four aims, are that 1) spatial CI performed better than non-spatial CIs; 2) growth of individual trees of karri and marri in the Mediterranean climate of SWWA can be predicted reasonably well by their size and age at the beginning of the growth period, but that predictability is improved by accounting for the effect of competing neighbouring trees; 3) the models developed in this study are useful for predicting growth on different nearby plots and across different time periods; and 4) up to 14 neighbouring competitors, or all competitors within a radius of up to 7 m, need to be considered for the best prediction ability.

4.1 Comparison of CIs

Our study showed negative correlations for all the CIs with ΔDBH , confirming the expected negative effect of competition on growth. The negative correlations of spatial indices were higher than those of non-spatial indices. These results were similar to the results reported by Bhandari et al. (2021a) in a study of *Eucalyptus marginata* in SWWA and Soares and Tome (1999) in a study of a *Eucalyptus globulus* plantation in Portugal. Other studies from around the globe also found a negative correlation of competition indices with individual tree growth of three tree species (*Pinus ponderosa*, *Pseudotsuga menziesii* and *Larix occidentalis*) growing in Western Montana, USA (Contreras et al., 2011) and for *Betula pendula* in Estonia (Maleki et al., 2015). Spatial indices have the limitation of

being more time consuming and costly to collect because the position of individual trees must be known (Bhandari et al., 2021a). Furthermore, there are some circumstances where non-spatial indices perform as well as spatial indices, at least for yield projection in plantations (Martin and Ek, 1984; Corona and Ferrara, 1989) mainly because of the similar inter-tree distance between individual trees in plantation. In agreement with the study of Contreras et al. (2011) and Bhandari et al. (2021a), our data indicate that correlations among spatial CIs or among non-spatial CIs are higher than correlations between spatial CIs and non-spatial CIs. The fact that we found spatial CIs to be better predictors than non-spatial supports the notion that proximity and size of competitors have a negative effect on growth of individual trees. However, the fact that CI₄ performed nearly as well as the best spatial CIs indicates that it would be the best measure of competition to use if we did not have individual location data.

4.2 Tree size, age, and competition

Our results showed that individual tree size (DBH), age and competition were all significant predictors of Δ DBH for both karri and marri. This finding is consistent with those from several other studies (Contreras et al., 2011; Weiskittel et al., 2011; Diaconu et al., 2015; Maleki et al., 2015; Lhotka, 2017; Sharma et al., 2017; Luo et al. 2019; Bhandari et al., 2021a). Even if used by itself, tree size (DBH) and age can help predict the variation in Δ DBH; however, including competition significantly improved the proportion of variation explained. Martins et al. (2014) showed that DBH was a significant predictor and described up to 98% of variation for Δ DBH in a hybrid stand of eucalypts (*Eucalyptus grandis* and *Eucalyptus urophylla*) in a plantation in northern Brazil. Similarly, Sharma et al. (2017) found that diameter and age together described more than 99% of variation in diameter growth of natural Norway spruce in Czech Republic. The higher percentage of variation explained by the diameter growth models of Sharma et al. (2017) may be attributed to species (conifer species). The stem is more cylindrical in most of the conifer species than in most of the broadleaved

species such as marri. The bark of marri is rough and may lead to error while measuring the DBH. In the present study, DBH only described up to 62% of variation in diameter growth. The lower amount of variance explained by DBH in our study may be due to how the variables have been measured (measured by tape / calliper versus measuring annual tree growth rings using tree core or tree discs), greater variation in size and inter-tree distance of individual trees growing in a stand, along with greater genetic diversity and greater environmental heterogeneity. One or two cores per tree extracted from breast height may not be representative and may lead to errors. Using stem discs at breast height or some other convenient point might be more representative option, however, stem discs require large-scale tree felling which is not possible in ongoing experimental plots or forests protected for conservation. Having annual diameter measurement data is obviously better than the data measured at the interval of longer period. We used data collected at intervals of 10 years or more in this study, which may be partly responsible for the lower percentage explained of variation in diameter growth.

Our study showed that larger trees had higher diameter growth rates than smaller trees (Fig. 2c, d). This is consistent with other studies and may be explained by the interaction of tree size with access to resources (Contreras et al., 2011; Lhotka and Loewenstein, 2011; Zhang et al., 2016; Acuna et al., 2017; Delgado-Matas and Pukkala, 2011; Bhandari et al., 2021a; 2021b, 2021c). It is well known that photosynthetic rate is dependent on the supply of water, light and nutrients (Coomes, 2006; Muller-Landau et al., 2006; Reich et al., 2006). Compared to small trees, larger individuals generally have more leaves, a higher photosynthetic surface area (Enquist 2002) and have greater access to light, nutrients and water and therefore grow faster in diameter (Coomes and Allen, 2007). Faster growth of larger trees in this forest also indicates that the larger trees of the forest have not reached at maturity.

This study showed a negative relationship between diameter growth and the age of individual trees. The diameter growth in each growth period was less than the previous period. The thinning carried out in 1992 reduced the inter-tree competition for resources (light, water and soil nutrients) and increased the growth from 1992 to 1997, however, the competition increased from 1997 to 2002 due to an increase in individual trees size and stand basal area. The gradual increase in age and inter-tree competition among individual trees resulted in a slow growth and thus a negative correlation. In general, individual tree growth increases with an increase in age, reaches a peak at middle age and then the growth rate starts to decrease with further increase in age (Schongart et al., 2015; Chaturvedi and Khanna, 2011). The individual trees in the studied forest are relatively young (49 years) and likely to still be growing at an increasing rate if there had not been any thinning. The decrease in growth rate with age observed in this study is thus likely to be due to a release of inter-tree competition immediately after thinning, followed by a slow increase in competition as the remaining trees fill in the gaps. However, it could also be due to climatic change such as the decreasing rainfall observed in southwest Western Australia over this period (Bates et al., 2008; BOM 2019). As the inter-tree competition increases with an increase in age, these two variables might be correlated with each other, but the inter-tree competition depends mainly on the initial basal area. Age increases at the same rate for all individuals and stands but competition might be significantly different to each individual and stand depending on the initial basal area. Therefore, using competition and age as predictor variables in a single model may provide a better prediction of individual tree growth.

As the study site consists of plots with different stand densities, ranging from heavily thinned to unthinned, the inter-tree distances are highly variable. The variation in inter-tree distances and size of the individual trees introduced variation in the magnitude of competition and its effect on growth, which is likely to be one of the reasons that we were able to find the significant effect of spatial CIs on growth prediction. Other studies have found competition to be a significant predictor in the growth

of eucalypts across temperate and sub-tropical mesic Australia (Prior and Bowman, 2014). Competition was the second-best predictor after tree size in the growth model of *Pinus koraiensis* in northeast China (Zhang et al., 2016). In irregular stands, inter-tree distances have proved useful in predicting individual tree growth (Lorimer, 1983). The CIs which we used in our models assumed that the size of the competitor trees had a positive correlation with magnitude of competition. Larger competitors likely imposed a higher competitive stress on the growth of the target tree due to their greater access to light, nutrient and water than smaller trees whose photosynthetic rate and therefore growth are negatively affected by limited access to light, nutrients and water. Distance from target tree to competitors had a negative correlation with magnitude of competition, most likely due to diminishing competition for light, nutrients and water.

When the non-spatial proxies of competition were added to the model along with CI₁₄, these proxies were not significant, demonstrating that our spatial competition index captured competition well. The fact that our spatial competition index outperformed the non-spatial proxies indicates that spatial data is useful. On the other hand, the fact that models with stand-level proxies were often nearly as good as models with spatial CIs indicates that stand BA per ha at plot level can be used as an alternative predictor variable in the absence of spatial data. This suggests that, in future work, the resources that would have been used to collect spatial data might be better spent in collecting data from a much higher number of plots covering a wider range of site and stand conditions.

Because of the lack of independent data, we could not validate our model with data from other sites and regions, which would be necessary to confirm whether the model can be used for accurate prediction in different geographical regions and different growing conditions. Leave one out cross validation is a commonly used method of validating predictive ability of models and makes best use of available data (Nord-larsen et al., 2009; Zhou et al., 2021), but only demonstrates predictive ability

within the range of conditions of the data used. Validation showed that the karri models had better predictive ability than the marri models. We had data from a larger number of plots for karri (N=19) compared to marri (N=8). The larger number of plots and individual trees of karri represented a larger amount of variation than that of marri, which may have contributed to the better predictive ability of karri models. The models with competition had better predictive ability than the models without competition, again showing that competition is an important and useful predictor of individual tree growth.

4.3 Testing distance and number of competitors

Establishing the optimum number and distance of competitors that need to be measured to predict the growth of a target tree is important to the development of efficient experimental designs and an efficient model. Other studies have based their models on established plot size and not tested optimum distances or number of competitor trees. For example, Contreras et al. (2011) used an 11 m radius and Stadt et al. (2002) used an 8 m radius. Maleki et al. (2015) used 10, 15, 20, 25 or 30 m radii, based on the size of the established plot, which varied depending on stand age and density, but did not explicitly test different radii in analysis. We tested a range of 1 to 15 competitors and 1 m to 10 m distance and found the optimum number of competitors in models to be 11 to 14, and the optimum distance to be 5 m to 7 m (roughly 1/3 of canopy height) from the base of the target tree. However, the optimal number and distance of competitors to include in predicting the growth of target trees may vary with species, stand density, soil fertility and water availability. In another eucalypt forest, 250 km north of the current study site, Bhandari et al. (2021a) found 12 competitors as optimal competitors and 10 m distance as optimal distance for explaining the growth of *Eucalyptus marginata*. Thus our hypothesis that the number of competitors to be considered would be higher for karri than for jarrah was supported. Our hypothesis that the distance of competitors to be considered would be higher for karri was not supported, maybe because the karri trees were younger, and because the plots

were not large enough to pick up longer range effects. Forrester et al. (2011) reported 5 m and 6 m distance as the optimal distances to be considered while estimating the competition for *E. globulus* and *Aacacia mearnsii* in eastern Australia. In another study Forester et al. (2013) reported 6.5 m as optimal distance to be considered while estimating the competition for *E. globulus*, *E. nitens*, *E. grandis* in Victoria, Australia. In a study in Canada, Canham et al. (2004) reported 8 m for western hemlock and 13 m for western red cedar as the maximum distance after which there was no competitive effect of neighbouring trees. Competitive effect of neighbour trees was dependent on social position (dominant, co-dominant or intermediate) of the target tree and the competitors for *Picea abies* in Austria (Ledermann and Stage, 2001). The competitive effect of neighbouring trees also depends on tree size and architecture and the way in which the root systems of the trees exploit the soil resources.

This study revealed that the optimum number and distance of competitors was greater in the second growth period for karri indicating that the magnitude of competition was dynamic, increasing with an increase in size, age and time. This result is consistent with the findings of Forrester et al. (2011) and Bhandari et al. (2021a), who also reported that magnitude of competition is dynamic and changes through time. Bhandari et al. (2021) explained the two possible reasons in explaining the difference in number and distance of competitors between first growth and second growth period are; 1) increase in age and size of individual trees; and 2) decrease in rainfall in SWWA since the 1970s (BOM, 2019). We also agree with those two reasons in explaining the difference in number and distance of competitors in karri and marri forest. The average annual rainfall at the nearest meteorological station (Manjimup, SWWA) from 1992 to 2002 was 920 mm and from 2002 to 2018 was 828 mm. The average rainfall for the last five years (2013-2018) was even lower i.e., 753 mm (BOM, 2019). In areas where water is limited, plants allocate more biomass to the roots, which results

in competition over a larger distance from their base (Casper et al., 2003; Deng et al., 2006). In SWWA moisture is a limiting factor for tree growth (Raper, 1998; Burrows et al., 2010).

Diameter growth of target trees may have been affected more by the competitors from a certain direction. In the southern hemisphere, competitors north of a target tree may exert a higher competitive effect for light than competitors south of the target tree. Such a directional effect is presumably not present for below-ground competition. In future research, accounting for the directional effect of competitors may help in more accurately predicting growth and gaining insight into the relative importance of above-ground versus below-ground competition.

The optimal number and distance of competitors found in this study could potentially help guide tree marking during thinning operations. Determining the distance and number of competitors may help in deciding the appropriate size of experimental plots for studying the effect of competition on individual trees. As competition from neighbours was a significant predictor with a negative effect on growth, it is recommended that neighbourhood competition be included when predicting growth and considering thinning treatments to minimize the effect of competition on growth while maximizing stand growth. Individual-based modelling could provide guidelines about what thinning strategies are best for different objectives (e.g., volume per ha vs large quality trees). Thinning strategies should presumably also be different for stands that are clear-felled vs selectively logged.

5 Conclusions

We developed a new crown diameter and distance-based competition index. This study showed that growth of karri and marri at the individual tree level can be predicted using DBH and age at the beginning of the growth period and this prediction could be improved by accounting for competition. The validation shows that our model had some independent predictive ability, with karri

growth models more predictive than marri growth models. Model prediction is optimized if 11 to 14 competitors or competitors within ~7 m from the base of the target tree are included in the model. As competition had a significant and negative correlation with diameter growth of individual trees, including neighbourhood competition in growth predictions is recommended where possible. Our results have potential to inform tree marking for thinning operations in order to optimize growth that may otherwise be impacted by competition from neighbouring trees. Future studies that differentiate the effects of competitors from different directions are recommended, as these may improve predictability and also help in identifying whether the competition is above-ground and/or below-ground.

Conflicts of interest: The authors declare that they have no conflict of interest.

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CHAPTER 7

Investigating above- vs. below-ground competition by accounting for azimuth of competitors in native eucalypt forests

PREAMBLE

This chapter presents three different new modelling approaches to investigating above- vs. below-ground competition by accounting for azimuth of competitors in the jarrah, karri and marri forests. It is presented as a manuscript intended for submission to *Functional Ecology*. Formatting is that specified by the journal with the exception of page numbering. S4 is the supplementary materials for online submission with the manuscript.

Investigating above- vs. below-ground competition by accounting for azimuth of competitors in native eucalypt forests

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Abstract

1. Competition for both above-ground and below-ground resources plays a crucial role in shaping the structure and dynamics of plant communities. Above-ground competition for light is more pronounced in areas with higher latitude because of the low sun angle than in lower latitude, and in plant communities with more dense foliage and vertical stratification. Below-ground competition is more dependent on below-ground resource availability. Above-ground competition may be more azimuthal and size-asymmetric than below-ground competition. However, there has been limited research on azimuthal effects on competition and related methods that may help distinguish between above- vs. below-ground competition.

2. The aim of this study was to investigate whether accounting for the azimuth of competitors in different ways could improve predictions of tree growth of dominant eucalypt species in mid-latitude

Mediterranean climate forest, and whether this could provide insights into the relative importance of above- vs. below-ground competition for the different species.

3. To achieve this aim, we developed, applied and evaluated three new approaches to evaluate azimuthal differences in competition, using models predicting DBH growth in two different forests (*Eucalyptus marginata*, jarrah and *E. diversicolor*, karri; and *Corymbia callophyla*, marri) of south-west Western Australia. The foliage density of karri/marri is relatively higher than that of jarrah, and the karri/marri site had higher rainfall. Both sites included thinned and unthinned plots. In the first approach (comparing azimuths), we compared the ability to predict growth using competitors in specific azimuths only vs. all competitors together. In the second approach (optimizing azimuth), we investigated whether weighting competitive effects of neighbours according to their azimuth could improve growth predictions. In the third approach (relative size and azimuth), we investigated whether growth prediction could be improved by accounting for relative size of competitors as well as their azimuth.

4. We found evidence of an azimuthal effect of competition on growth in jarrah, karri and marri forest through all three modelling approaches. The third modelling approach (relative size and azimuth) showed the existence of size-asymmetric competition. Improvement in model prediction was relatively small when accounting for the azimuth and therefore we believe that the above-ground competition for light is low and the remaining larger proportion of competition that occur in the growth of jarrah, karri and marri forest may have occurred for the below-ground competition. The three modelling approaches used in this study can potentially help identify, distinguish and understand above- vs. below-ground competition for tree species in different parts of the world where competition among trees is one of the limiting factors of forest growth, dynamics and health.

Keywords: above- vs. below-ground competition, azimuth, direction, growth, model

1 Introduction

Individual plants in a plant community may compete for resources including light, water, nutrients, and space (Harper, 1977; Weiner, 1993; Forrester et al., 2011). Competition inhibits the growth and development of individual plants; however, its magnitude depends on resource availability, stand structure, site quality and the number of individual plants competing for resources at a given point of time and space (Stoneman et al., 1996; Forrester et al., 2013a; Forrester et al., 2013b; Acuna et al., 2017; Bhandari et al., 2021a or Chapter 2; Chapter 3). Negative competitive effects increase as the number of individual trees per unit area increase, size of the neighbouring competing plants increase and the distance between the subject plant and neighbouring competitors decreases (Bhandari et al., 2021b or Chapter 5; Chapter 6). This competition plays a determining role in the dynamics of plant communities and the distribution of plant species (Craine & Dybzinski, 2013). Competition among individual plants in a plant community takes place for above-ground resources and/or below-ground resources (Schnitzer et al., 2005; Murphy & Dudley, 2007).

Individual plants compete above-ground for light and this competition varies according to the sun elevation, height of individual plant and number of plants per unit area (Rijkers et al., 2000; Kohyama & Takada, 2012). Light is a directional resource; for example, light tends to come more from above than from below, and therefore larger and taller plants are likely to receive more light than smaller and shorter ones (Aerts, 1999). Because of the directional nature of light, the competition for light is known as size-asymmetric or one-sided competition (Kohyama & Takada, 2012). This means that larger and taller plants exert a competitive effect on smaller and shorter plants (Kikuzawa & Umeki, 1996; Onoda et al., 2014). Light intensity varies with the sun angle, which shifts daily and seasonally (Craine & Dybzinski, 2013). The impact of light competition mainly depends on the density of the canopy and maybe lower in uneven-aged forests because for a given canopy density, the crowns are not all at a similar level and hence more light can penetrate to lower levels in the

canopy (Laurans et al., 2014). The influence of light direction and intensity are comparatively more important for plants that grow far from the equator (Kuuluvainen, 1992). Sun elevation becomes lower with an increase in latitude. In the southern hemisphere, plants growing on north-facing slopes receive more light compared to plants growing on south-facing slopes. In an area where the sun elevation is low, relative position of individual plants may affect light availability. An individual plant may receive shade from a plant growing north of its position while simultaneously shading a plant south of its position (Kuuluvainen & Pukkala, 1989). Because of low light availability and shade, the individual trees growing on the northern side of a subject tree may exert more competition to that subject tree than trees growing to its south (Aakala et al., 2016).

Below-ground competition occurs mainly for water, space, and mineral nutrients (Casper & Jackson, 1997). In many cases, the magnitude of below-ground competition is higher than that of above-ground competition, and therefore below-ground competition is more likely to reduce the growth of individual plants (Wilson, 1988; Cahill, 2003). Below-ground competition is often two-sided and/or size-symmetric (Kohyama & Takada, 2009) whereby both large and small plants compete for the same resources. The presence of below-ground competition can change the growth pattern of fine roots (Gersani et al., 2001) and root depths (Wardle & Peltzer, 2003) affecting both root development and development of the plant overall. Below-ground competition is very important in Mediterranean environments characterised by low soil fertility and seasonally limited moisture availability (Vilà & Sardans, 1999; Sardans & Peñuelas, 2013).

Competition among individual plants can be estimated using various competition indices (CIs) (Lorimer, 1983; Dale et al., 1985; Contreras et al., 2011; Maleki et al., 2015; Bhandari et al., 2021b or Chapter 5; Chapter 6). These indices are broadly categorised into spatial and non-spatial CIs. Non-spatial CIs use average stand properties relating to the size (DBH, height, crown measures)

of the competitor plants and subject plant in estimating the magnitude of competition (Hamilton, 1986; Corona and Ferrara, 1989; Wykoff, 1990). Since non-spatial CI assume that individual plants are uniformly distributed in space throughout the community, they do not consider the proximity of the competitors (Weiskittel et al., 2011). Non-spatial CIs are better suited to measure competition in even-aged and homogeneous forests (such as plantations) than in uneven-aged and mixed forests with more complex and heterogeneous species composition, size distributions and stand structure. Many studies use non-spatial CIs because of their simplicity; however, they do not have the ability to differentiate intensity of competition for individual trees (Reineke, 1933; Hamilton, 1986; Corona & Ferrara, 1989; Wykoff, 1990; Lhotka & Loewenstein, 2011; Diaconu, Kahle & Spiecker, 2015; Lhotka, 2017). In contrast, spatial CIs use the size and distance between competitors and subject plants to estimate the magnitude of competition (Hegyi, 1974; Braathe, 1980). Spatial CIs are more accurate than non-spatial indices, but the cost and time to collect the information required for spatial CIs are more than that required for non-spatial CIs (Bhandari et al., 2021b or Chapter 5; Chapter 6).

Jarraah (*Eucalyptus marginata*), karri (*Eucalyptus diversicolor*) and marri (*Corymbia callophyla*) are the dominant tree species in the Mediterranean forest in the south-west of Western Australia (SWWA) (Bradshaw, 2015a; Bradshaw, 2015b; Bhandari et al., 2021a or Chapter 2; Chapter 3). Forest growth in SWWA is constrained by nutrient-poor soils with low available phosphorus (Hingston et al., 1981; Handreck, 1997) and low moisture availability during the dry summer and autumn months. Annual rainfall in SWWA has also declined since the 1960s (Bates et al., 2008; BOM, 2020). Competition for resources can be high in dense stands of regrowth forest as evident in the diameter growth of jarraah, karri and marri which have been found to be 7, 1.5, and 1.1 times higher in heavily thinned plots compared to unthinned plots (Bhandari et al., 2021a or Chapter 2; Chapter 3). Further evidence of competition was reported by Bhandari et al. (2021b or Chapter 5) and Chapter 6 while predicting the growth of these species using CIs as one of the predicting

variables. They found that inclusion of CI improved growth prediction by up to 30% and 7% in jarrah and karri, respectively. However, they did not examine if there were strong azimuthal effects of competition on these tree species.

Investigating the extent to which the azimuth of competitors affects competition, in addition to their size and distance, may provide greater insight into above vs. below-ground competition since above-ground competition is likely to be more azimuthal than the below-ground competition. If competitive effects are stronger from neighbours situated in the direction of the sun, this may indicate the importance of above-ground competition for light, while a lack of azimuthal effects may indicate more importance of below-ground competition. While estimating the competition in these tree species, Bhandari et al. (2021b) or Chapter 5; Chapter 6 used the size and distance between the subject tree and competitors. Contreras et al. (2011), studying competition as predictor of basal area increment in a montane forest in the western USA, used CIs based on estimated light interception in addition to size and distance; however, the performance of light-based CIs was lower than the CIs based on size and distance between the subject tree and competitors. A few studies have considered azimuths of competitor trees (Puettmann et al., 1993; Boivin et al., 2010; Richards et al., 2010) in different parts of the world, however, no other published studies have looked at the azimuthal effect of competitors in addition to their size and distance in West Australian forests.

The aim of this study was to examine the effect of azimuth of competitors as a potential indicator of the importance of above- vs. below-ground competition in the jarrah, karri and marri forest. To achieve this aim, we considered models of the DBH growth of three tree species (jarrah, karri and marri) in two forest types and developed, applied, and evaluated three new approaches to evaluate the azimuthal effect of competition.

2 Materials and methods

2.1 Study area

This research used data collected from two study areas in SWWA. The first study area is in jarrah-dominated forest at Inglehope (32° 45' S, 116° 11' E) (altitude = 268 m), 12 km east of Dwellingup, SWWA

(Figure 1). This is a regrowth forest regenerated in 1924 and was thus 86 years old in 2010 when the most recent measurement was carried out. The soil of this area is yellow in colour and sandy ferruginous in nature with

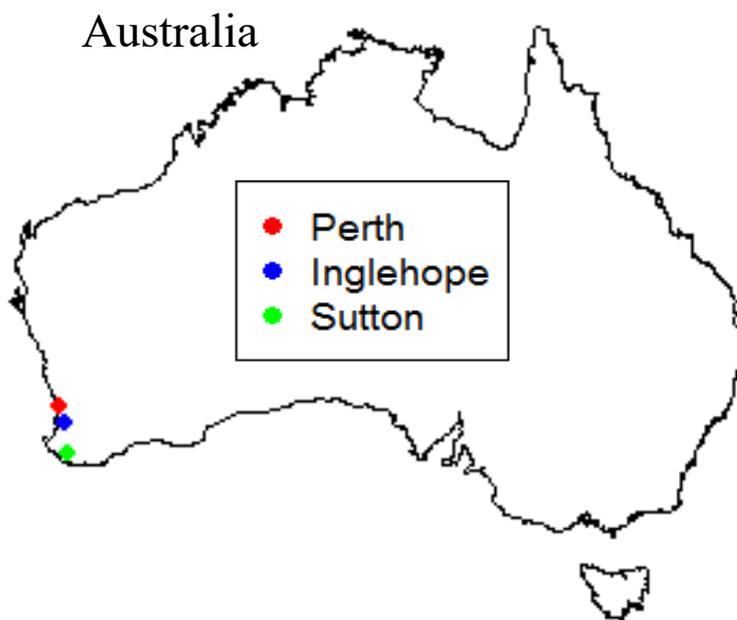


FIGURE 1 Map of Australia showing the location of the two study areas, Inglehope and Sutton, near Perth, Western Australia.

low fertility (Hingston et al., 1981). The area has a Mediterranean climate with an average annual rainfall concentrated in the winter months. Average annual rainfall at the Dwellingup station from 1934 to 2010 was 1245 mm (BOM, 2019) (Figure 2a), but rainfall at Inglehope is about 200 mm lower than at Dwellingup (Stoneman et al., 1996). The lowest minimum and the highest maximum daily temperature in Dwellingup ranges from -3.9°C to 43.5°C. The average monthly wetness index in Dwellingup was -92.9 mm (Figure 2c). The second study area is in karri dominated forest at Sutton (34° 28' S and 116° 20' E) (altitude = 205 m), 38 km south-east of Manjimup (Figure 1). This is a regrowth forest regenerated in 1969 using clear-felling with retained seed trees and was 49 years old in 2018 when the most recent measurement was carried out. The site has a Mediterranean climate with an average annual rainfall of 980 mm (1915-2019) measured at Manjimup station which is

located 38 km to the north-west of Sutton (BOM, 2019). The lowest minimum and the highest maximum daily temperature at Manjimup ranges from -0.6°C to 42.7°C . The average monthly wetness index in Manjimup was -74.2 mm (Figure 2c). Average monthly rainfall and maximum temperature are higher at Dwellingup than at Manjimup (Figure 2a). Average monthly minimum temperature is lower at Dwellingup than at Manjimup between April and September during the austral autumn and winter (Figure 2b).

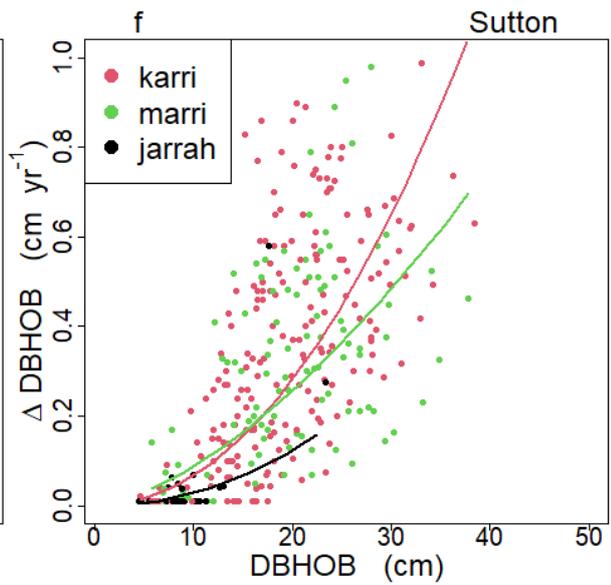
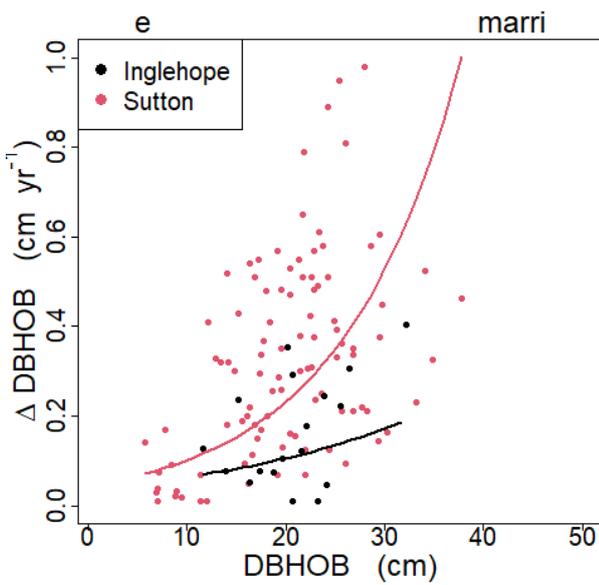
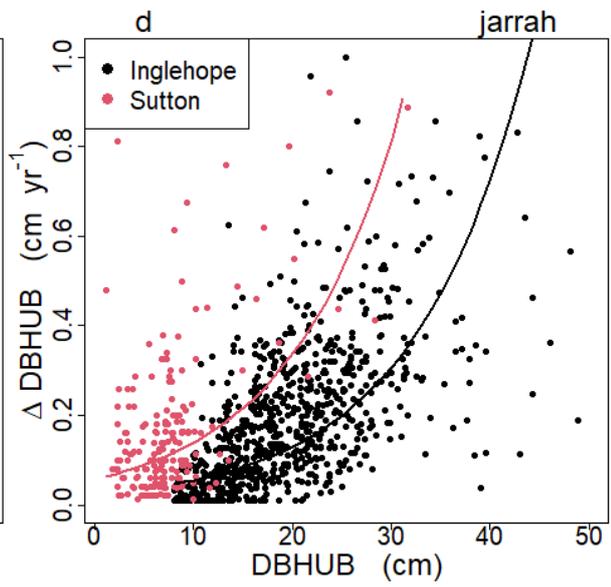
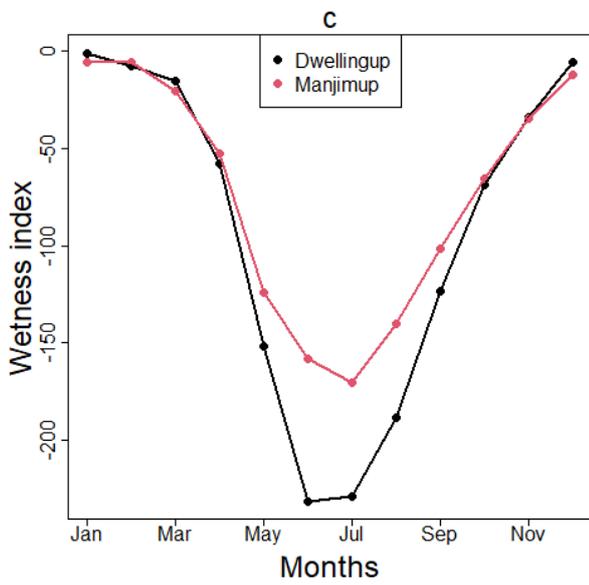
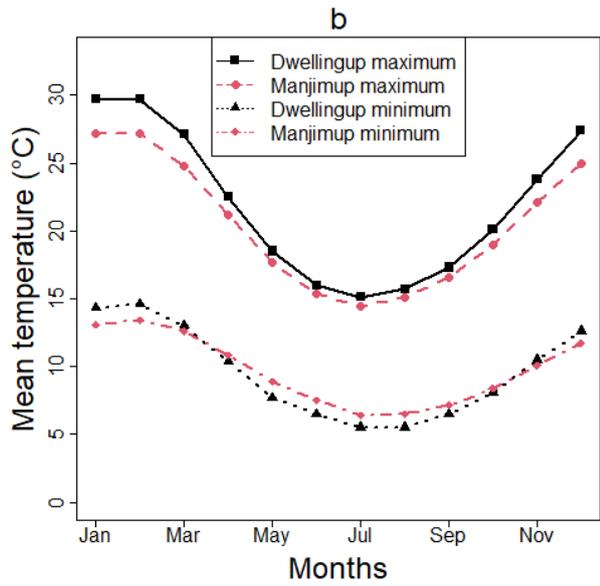
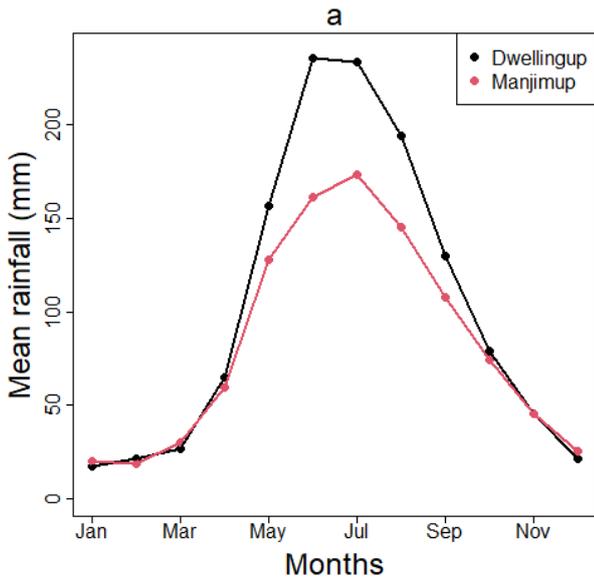


FIGURE 2 Variation in; (a) monthly rainfall (mm); (b) monthly temperature ($^{\circ}$ c) in Dwellingup and Manjimup; (c) monthly wetness index in Dwellingup and Manjimup (wetness index = monthly evapotranspiration - monthly rainfall, where monthly evapotranspiration (ET_0) was calculated following Hargreaves (1975): $ET_0 = 0.0023 \times R_a \times (T_{\text{mean}} + 17.8) \times (T_{\text{max}} - T_{\text{min}})^{0.5}$, where T_{mean} , T_{max} , T_{min} are monthly mean, mean maximum and mean minimum temperatures and R_a is extra-terrestrial radiation; (d) diameter growth under bark (DBHUB) of jarrah at Inglehope and Sutton; (e) diameter growth over bark (DBHOB) of marri at Inglehope and Sutton; (f) diameter growth over bark (DBHOB) of karri, marri and jarrah at Sutton.

2.2 Treatments (thinning and fertilizer)

2.2.1 Inglehope thinning trial

The Inglehope thinning trial consists of 30 plots with six replicates of five different stand densities. The first thinning was carried out in 1965 with a retained basal area under bark (BAUB) of 6.99 (T1), 11.04 (T2), 15.40 (T3), 18.33 (T4) and 21.94 (T5) $\text{m}^2 \text{ha}^{-1}$. Stand density T5 represents unthinned plots (control). The size of the thinned plot is 40×40 m (with an 8 m buffer on all sides) and of unthinned is 20×20 m. A second thinning was carried out in 1986. At this time, a fertilizer treatment (F0 unfertilized and F1 fertilized with 400 kg ha^{-1} N and 229 kg ha^{-1} P) was also applied to three of the six replicate plots in a completely randomized design. Further details of the thinning trial are reported in Bhandari et al. (2021a) or Chapter 2.

2.2.2 Sutton thinning trial

The Sutton thinning trial consists of 27 plots (size 30 m × 30 m plus an outer 10 m buffer on all sides). Separate plots were established for karri (19 plots) and marri (eight plots). Karri plots were thinned non-commercially to six different stand densities in 1992 as follows: 34 (T1), 20 (T2), 16

(T3), 13 (T4), 10 (T5) and 7 (T6) $\text{m}^2 \text{ha}^{-1}$ basal area over bark (BAOB). Similarly, the marri stand was thinned to four stand densities as follows: 37 (T1), 19 (T2), 15 (T3) and 10 (T4) $\text{m}^2 \text{ha}^{-1}$ BAOB. Stand density (T1) represents unthinned plots (control) in case of karri and marri plots. Details of the thinning trial are reported in Chapter 3.

2.3 Sampling and measurement

2.3.1 Inglehope thinning trial

In this trial, the DBH of all trees and height of sample trees were measured in 1965, 1984 and 2010. The location of the centre and corner of each plot was measured using a theodolite in 1985 and the position of each tree was mapped using the azimuth and distance from the plot centre. A detailed tree and plot measurement procedure for the Inglehope thinning trial is described in Bhandari et al. (2021a) or Chapter 2.

2.3.2 Sutton thinning trial

At Sutton, the DBH of all the trees and heights of sample trees were measured in 1992, 2002 and 2018. In 1992, GPS was used to measure the coordinates for the centre of each plot. The position of each tree was mapped using the azimuth and distance from the plot centre. A detailed tree and plot measurement procedure in Sutton thinning trial is described in Chapter 3. A summary of the stand characteristics at different time points for both study areas is presented in Table 1.

Table 1 Descriptive statistics (mean, standard deviation and range) of the data for jarrah, karri and marri at different time points that were used in this study. Under bark diameter at breast height (DBHUB), over bark diameter at breast height (DBHOB), and height are individual tree level variables, and under bark basal area (BAUB) and stem number per ha are stand level variables. The figures presented under ‘jarrah thinned’ represent the data from all thinning intensities.

Site	Species	Variables	Mean±std.(range)		
			1965	1984	2010
Inglehope	Jarrah thinned	DBHUB (cm)	18.16±5.99(5.90-48.80)	21.82±7.62(7.90-53.40)	29.94±10.34(9.90-72.55)
		Height (m)	19.14±3.46(7.74-32.01)	21.24±3.85(9.00-34.00)	23.60±3.74(11.50-36.00)
		BAUB (m ² ha ⁻¹)	13.22±4.32(6.49-19.35)	19.05±4.66(11.05-25.56)	21.02±8.17(7.62-34.45)
		Stem number (ha ⁻¹)	460±249(125-881)	454±242(125-869)	266±201(25-700)
	Jarrah unthinned	DBHUB (cm)	14.21±5.72(8.10-49.60)	15.59±6.46(7.80-54.30)	18.16±7.91(8.85-59.45)
		Height (m)	16.58±3.46(11.09-29.09)	17.88±3.88(7.00-30.00)	18.53±4.35(3.10-29.50)
		BAUB (m ² ha ⁻¹)	21.95±1.83(20.11-23.79)	26.66±1.78(24.75-28.26)	32.84±3.31(29.71-36.32)
		Stem number (ha ⁻¹)	1192±52(1150-1250)	1183±58(1150-1250)	1067±88(975-1150)
Sutton	Karri		1992	2002	2018
		DBHOB (cm)	16.54±5.78(1.90-34.70)	22.28±6.93(4.10-45.00)	29.81±8.71(10.10-55.10)

Marri	Height (m)	18.28±3.05(2.30-25.60)	23.34±3.49(12.20-32.70)	30.68±4.96(14.50-42.10)
	BAOB (m ² ha ⁻¹)	15.39±7.75(6.85-36.84)	23.86±8.70(13.21-48.08)	34.59±7.49(23.33-55.74)
	Stem number (ha ⁻¹)	627±564(178-2378)	574±426(178-1833)	487±252(178-1200)
	DBHOB (cm)	16.02±6.31(1.70-35.30)	19.86±7.73(3.40-47.40)	24.36±9.23(3.70-65.20)
	Height (m)	15.95±2.40(9.80-20.50)	18.90±3.23(10.00-29.00)	22.41±4.18(10.90-33.80)
	BAOB (m ² ha ⁻¹)	20.07±10.69(10.03-36.57)	29.47±11.58(17.26-47.68)	41.10±14.34(24.65-62.21)
	Stem number (ha ⁻¹)	1021±1152(233-3389)	921±958(244-2856)	790±738(200-2289)
Jarrah	DBHOB (cm)	8.6±3.3(2.0-24.0)	9.3±4.1(2.7-33.2)	11.3±5.3(4.5-42.9)
	Height (m)	11.3±2.9(8.3-16.7)	17.9±4.6(12.7-21.6)	22.1±8.9(15.8-28.5)
	BAOB (m ² ha ⁻¹)	2.3±2.5(0.3-6.3)	2.5±2.5(0.5-6.5)	2.7±2.4(0.7-6.2)
	Stem number (ha ⁻¹)	340±471(11-1133)	309±442(11-1067)	218±314(11-767)

2.4 Previous DBH growth modelling

2.4.1 Inglehope thinning trial

For our previous study (Bhandari et al., 2021b or Chapter 5), we estimated periodic annual increment as the difference in DBH over the time period divided by the number of years; this periodic annual increment is hereafter referred to as the Δ DBH. For modelling purposes, we defined a core inner plot of 20 m \times 20 m for thinned plots and 10 m \times 10 m for unthinned plots. Only trees in the inner core plot were considered as subject trees for modelling purposes, to ensure sufficient information was available for all competitors for all subject trees; this ensured we had full details on all competitor trees within 10 m of every subject tree in the thinned plots, and within 5 m of every subject tree in the unthinned plots. Separate models were developed for two different time periods (1965 to 1984, and 1984 to 2010) and in each period, separate models were developed for the thinned and unthinned plots (because they had different sizes). We found a power-law model (Eq. 1) to be the best model of jarrah growth for this site (Bhandari et al., 2021b or Chapter 5).

$$\log(\Delta DBHUB) = \alpha_1 + \alpha_2 \log(DBHUB) + \alpha_3 \text{fertilizer} + \alpha_4 CI \dots \dots \dots 1$$

$$CI = \sum_{j \neq i}^n DBHUB_j * \exp(-k * DIST_j) \dots \dots \dots 2$$

In this equation 1, DBHUB is under bark diameter at breast height at the beginning of the growth period, CI is the spatial competition index defined in Eq. 2 which was found to be the best out of 12 tested competition indices (Bhandari et al., 2021b or Chapter 5). In equation 2, $DBHUB_j$ is DBHUB of the j^{th} competitor and $DIST_j$ is distance between the subject tree and its j^{th} competitor tree. With this index, we thus assume that the competitive effect of each neighbouring tree depends linearly on the diameter of the tree and declines exponentially with distance, and that the total competitive effect on a subject tree is the sum of the competitive effects of all other individual trees within 10 m of the subject tree. We used all competitors within 10 m distance of a subject tree because a 10 m

distance was optimal in predicting the growth of individual trees of jarrah in this forest (Bhandari et al., 2021b or Chapter 5). The rate of this exponential decline is determined by a parameter k , and the numerical value of k was estimated by finding the value that gave the best model fit (based on model AIC). We also fitted another model which did not include competition as a prediction variable.

2.4.2 Sutton thinning trial

For our previous study (Chapter 6), we defined a core inner plot of 10 m × 10 m for all plots. Only trees in the inner core plot were considered as subject trees for modelling purposes, to ensure sufficient information was available for all competitors for all subject trees; this ensured we had full details on all competitor trees within 10 m of every subject tree. Separate models were developed for two different time periods (1992 to 2002, and 2002 to 2018) and in each time period, separate models were developed for karri and marri plots. We used a linear model (Eq. 3) to predict the karri and marri growth because this form of model had previously been found to be the best model for karri and marri growth on the same site (Chapter 6).

$$\Delta DBHOB = \alpha_1 + \alpha_2 DBHOB + \alpha_3 CI \dots \dots \dots 3$$

In equation 3, DBHOB is diameter at breast height at the beginning of the growth period, CI is the spatial competition index defined in Eq. 2 which was found to be the best out of 14 tested competition indices (Chapter 6). The models described above assume that the competitive effect of competing trees depends on their size and their distance from the subject tree but is not affected by their azimuth. In this study, we now used three different approaches to evaluate whether trees positioned in certain azimuths exerted greater competition on subject trees than trees positioned in other azimuths.

2.5 Modelling approaches

2.5.1 First modelling approach (comparing azimuths)

In this approach we simply tested whether considering competition from trees in certain azimuths gave better predictions than considering competition only from trees in other azimuths. Diameter growth was predicted separately (with Eq. 1 or Eq. 3 depending on site) using competitor trees from the following azimuths.

- i. North (0° to 90° and 270° to 360°)
- ii. South (90° to 270°)
- iii. East (0° to 180°)
- iv. West (180° to 360°)
- v. Northeast (0° to 90°)
- vi. Southeast (90° to 90°)
- vii. Southwest (180° to 270°)
- viii. Northwest (270° to 360°)

The CI which is used in Eq. 1 or Eq. 3 was estimated using Eq. 2. Only neighbouring trees were considered that have a position relative to the reference tree within the respective range of the cardinal directions defined by items i to viii were used and other trees outside this range were not considered at all. The idea underlying this approach was that if competition came more from a certain azimuth (e.g., from trees to the north) then we should find better predictions when considering trees from that azimuth compared to those obtained when considering trees from other azimuths (e.g., trees to the south).

2.5.2 Second modelling approach (optimizing azimuth)

Diameter growth was predicted similarly to the original approach (Eq. 1 or 3), but with a CI that also accounted for azimuth of competing trees as well as their distance and size (Eq. 4). All trees

of the subject tree, while below-ground competition would come from all nearby trees regardless of size or azimuth. We therefore fitted models with two CIs as explanatory variables, one for above-ground competition (Canopy CI) and one for general (including below-ground) competition (General CI). We considered two possibilities for the Canopy CI: one that included only trees positioned to the north of the subject tree that were also larger than the subject tree, and one that included all trees positioned to the north of the subject tree, regardless of size. The General CI included trees in all azimuths and of all sizes, as before. We then tested whether adding either of these Canopy CIs to the model with the General CI significantly improved growth predictions, compared to the model with only the General CI. In all cases, Eq. 2 was used for the CI, but with different trees included or excluded.

For all approaches, the predictive ability of the models was evaluated using three fit statistics: coefficient of determination (R^2), root mean squared error (RMSE) (Montgomery et al., 2001) and Akaike information criteria (AIC) (Akaike, 1972).

We also explored the variation in size (height) using the coefficient of variance (CV) in jarrah (thinned and unthinned), karri and marri forest as a measure of the probability of size-asymmetric competition. The idea underlying this analysis is, if the CV of height increases, there will be a higher possibility of size-asymmetric competition and thus above-ground competition (Kikuzawa & Umeki, 1996).

3 Results

3.1 First modelling approach (comparing azimuths)

For thinned jarrah forest, for both growth periods, none of the azimuthal models (the eight models with competitors from only one azimuth) had a higher R^2 (or a lower RMSE or AIC) than the

model with all competitors included (Figure 3, Table S1). Of the azimuthal models the model accounting for competitors from the east had the highest R^2 in both growth periods. Competition was highly significant for all models regardless of azimuth (Table S1).

For unthinned jarrah forest, R^2 was highest when the competitors were restricted to the southeast (in the first growth period) or from the east (in the second growth period) (Figure 3, Table S1). In both cases, the R^2 from the azimuthal model was considerably higher (and AIC and RMSE considerably lower) than with the model including competitors from all azimuths. Furthermore, the competition index was significant in these azimuthal models, but not in all azimuth models.

For karri, in both growth periods, none of the azimuthal models had a higher R^2 (or a lower RMSE or AIC) than the model with all competitors included (Figure 3, Table S2). For the first growth period, the models with competitors from the north and from the west described ~3% more variability in growth (and had considerably lower AIC and RMSE) than the models with competitors from the south and east (Table S2). For the second growth period, the models with competitors from the north and from the west were again the best of the azimuthal models in terms of R^2 , AIC and RMSE, and were also the only azimuthal models where the competition index was significant.

For marri, in the first growth period, none of the azimuthal models had a higher R^2 than the model with all competitors included (Figure 3, Table S2). The best of the azimuthal models were the ones with competitors to the south and west. In the second growth period of marri, competition was not a significant predictor for any model.

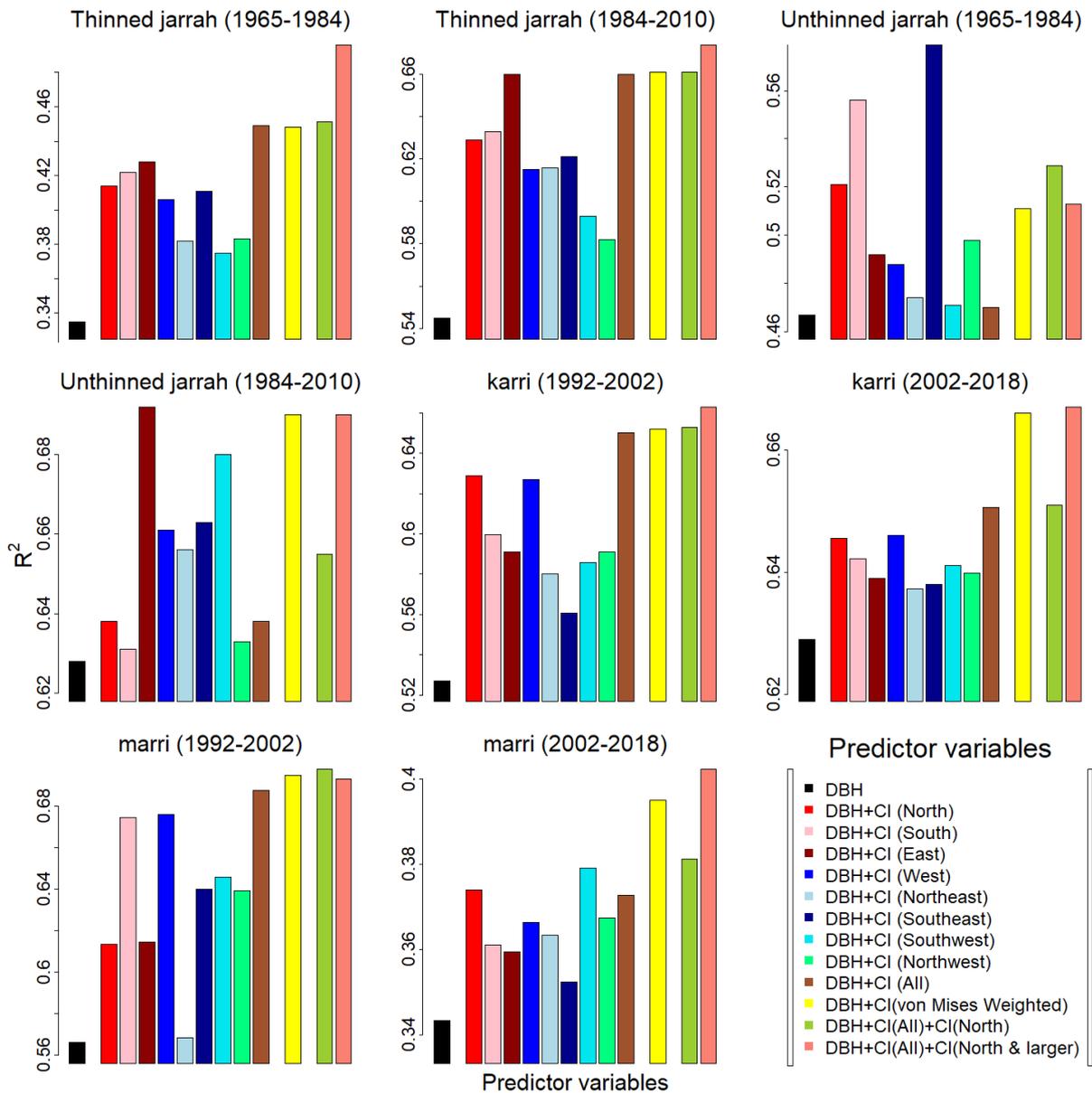


FIGURE 3 Predictive ability of the different models for DBH growth that were considered in this study, as measured using coefficient of determination (R^2). The groupings of the bars indicate the approaches used in this study: the first bar represents the baseline model without competition, the next nine grouped bars represent the models used in the first approach, the next single bar represents the optimised azimuth model of the second approach, and the final two bars represent the models used in the third approach.

3.2 Second modelling approach (optimizing azimuth)

For thinned jarrah forest, in both growth periods, R^2 was not different when the competitive effect was weighted by angle as well as distance (Table 2; Figure 3). For unthinned jarrah forest, in both growth periods, R^2 was considerably higher and AIC improved by more than two units when the competitive effect was weighted by angle as well as distance. The p-value of the CI was also much lower when azimuth was considered, although it only became <0.05 in the second growth period.

In karri forest, R^2 was higher, and AIC improved by more than two units when the competition effect was weighted by angle as well as distance, in the second growth period (Table 3). In the marri forest, R^2 was higher when the competition effect was weighted by angle as well as distance, but AIC was not improved by more than two and the CI was significant only in the first growth period.

Table 2 Fit statistics (R^2 , RMSE and AIC) for the model with non- azimuthal CI (Eq. 2) and the model based on azimuthal CI used in the second modelling approach (optimizing azimuth) (Eq. 4) in jarrah forest (thinned and unthinned) for two growth periods. Best angle is the bearing of the optimal mean angle of competition, relative to North. The given p-value is for azimuthal (Eq. 4) and non- azimuthal (Eq. 2) CI in the model (not for the overall model). k is the numerical power value that gave the best model fit for all data across all plots (based on model AIC). NA is not applicable.

Growth period	Models based on	Thinned plots						Unthinned plots					
		Best angle	p-value	k	R^2	RMSE	AIC	Best angle	p-value	k	R^2	RMSE	AIC
1965-1984	Non- azimuthal CI	NA	<0.001	0.344	0.439	0.116	1021.51	NA	0.661	2.500	0.470	0.078	92.48
	Azimuthal CI	0°	<0.001	0.340	0.439	0.116	1021.51	133°	0.111	0.110	0.511	0.074	89.85
1984-2010	Non- azimuthal CI	NA	<0.001	0.205	0.650	0.123	398.05	NA	0.402	0.426	0.628	0.052	68.41
	Azimuthal CI	322°	<0.001	0.200	0.651	0.124	397.06	76°	0.031	0.010	0.680	0.051	63.96

Table 3 Fit statistics (R^2 , RMSE and AIC) for the model with non- azimuthal CI (Eq. 2) and the model based on azimuthal CI used in the second modelling approach (optimizing azimuth) (Eq. 4) in karri and marri forest for two growth periods. Best angle is the bearing of the optimal mean angle of competition, relative to North. The given p-value is for azimuthal (Eq. 4) and non- azimuthal (Eq. 2) CI in the model (not for the overall model). k is the numerical power value that gave the best model fit for all data across all plots (based on model AIC). NA is not applicable.

Growth period	Models based on	Karri						Marri					
		Best angle	p-value	k	R^2	RMSE	AIC	Best angle	p-value	k	R^2	RMSE	AIC
1992-2002	Non- azimuthal CI	NA	<0.001	0.169	0.650	0.1644	-74.66	NA	0.010	0.363	0.6778	0.1339	-45.19
	Azimuthal CI	76°	<0.001	0.17	0.652	0.1640	-75.18	19°	<0.001	0.360	0.6853	0.1324	-46.25
2002-2018	Non- azimuthal CI	NA	0.019	0.069	0.650	0.1362	-99.98	NA	0.190	0.758	0.3727	0.1354	-39.55
	Azimuthal CI	57°	0.001	0.03	0.666	0.133	-104.30	322°	0.079	0.640	0.3952	0.1330	-41.05

In jarrah forest, the azimuth of the best angle was towards the north except in the first growth period of unthinned plots (Figure 4.). In both karri and marri forest, the azimuth of the best angle was towards the north in both growth periods.

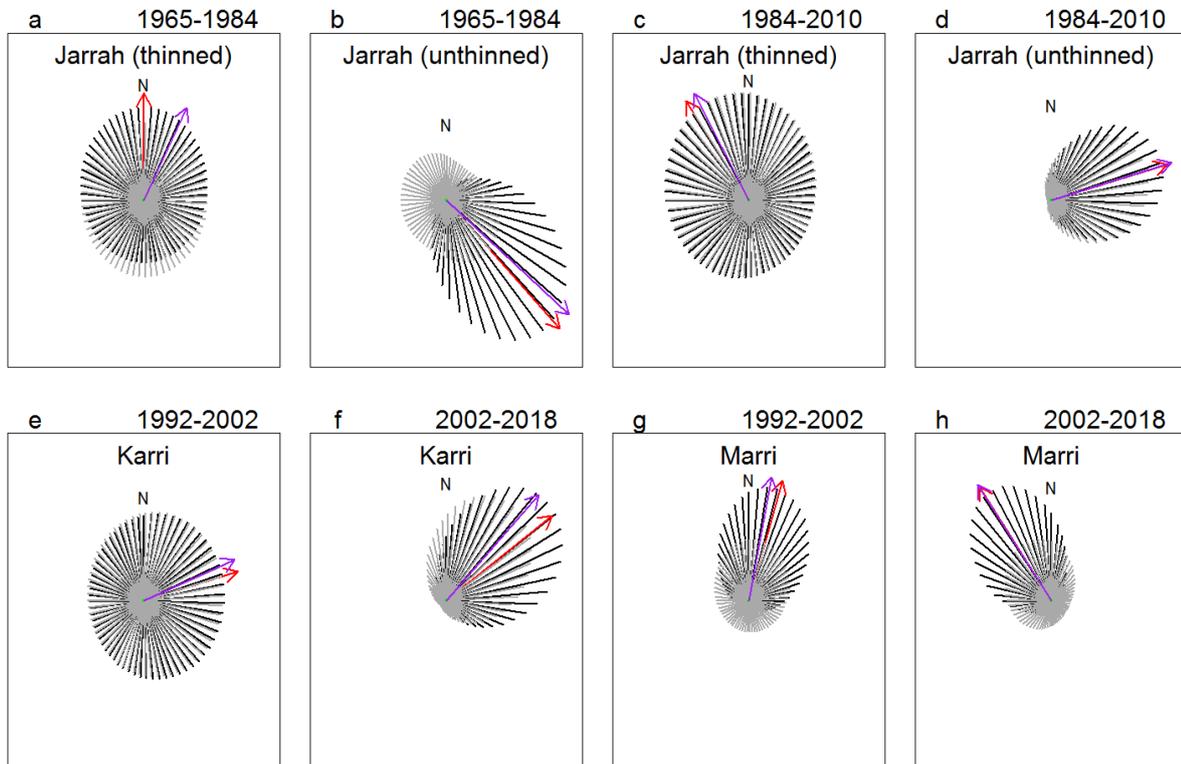


FIGURE 4 Graphical representation of the azimuth of competition for jarrah, karri and marri for two different growth periods, as indicated by the fitted von Mises distributions. (N denotes north; the red-coloured arrow denotes the azimuth of greatest competition, according to the best model (lowest AIC); length of black lines indicates the relative amount of competition coming from different azimuths, according to the best model; the purple-coloured arrow and grey lines denote the azimuth of greatest competition and the relative amount of competition coming from different azimuths according to an AIC weighted average of all models within 2 AIC of the best model). Differences in the length of arrows among subfigures is not meaningful.

3.3 Third modelling approach (relative size and azimuth)

For the thinned jarrah forest, in both growth periods, the second competition factor (Canopy CI) was not a significant predictor in the model with all competitors from the north, but it was a significant predictor when the model used only competitors larger than subject trees and from the north (Table 4). For the unthinned jarrah forest, competition was not a significant predictor in either growth period, although Canopy CI was very close to significant in the second growth period when the model used competitors larger than subject trees and from the north (Table 4).

For karri, Canopy CI was not a significant predictor in the model with competitors from the north in either growth period, but it was a significant predictor in both periods when the model used competitors larger than subject trees and from the north (Table 5). For marri, Canopy CI was not a significant predictor in either growth period, but the general CI was a significant predictor in the first growth period (Table 5).

Table 4 Fit statistics (R^2 , RMSE and AIC) for models based on all possible competitors, competitors only from the north, and competitors larger than subject trees and from the north in jarrah forest (thinned and unthinned) for two growth periods. P-value is for general CI (above- and below-ground competition) and canopy CI (above-ground competition). k is the numerical value that was estimated by finding the power value that gave the best model fit for all data across all plots (based on model AIC). North trees in this table denotes the tree to north of the subject tree. NA is not applicable.

Growth period	Competitors	Thinned plots						Unthinned plots					
		p-value		k	R^2	RMSE	AIC	p-value		k	R^2	RMSE	AIC
		General CI	Canopy CI					General CI	Canopy CI				
1965-1984	All Trees	<0.001	NA	0.344	0.439	0.116	1021.51	0.661	NA	2.500	0.470	0.078	92.48
	North trees	<0.001	0.240	0.847	0.441	0.116	1022.11	0.483	0.067	0.033	0.529	0.071	90.60
	North + >subject tree	<0.001	<0.001	0.104	0.486	0.107	985.05	0.156	0.119	0.734	0.513	0.077	91.67
1984-2010	All trees	<0.001	NA	0.205	0.650	0.123	398.05	0.402	NA	0.426	0.628	0.052	68.41
	North trees	<0.001	0.421	1.443	0.651	0.123	399.38	0.204	0.285	2.500	0.645	0.053	69.06
	North + >subject tree	<0.001	0.002	0.767	0.664	0.117	390.69	0.704	0.050	0.223	0.680	0.049	65.91

Table 5 Fit statistics (R^2 , RMSE and AIC) for models based on all possible competitors, competitors only from the north, and competitors larger than subject trees and from the north in karri and marri forest for two growth periods. P-value is for general CI (above- and below-ground competition) and canopy CI (above-ground competition). k is the numerical value that was estimated by finding the power value that gave the best model fit for all data across all plots (based on model AIC). North trees in this table denotes the tree to north of the subject tree. NA is not applicable.

Growth period	Competitors	Karri						Marri					
		p-value		k	R^2	RMSE	AIC	p-value		k	R^2	RMSE	AIC
		General CI	Canopy CI					General CI	Canopy CI				
1992-2002	All trees	<0.001	NA	0.169	0.650	0.164	-74.66	<0.001	NA	0.363	0.6778	0.1339	-45.19
	North trees	0.006	0.348	0.118	0.653	0.163	-73.57	<0.001	0.251	0.166	0.6881	0.1318	-44.65
	North+ >subject tree	<0.001	0.050	0.212	0.663	0.161	-76.33	0.001	0.404	0.097	0.6833	0.1328	-43.96
2002-2018	All trees	0.019	NA	0.069	0.650	0.136	-99.98	0.190	NA	0.758	0.3727	0.1354	-39.55
	North trees	0.021	0.599	2.500	0.651	0.136	-98.27	0.488	0.479	0.268	0.3812	0.1345	-38.11
	North+ >subject tree	0.027	0.035	0.139	0.667	0.132	-102.62	0.123	0.183	0.700	0.4024	0.1322	-39.54

Coefficient of variation of tree heights increased with time in unthinned jarrah plots from 22% to 27% and in marri plots from 33% to 36%; however, it did not increase in thinned jarrah and karri plots (Figure 5).

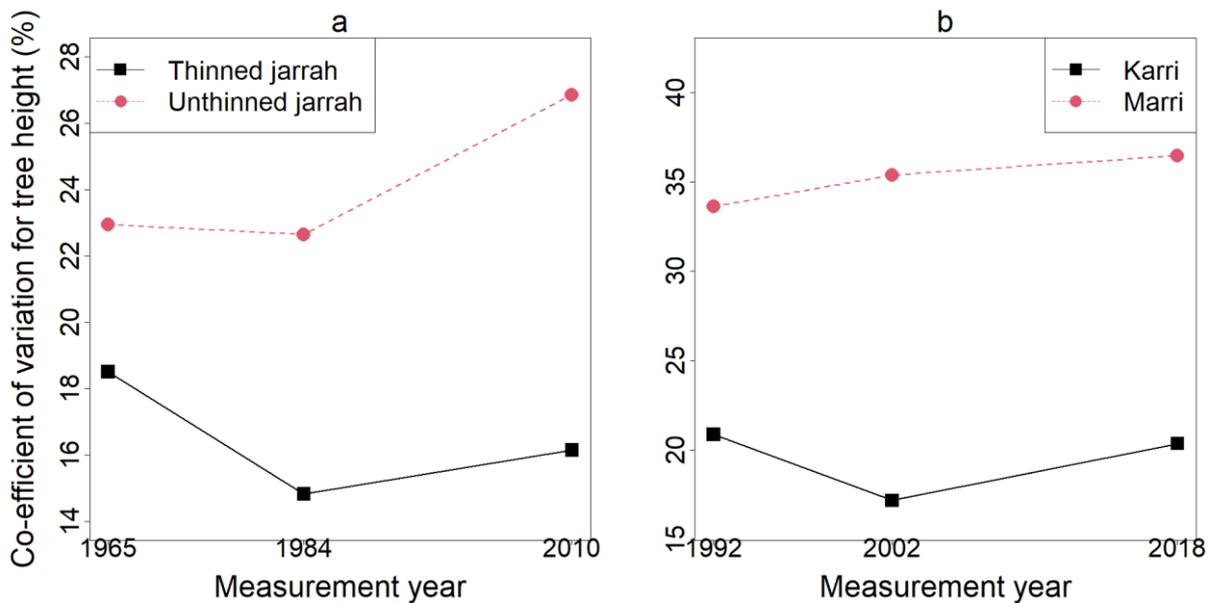


FIGURE 5 Variation in co-efficient of variation (CV) for tree height at stand level between growth periods for (a) thinned and unthinned jarrah plots, and (b) karri and marri plots.

4 Discussion

All three modelling approaches showed clear evidence of the azimuthal effects of competition on the growth of the jarrah, karri and marri forests, but also indicated that these azimuthal effects were relatively small. The magnitude of the azimuthal effect was higher in the unthinned jarrah forest than in thinned jarrah forest. The third modelling approach further provided evidence of size-asymmetric competition and the azimuthal effect of competition as competitors larger than subject tree and from the north had a significant effect on the growth of subject trees. The relatively small azimuthal effects in these forests suggest that the major competition in these forests is for below-ground resources, but a relatively smaller degree of competition for above-ground resources does also occur.

4.1 First modelling approach (comparing azimuths)

The first modelling approach indicated clear evidence of an azimuthal effect of competition in the thinned and unthinned jarrah forest. In the thinned jarrah forest, competitor trees from the east described more variability in growth compared to competitor trees from other azimuths. The model based on competitors from the east explained 6% more of the variability than the model based on competitors from the west (Table S1). In the unthinned jarrah forest, competitor trees from the south-east described 23% more variability in diameter growth compared to the competitor trees from the south-west azimuth in the first growth period, and competitors from the east described 5% more variability in diameter growth compared to the competitor trees from west azimuth in the second growth period (Table S1). This suggests that above-ground competition, especially for light, is higher in the unthinned jarrah forest than in the thinned jarrah forest. The higher competitive effect in unthinned jarrah forest is expected, because the unthinned forest had 1067 trees per hectare, which was four times higher than that in thinned forest (266) (Table 1). A significantly lower diameter growth due to higher competition in unthinned plots of jarrah than in thinned plot was found by Bhandari et al. (2021a) or Chapter 2 on the same experimental site. A greater effect of competitors from the east and south-east may indicate that morning light is very important for photosynthesis and growth of jarrah trees in these forests (Table S1). Jarrah trees tend to photosynthesize more in the morning, especially in the summer because that's when they have to close their stomata later in the day because of water scarcity. The morning light is restricted by the competitors from the east. Many eucalypt leaves tend to be vertical and capture more light in the morning (low sun angle) than at midday (King, 1997; Smith et al., 1998; James and Bell, 2000), reducing radiation intensity and heat load at midday, while allowing adequate light absorption in the early morning (east) and late afternoon (west) (Falster and Westoby 2003). However, the leaf angle distribution of jarrah is more spherical, so this effect is probably small in this species. Stomatal conductance and photosynthetic rates tend to be highest in the morning (Tenhunen et al., 1987; Lambers et al., 2014). In situations of

low water availability, midday stomatal closure reduces excessive water loss and enhances water-use efficiency (Cowan, 1982; Jones, 1992). Lower sun angles in the morning presumably also contribute to the greater effect of competitors from the east, compared to competitors from the north which cast shorter shadows due to the higher sun angle at midday.

For karri, in both growth periods, competitors from the north and west azimuth described a higher proportion of growth variability than the competitors from other azimuths, demonstrating evidence of azimuthal effect. Evidence of azimuthal effect was also present in both growth periods of marri; however, the effect of competition was not significant in the second growth period.

4.2 Second modelling approach (optimizing azimuth)

The second modelling approach showed a small effect of azimuth on above-ground competition in the thinned jarrah forest, and a clearer effect of azimuth in the unthinned plots. For the unthinned jarrah forest, in both growth periods, model prediction as measured by fit statistics (R^2 , RMSE and AIC) was significantly improved when the competitive effect was weighted by angle as well as distance (Table 2), but the moderate size of these improvements suggest that the role of azimuth is relatively small. Similar to the jarrah forest, evidence of azimuth effect was also observed in both the karri and marri forest with a significant improvement in fit statistics when the competitive effect was weighted by angle as well as distance (Table 3).

The azimuth of greatest competition in all the models for all species and periods was towards the north or east (Figure 4). This indicates that the competition for above-ground resources, such as light, comes from the north and east. This is expected for the individual trees growing in the southern hemisphere, where the sun moves through the northern sky. Thus, trees to the north cast shade on the subject tree, exerting a more competitive effect. The competitive effect of trees in the north of the

subject tree increases as latitude increases because of the decrease in sun elevation (Kuuluvainen & Pukkala, 1989). The influence of trees to the east of the subject tree was discussed in the previous section.

4.3 Third modelling approach (relative size and azimuth)

The third modelling approach of this study showed evidence of azimuthal and size-asymmetric competition (Table 4 and 5). When we used competitors from the north, canopy competition was not significant, but when we restricted the analysis to competitors from the north that were larger than the subject tree, canopy competition became a significant predictor (Table 4). Many other studies have also reported that large-sized trees may impose greater light competition to the small-sized trees and that light competition is thus at least partly size-asymmetric (Onoda et al., 2014; Forrester, 2019).

Our study showed an increase in the coefficient of variance (CV) in the unthinned plots and a decrease in the CV in the thinned plots of jarrah. This may be due to the small-sized trees being removed from the forest during thinning. This also suggests that competition in unthinned jarrah plots was more size-asymmetric than in the thinned jarrah plots. Similarly, we found a greater increase in the CV of marri plots compared to karri plots suggesting that competition in marri plots is more size-asymmetric than in karri plots. However, this increase was small in comparison to the increase in the unthinned plots of jarrah. Other studies have found more generally that variation in height increases over time when one-sided or size-asymmetric competition is high (Ellison & Rabinowitz, 1989; Kikuzawa & Umeki, 1996). Size-asymmetric competition promotes size inequality, and therefore supports the formation of a strong hierarchy in size distribution, which is important for population dynamics in plant species (Weiner, 1990). However, while larger trees reduce light incident on smaller trees, they can also provide protection against wind (Lomnicki, 1988; Lomnicki & Sedziwy,

1989). One-sided or size-asymmetric competition for light is also reported to promote the coexistence of forest tree species with similar adult height (Kohyama & Takada, 2012).

The presence of competition in the jarrah, karri and the marri forest has been observed in many other studies (Stoneman et al., 1996; Bhandari et al., 2021a or Chapter 2; Chapter 3; Bhandari et al., 2021b or Chapter 5; Chapter 6). Our study adds to these studies by showing that tree growth models are improved when competition is used as one of the predictor variables. However, the improvement in model prediction is relatively small when accounting for azimuth. This demonstrates that above-ground competition for light exists in these forests but its intensity is low. We therefore believe that below-ground competition is more important for the growth of individual trees in the jarrah, karri and marri forest of SWWA. For jarrah this contention is further supported by the observation that production of a vigorous central stem is delayed in young plants while a lignotuber, and a root system capable of exploiting subterranean root channels and deep-water tables is developed (Abbott and Loneragan, 1986; Bradshaw, 2015a). Together with a slow growth rate and highly seasonal Mediterranean rainfall, this indicates the plants have strategies focused on root development in preference to canopy or stem development (Abbott and Loneragan, 1983). The role of apical dominance in the early growth of karri indicates that competition for light is stronger in karri than in jarrah (Jacobs, 1955; Bradshaw, 2015b). Similarly higher self-thinning in karri should indicate a greater importance of above-ground competition compared to jarrah (Chapter 2 and Chapter 3). The site of this study has a Mediterranean climate with hot, dry summers and infertile soil, and thus water and mineral nutrients are limiting factors for the growth of jarrah, karri and marri. Competition for water and nutrients is size-symmetric, and no azimuth effect is expected. Experimental studies are needed for further evidence of below-ground and above-ground competition, and that may include thinning designs that ensure that trees experience greatly different levels of competition from different azimuths.

5 Conclusions

We developed, applied and evaluated three different modelling approaches in this study to investigate above- vs. below-ground competition by accounting for the azimuth of competitors in the dominant species of Mediterranean climate forest. We observed evidence of the azimuthal effect of competition on growth of jarrah, karri and marri through all three modelling approaches. The third modelling approach (relative size and azimuth) further showed the potential existence of azimuthal and size-asymmetric competition. As the improvement in model prediction was small when accounting for azimuth, we believe that above-ground competition for light is relatively small, and the majority of competition in these forests is mainly for below-ground resources. The modelling approaches accounting for azimuth of competitors developed in this study are likely to be useful methods for understanding above- vs. below-ground competition for different species world-wide in areas where competition among trees is one of the limiting factors for forest growth, dynamics and health.

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Supplementary Materials: S4

Table S1 Fit statistics (R^2 , RMSE and AIC) for models based on without CI (Eq. 1), with CI (Eq. 2) and CI from different azimuths ((Eq. 2) in jarrah forest (thinned and unthinned) for two growth periods. k is the numerical value that was estimated by finding the power value that gave the best model fit for the data used according to azimuths of competitors (based on model AIC). NA is not applicable.

Growth period	Competitors	Thinned plots					Unthinned plots				
		p-value	k	R^2	RMSE	AIC	p-value	k	R^2	RMSE	AIC
1965-1984	No CI	NA	NA	0.325	0.132	1101.07	NA	NA	0.467	0.078	90.69
	All	<0.001	0.344	0.439	0.116	1021.51	0.661	2.500	0.470	0.078	92.48
	North	<0.001	0.192	0.404	0.119	1048.27	0.074	0.051	0.521	0.071	89.15
	South	<0.001	0.353	0.412	0.119	1042.69	0.019	0.015	0.556	0.071	86.61
	East	<0.001	0.314	0.418	0.116	103782	0.226	0.062	0.492	0.074	91.05
	West	<0.001	0.200	0.396	0.123	1054.31	0.276	0.010	0.488	0.075	91.36
	Northeast	<0.001	0.188	0.372	0.124	1071.66	0.511	0.010	0.474	0.078	92.21
	Southeast	<0.001	0.365	0.401	0.118	1050.81	0.008	0.010	0.579	0.061	84.88

	Southwest	<0.001	0.219	0.365	0.129	1076.21	0.614	0.010	0.471	0.077	92.41
	Northwest	<0.001	0.129	0.373	0.123	1070.55	0.184	0.139	0.498	0.072	90.72
1984-2010	No CI	NA	NA	0.535	0.151	457.68	NA	NA	0.618	0.051	67.20
	All	<0.001	0.205	0.650	0.123	398.05	0.402	0.426	0.628	0.052	68.41
	North	<0.001	0.169	0.619	0.129	416.22	0.405	0.446	0.628	0.053	68.42
	South	<0.001	0.118	0.623	0.134	414.06	0.650	2.500	0.621	0.051	68.97
	East	<0.001	0.237	0.650	0.126	397.41	0.027	0.244	0.682	0.040	63.71
	West	<0.001	0.010	0.605	0.136	424.21	0.123	0.132	0.651	0.042	66.50
	Northeast	<0.001	0.197	0.606	0.134	423.49	0.162	0.283	0.646	0.050	66.99
	Southeast	<0.001	0.172	0.611	0.139	421.01	0.110	0.010	0.653	0.041	66.31
	Southwest	<0.001	0.010	0.583	0.139	436.09	0.049	0.104	0.670	0.044	64.82
	Northwest	<0.001	0.010	0.572	0.143	441.53	0.558	0.080	0.623	0.048	68.81

Table S2 Fit statistics (R^2 , RMSE and AIC) for models based on without CI (Eq. 3), with CI CI (Eq. 2) and CI from different azimuths (Eq. 2) in karri and marri forest for two growth periods. k is the numerical value that was estimated by finding the power value that gave the best model fit for the data used according to azimuths of competitors (based on model AIC). NA is not applicable.

Growth period	Competitors	Karri					Marri				
		p-value	k	R^2	RMSE	AIC	p-value	k	R^2	RMSE	AIC
1992-2002	No CI	NA	NA	0.527	0.191	-44.39	NA	NA	0.5564	0.157	-32.80
	All	<0.001	0.169	0.6502	0.1644	-74.66	0.010	0.363	0.6778	0.1339	-45.19
	North	<0.001	0.153	0.6289	0.1693	-68.32	0.030	0.374	0.6038	0.1485	-35.88
	South	<0.001	0.183	0.5996	0.1759	-60.19	<0.001	0.302	0.6649	0.1366	-43.42
	East	<0.001	0.143	0.591	0.177	-58.02	0.028	0.331	0.6049	0.1483	-36.01
	West	<0.001	0.170	0.627	0.169	-68.04	<0.001	0.319	0.6661	0.1364	-43.58
	Northeast	<0.001	0.114	0.5801	0.1801	-55.10	0.634	0.01	0.5588	0.1567	-31.05
	Southeast	0.005	0.224	0.5606	0.1843	-50.24	0.005	0.329	0.6302	0.1435	-38.99
	Southwest	<0.001	0.127	0.5858	0.1789	-56.55	0.004	0.268	0.6362	0.1423	-39.73
	Northwest	<0.001	0.146	0.5909	0.1778	-57.89	0.0117	0.301	0.6194	0.1456	-37.69

2002-2018	No CI	NA	NA	0.629	0.140	-96.35	NA	NA	0.3433	0.1386	-39.68
	All	0.019	0.069	0.6506	0.1362	-99.98	0.190	0.758	0.3727	0.1354	-39.55
	North	0.042	0.089	0.6455	0.1372	-98.62	0.180	0.322	0.3740	0.1353	-39.64
	South	0.070	0.055	0.6422	0.1378	-97.75	0.310	1.202	0.3611	0.1367	-38.80
	East	0.104	0.097	0.639	0.1383	-97.10	0.333	1.700	0.3595	0.1368	-38.70
	West	0.036	0.033	0.646	0.137	-98.89	0.248	0.431	0.3663	0.1361	-39.13
	Northeast	0.152	0.177	0.6373	0.1388	-96.48	0.281	2.500	0.3634	0.1364	-38.95
	Southeast	0.133	1.623	0.6381	0.1386	-96.69	0.474	1.516	0.3523	0.1376	-38.24
	Southwest	0.082	0.022	0.6411	0.1380	-97.48	0.147	0.01	0.3791	0.1347	-39.97
	Northwest	0.100	0.013	0.6399	0.1382	-97.16	0.236	0.074	0.3675	0.1360	-39.21

GENERAL DISCUSSION

1 Main findings

Chapters 2, 3 and 4 presented in this thesis confirm that, based on the experiments carried out at Inglehope and Sutton of Western Australia, jarrah and marri are slow-growing tree species compared to the moderately fast-growing karri. The rate of self-thinning is also lower in jarrah ($0.20\% \text{ yr}^{-1}$) and marri ($1.22\% \text{ yr}^{-1}$) compared to karri ($1.99\% \text{ yr}^{-1}$). Thinning improved the growth of individuals of all three species (jarrah, karri and marri) but the amount of improvement was species-specific. Heavy thinning resulted in seven times more diameter growth in jarrah, 1.5 times in karri and 1.08 times in marri. Dominant trees showed significantly higher growth compared to all other trees in both unthinned plots and slightly thinned plots, however the difference was negligible in heavily thinned plots. Heavily thinned plots contain a small number of individual trees and therefore all the trees have similar access to resources. The presence of competition among individual trees is clearly illustrated, as growth in thinned plots was significantly higher than in unthinned plots.

Two new spatial competition indices (CIs) were developed in Chapter 5 and 6 of this thesis. One new index is based on DBH of each competing tree and the distance between the subject tree and each competing tree. The other is based on crown width of each competing tree and the distance between the subject tree and each competing tree. For these indices, it was assumed i) that the competitive effect of each neighbouring tree depends linearly on the diameter or crown width of the tree and declines exponentially with distance; and ii) that the total competitive effect on a subject tree is the sum of the competitive effects of all other individual trees. Spatial competition indices

performed better than non-spatial indices for explaining/predicting the growth of individual trees. Competition among individual trees was the another most important significant predictor of tree growth after size (DBH and/or height) and/or age in thinned plots of jarrah, karri and marri. Validation of models developed for growth prediction of karri and marri showed that they have a good predictive ability within the range of conditions of the data used. As the age and size of individual trees increased over time, the number and distance of competitors was greater in the second growth period than in the first growth period. The optimum number and distance of competitors identified in this thesis may help in identifying trees to be removed during thinning operations. All three modelling approaches developed, applied, and evaluated in Chapter 7 of this thesis showed evidence of azimuthal effect of competition on the growth of the jarrah, karri and marri forests, but the small effect observed suggests that the major competition in these forests is for below-ground resources.

2 Effect of thinning on tree growth

Chapters 2, 3 and 4 of this thesis showed evidence of an increase in diameter growth of individual trees, when thinning was introduced as a management tool in the jarrah, karri and marri forests of south-west Western Australia (SWWA). The observed increase in growth due to thinning, or reduction in stand density, is consistent with the results from several other studies (Stoneman et al., 1995; Stoneman et al., 1996; Forrester et al., 2003; Koch and Ward, 2005; Grigg and Grant 2009; Forrester and Baker, 2012; Parrott et al., 2012; Forrester et al. 2013a; Forrester et al. 2013b; Lhotka, 2017; Acuna et al., 2017; Volkova et al., 2017; Hackworth et al., 2020). A study carried out in SWWA by Grigg and Grant (2009), found higher growth in diameter of jarrah trees in thinned plots than in unthinned plots. Similarly, in SWWA, Acuna et al. (2017) found a significantly higher volume increment in heavily thinned plots of *Eucalyptus globulus* compared to unthinned and lightly thinned plots. In south-eastern Australia, Volkova et al (2017) found that thinning increased canopy openness

and enhanced the growth of *Eucalyptus delegatensis*. Hackworth et al. (2020) in the USA, found that midstory removal on oak stands improved the light availability to seedlings and thus increased the survival rate, height growth and diameter growth. All these studies indicate that thinning or reduction in stand density reduces inter-tree competition for light, nutrients and water, and facilitates the enhanced and healthy growth of retained trees. The response of individual trees or of the whole stand to thinning may however vary, depending on species, thinning intensities, thinning methods and nutrient availability.

Thinning resulted in a greater relative increase in growth in jarrah than in karri and marri suggesting that growth response to thinning is highly species specific. Lhotka (2017) also reported that the rate of growth after thinning was different for different species in *Quercus* stands. This higher growth in jarrah after thinning can be attributed to the low rate of self-thinning (Burrows et al., 2010; Chapter 2). The rate of self-thinning is lowest in jarrah and highest in karri forest. As self-thinning is low in jarrah forest, inter-tree competition is high, which suppresses potential growth. The low rate of self-thinning could have been influenced by the fact that the stands were not at full stocking during the initial thinning operation, but note that this estimate is similar to the rate of self-thinning measured by Burrows et al. (2010) who found mortality of jarrah as 0.12% per year.

The effect of thinning was also observed to be site-specific for the same species. For example, marri trees grew more rapidly at Sutton than at Inglehope. This may be attributed to the higher site quality at Sutton block, where the soil is relatively more fertile than at Inglehope.

Stand-level basal area growth showed a different pattern than individual-tree diameter and/or individual-tree basal area growth in jarrah, karri and marri (Chapter 2, 3 and 4). Diameter growth increased continuously with an increase in thinning intensity in all three species; however, stand-level

basal area growth was maximum at intermediate thinning intensities in jarrah and karri, and in unthinned plots in marri. After thinning, the number of individual trees was significantly lower in heavily thinned plots compared to lightly thinned or unthinned plots. Because of the significantly lower number of individual trees in heavily thinned plots, stand-level growth was lower despite higher growth of individual trees. As the number of trees increased in plots with successively lower thinning intensities, stand-level basal area growth increased, though the basal area growth of individual trees decreased slightly. This trend continued up to a certain level (generally intermediate thinning intensity) and then stand-level basal area growth decreased with further increase in the number of individual trees. As the number of individual trees increased in lower thinning intensity plots, the inter-tree competition increased and growth in basal area of individual trees decreased significantly. When basal area growth of individual trees was significantly low, stand-level basal area growth was also low, despite the relatively higher number of individual trees. This is a common pattern of stand-level basal area growth under thinning operations (Moller, 1954; Grigg and Grant, 2009; Bradshaw, 2015a, 2015b; Chapter 2 and 3).

A different pattern of stand-level basal area growth was found in marri plots. Stand basal area growth increased continuously with decreasing thinning intensity. This may be because of the higher thinning intensity (46% in T2, 54% in T3, and 70% in T4) on the thinned plots of marri and a significantly larger number of individual trees per ha in unthinned plots of marri (1905 in 2018) compared to the number of individual trees per ha in the unthinned plot of jarrah (1067 in 2010) and karri (1016 in 2018). As the number of individual trees was large in the unthinned plot of marri, it resulted in a larger amount of growth even though the growth rate of individual trees was low.

Thinning in the forests may be costly from an economic point of view but may also generate economic benefits through the sale of forest products though the income generated from the sale of

forest products may be smaller than the cost of thinning. The costs of thinning depend on the quantity and commercial value of products removed, the cost of harvesting and extraction, and the distance from market. In some situations, non-commercial thinning may be justified where non-market values such as forest health, visual amenity, climate resilience, fire protection will be enhanced by thinning. Positive benefits of thinning include reduction of forest fire (Volkova et al., 2017); increased drought resistance (Vernon et al., 2018); increased groundwater storage and discharge (Bari and Ruprecht, 2003); improved forest health and promotion of regeneration (Wang et al., 2019). Detrimental effects of thinning include disturbance of soil (Nikooy et al., 2020) and wildlife habitat (Meiman et al., 2003). The negative effects of thinning depend mainly on how the thinning operations are conducted and the measures put in place to protect recognized values such as soil structure, habitat elements and wildlife. For example, large mature trees that potentially provide habitat for hollow-nesting fauna can be identified and protected during thinning and any subsequent fire management operations that accompany thinning. Silvicultural prescriptions (controlled burning, thinning, harvesting, regeneration promotion, gap creation) used in SWWA recognize these values and put in place measures to avoid or minimise potential negative effects (Burrows et al., 2011).

3 Effect of fertilizer on tree growth

Chapter 2 of this thesis showed that the application of nitrogen and phosphorus increased the growth of jarrah trees. Our finding of increase in jarrah growth after fertilizer application is consistent with Koch and Ward (2005), Grigg and Grant (2009) and Walters et al. (2021). Grigg and Grant (2009) reported that application of fertilizer (DAP with added KCl, Cu, Zn, Mn and Mo) increased diameter growth in 10-13-year-old rehabilitated jarrah in SWWA. Walters et al. (2021) found that application of nitrogen and phosphorus fertilizer increased diameter growth in the northern jarrah forest of Western Australia only up to 20 years after fertilizer application, suggesting that the effect of fertilizer on jarrah growth did not remain for a longer time. Application of fertilizer (nitrogen,

phosphorus and potassium) has also enhanced growth in other species, for example *Platanus occidentalis* in the USA (Brinks et al., 2011), *Pinus sylvestris* and *Picea abies* in Sweden (From et al., 2015), and *Ginkgo biloba* in China (Guo et al., 2016).

The soils of Western Australia are relatively nutrient-poor and plant growth is significantly limited by low availability of phosphorus (Handreck, 1997). Jarrah is well adapted to these types of soils and grows well, though the growth rate is low (Stoneman et al., 1996). The applied quantity of fertilizer caused higher growth of individual trees of jarrah in low stand density plots compared to high stand density plots (Chapter 2), indicating that either the applied quantity of fertilizer was not enough for high stand density plots, or that other factors such as water or light may have limited the response. Because of the larger number of individual trees in high stand density plots, the available nutrients were insufficient for maximizing growth. Although phosphorus fertilizer improved the growth of jarrah, it may be toxic to other plant species growing in the same forest in Western Australia (Lambers et al., 2013; Williams et al., 2019; Daws et al., 2021). The application of fertilizer, particularly phosphorus, has also been reported to decrease plant species diversity in jarrah forest ecosystem (Daws et al., 2013, 2015, 2021). It is clear, therefore, that whilst fertilisation enhances forestry outcomes, this comes at a cost for ecological values.

In addition to direct negative effects of fertiliser on many endemic plant species in SWWA, the use of fertiliser can have additional negative consequences for the natural environment. In high rainfall areas (>600 mm annual rainfall), the nitrogen and phosphorus can be leached into groundwater and washed into waterways. An excessive amount of phosphorus may contribute to algal blooms in waterways and estuaries in Western Australia (DPIRD, 2020). However, fertilizer application is not common as a management tool in jarrah forest except in mine-site restoration. Application of fertilizer in jarrah forest is currently uneconomic. As an experimental treatment in the

study presented in this thesis, fertilisation effects demonstrated the presence of below-ground competition for nutrients in jarrah forests.

4 Predicting/explaining individual tree growth

Growth of jarrah, karri and marri at the individual-tree level can be predicted by size (DBH and/or height) and/or age of the individual trees at the beginning of the growth period, however, the proportion of variation in growth explained/predicted by tree size varied with species. Height and/or DBH and/or age at the beginning of the growth period described the highest proportion of growth in jarrah (64%) (Chapter 5) followed by karri (56%) and the lowest in marri (38%). The prediction ability of size (DBH and/or height) at the beginning of the growth period is significantly lower in thinned plots (33%) of jarrah compared to unthinned plots (64%) (Chapter 5).

Growth prediction using the size of individual trees at the beginning of the growth period may depend on species, stem bark (smooth or rough) and measurement accuracy. Rough bark present in the stem of the individual trees reduces the accuracy of diameter measurement and therefore affects growth prediction. Chapter 6 of this thesis observed that the relatively low growth predictability in marri may be attributed to the rougher bark of marri compared to the bark of karri and jarrah. The diameter of each individual tree was measured after removing rough and loose bark to minimize error; however, depth of bark removal was highly subjective and therefore may not have reduced error completely.

As individual tree size increases gradually with age, the rate of diameter growth also increases, however the increasing rate of diameter growth does not continue throughout a tree's life. On average, diameter growth rate stabilizes during the middle stage of the trees life cycle. After that, the diameter growth rate starts to decline with further increase in age and becomes almost negligible when the tree

enters senescence. This typifies the general relationship between the diameter growth rate of an individual tree and its age (Chaturvedi and Khanna, 2011; Schongart et al., 2015). As trees get larger, they encounter their neighbours and begin to compete for resources. The slowdown in growth is also likely to be driven by competition. The relationship between age and tree diameter growth may deviate if some management interventions are applied in the forest. For example, if a thinning experiment is applied at the sapling or pole stage, the diameter growth rate of an individual may accelerate for a period after thinning but may again decrease before it reaches its normal growth peak. Chapter 6 showed a negative correlation between age and diameter growth in karri and marri forests which were relatively young (49 years). According to the general relationship between age and diameter growth, they were likely to be growing at an increasing rate (positive correlation with age). As a thinning treatment was applied when the karri and marri forests were 23 years old, the diameter growth rate increased rapidly right after thinning but declined gradually with increasing time after thinning. As the time after thinning increases, the size of individual retained trees increases and thus the inter-tree competition increases. The increased competition may have played a role in decreasing the diameter growth rate in karri and marri forest.

Individual trees in a forest grow with neighbouring trees and therefore, the growth of each one of them affects each of the others. The competition of neighbouring trees is one of the predictor variables in explaining and/or predicting the growth of a subject tree. Consistent with several other studies (Contreras et al., 2011; Lhotka and Loewenstein, 2011; Vanclay et al., 2013; Maleki et al., 2015), chapter 5 and 6 of this thesis observed a significant improvement in growth prediction when competition was included in the model, along with tree-size and/or age. Competition improved growth prediction (in terms of R^2) by 7% in overall (thinned plus unthinned) karri, 8% in overall (thinned plus unthinned) marri and 36% in thinned plots of jarrah. However, competition was not a significant predictor in unthinned plots of jarrah. In unthinned plots of jarrah, the inter-tree distance

was less variable and the rate of self-thinning in jarrah was relatively low. Therefore, the level of competition exerted on all individual trees was more or less similar and thus the competition was less likely to be a significant predictor. This should not be taken to mean that competition was not occurring. Competition alone has also been used as an explanatory variable in predicting individual tree growth (Forrester et al., 2013a).

Spatial competition indices performed better at predicting individual tree growth of jarrah, karri and marri than non-spatial competition indices, consistent with studies of other tree species (Contreras et al., 2011; Maleki et al., 2015). The correlation between the best non-spatial indices and diameter growth was 0.57 for jarrah forest and 0.56 for karri and marri which contrasted with correlations between the best spatial indices and diameter growth of 0.66 for jarrah and 0.58 for karri and marri. Spatial indices need extra effort in terms of cost and time to collect the location information of individual trees in the sample plot, however, non-spatial indices can also be used in growth prediction where the spatial information for individual trees is not available.

In chapter 5 and 6 of this thesis, the optimum number of competitors was found to be 10 to 14 and the optimum distance found for assessment of competitors was up to 10 m for explaining/predicting the individual tree growth of jarrah, karri and marri. This information (optimum number and distance to competitors) is crucial in designing the appropriate size of sample plot required for studying the effect of competition on growth and deciding which trees to remove in thinning operations. Besides the size and distance of neighbouring competitor trees, a further model was developed by including the growth rate of neighbouring competitor trees. Chapter 5 of this thesis showed that the growth rate of neighbouring trees is a significant predictor of a subject tree's growth but not better than the size of neighbouring trees. For the light competition, crown size (crown width and crown length) may be considered a better predictor than DBH because the crown size determines

how much light it intercepts. Individual tree growth is also directly proportional to the number of leaves on a tree or its leaf area (Enquist, 2002; Coomes and Allen, 2007). However, competition indices based on crown width only did not perform better than those based on DBH in the present study (Chapter 6). This could possibly be because crown width is more difficult to accurately estimate/measure than DBH, or because crown width in the absence of crown length may not be able to predict better than DBH, or because the above-ground competition was relatively unimportant.

As competition from neighbours was a significant predictor with a negative effect on the growth of individual trees of jarrah, karri and marri, it is recommended that neighbourhood competition be included when predicting growth and considering thinning treatments to minimize the effect of competition on growth. Stand-level modelling can also be applied to predict the growth and yield of a whole forest or stand, however, individual-based modelling can provide more accurate and detailed information for individual trees in the forest. Individual-based modelling could provide guidelines as to which thinning strategies are best for specific outcomes (e.g., volume per hectare or large-sized individual trees). Thinning strategies might be different for stands that regenerated after clear-felling or selective logging. A stand regenerated after clear-felling is likely to be even-aged with a high stand density but a stand regenerated after selective logging is likely to be uneven-aged because of the continuous regeneration which occurs using that system. For even aged stands, both stand level modelling and individual-tree level modelling are likely to be useful in predicting/explaining growth. For uneven-aged stands, individual-tree level modelling is likely to be the more useful method for predicting/explaining growth though the application of stand level models to uneven-aged forests is also reported (Forester et al., 2021).

In addition, thinning strategies might differ according to the objective of forest management. Intermediate thinning (thinning at intermediate age) is more appropriate for maximizing the economic

benefit derived from the forest. Thinning from below is more appropriate in late intervention, to maximize volume production per unit area, to improve saw log quality and to create a uniform stand structure (Opie et al., 1984). Thinning from above is more appropriate in early intervention, for maximizing the growth of retained individual trees and diversifying stand structure. Selective thinning is appropriate for maintaining straightness of retained trees and continuous canopy cover in the forest, along with some economic return from intermediate products (Stirling et al., 2000; Cameron, 2002). The impact of thinning also depends on thinning type, thinning intensity and thinning cycle. Different thinning strategies have been implemented for different species groups (conifer and/or broadleaved). Intermediate thinning at marginal intensity has been applied to conifer stands to maximize volume production in Britain (Kerr and Haufe, 2011). On the other hand, crown thinning has been applied to broadleaved stands for quality and high-value products.

5 Azimuthal effect of competitors on above-vs. below-ground competition

The modelling approaches developed, applied and evaluated in chapter 7 of this thesis found that competitors from a particular azimuth had higher predictability of growth compared to the competitors from other azimuths, demonstrating the presence of azimuthal competition in the jarrah, karri and marri forest of SWWA. As the predictive power of azimuthal effect is relatively low, it suggests that the greatest competition in these forests is for below-ground resources. Competitor trees from the north or east imposed the greatest competition because the forest occurs in the southern hemisphere. In contrast, in the northern hemisphere, greater competition is expected from individual trees from the south. As the sun elevation decreases with an increase in latitude, the competitor trees from the north may exert higher competition in higher latitude areas.

This study found that competition in the jarrah, karri and marri forest is not only azimuthal but also size-asymmetric. Canopy competition, an additional competition index apart from the general

competition index, was not a significant predictor when all competitors from the north were used but was a significant predictor when only those competitors from the north which were larger than the subject tree were used. Chapter 7 of this thesis also showed higher variation in the height of individual trees in unthinned jarrah forest compared to thinned jarrah forest. This demonstrates that size-asymmetric competition was higher in unthinned jarrah forest than in thinned jarrah forest. Because of the higher stand density in unthinned jarrah forest, insufficient light may have reached smaller and shorter individual trees compared to larger and taller ones. The azimuth of competitor trees and variation in size (height) can be considered as proxies for size-asymmetric competition.

Competitive stress influences total biomass production and its allocation to roots and shoots. In a study carried out in *Quercus liaotungensis* forest in China, Yang et al. (2019) found that a higher degree of competition among individual trees resulted in a greater allocation of root biomass compared to the shoot biomass. They further concluded that the greater allocation of biomass to roots is mainly because of the limited water availability for the growth of *Quercus liaotungensis* in the study site. Individual trees allocate more biomass to roots to make them stronger in the search for soil moisture and nutrients. The allocation of biomass to roots is proportionately higher in areas where below-ground competition is more intense than above-ground competition. In contrast, Cahill (2003) found that root biomass allocation was not increased with an increase in below-ground competition for 10 species he studied in Central Alberta, Canada. In a pot experiment using central European tree species, Kawaletz et al. (2013) found an increase in root competition over time and the increase in root competition was much higher for native species if mixed with exotic species compared to a monoculture or inter-native mixture. They also reported that native species allocated a higher amount of biomass to roots at the expense of branch or leaf biomass when the native species encountered higher root competition from exotic species. In another example, Rewald and Leuschner (2009) found that root competition was ubiquitous (present everywhere), size-asymmetric and species-specific in

broadleaved temperate mixed forest. Chapter 7 of this thesis found that the main type of competition in the jarrah, karri and marri forest is below-ground competition though a relatively smaller degree of above-ground competition also exists. Having knowledge about above or below-ground competition in a forest stand always provides important information for its sustainable management.

6 Relevance to forest-based industries in Australia

Australia has a large number of wood-based industries (257 sawmills, 23 wood-based panel mills and a small number of pulp and paper facilities) and these industries provide significant regional employment particularly in forest management, harvesting, transport and primary processing. In 2018/2019, forest industries in Australia generated \$23.9 billion of sales and service income and employed around 52,000 people (ABARES, 2018). The findings of this thesis may be useful in planning and implementation of forest-based industries. Chapter 2, 3 and 4 of this thesis provided evidence that the management intervention of thinning increased diameter, height and basal area growth and thus increased total yield from the forest. This may have implications for planning for profit generation by forest-based industries. The models developed in chapter 5 and 6 of this thesis are applicable to the prediction of growth of individual jarrah, karri and marri trees, for identifying patterns of forest stand dynamics and may provide improved predictions for use in forest management planning. They could even possibly be useful for identifying individual trees to be thinned. These findings could be useful in preparing management plans for the forests by Government authorities in Western Australia.

7 Recommendations

This thesis used 45-years long-term datasets for jarrah and 26-years long-term data sets for karri and marri in investigating the effects of thinning and neighbourhood competition on growth of endemic eucalypts of SWWA. For such slow-growing species like jarrah and marri, trials of this

length are essential but rarely undertaken. Collecting a similar dataset from another trial will necessarily take a long time-period and incur significant cost, highlighting the value of these existing long-term datasets. However, these datasets do have some limitations. These limitations include inconsistent interval of the measurement period, lack of data before thinning the stand, second thinning and fertilizer was not applied in the same year in jarrah forest, height was not measured for all trees in the plot and height was not measured when fertilizer was applied. These limitations also offer lessons for improvement of data collection in future experimental trials. The following recommendations may be useful for the future planning.

- i. Considering the relatively slow growth of tree species, data collection at the interval of five years would be one of the best options for long-term forest research experiments.
- ii. Measurement of height of all the individual trees inside the sample plot at each measurement time. Ground-based lidar 3-D mapping can be utilized to estimate the total height of the trees which can produce more accurate height of individual trees than the height measured by other methods.
- iii. Continuing the thinning experiment, as this reduces the inter-tree competition and provides a positive effect on forest growth.
- iv. A large number of sample plots need to be established at different geographical regions and climate gradients (temperature, rainfall), covering an appropriate range of ages and stand densities, to generalise the results for larger and wider areas. Studies carried out across a larger geographical and climate gradient may provide the opportunity to evaluate the effect of site and climate on forest growth and therefore may be an interesting and valuable topic for future study. The twin-plots concept (a pair of control and treated plots established 15 m – 20 m away from the permanent inventory plots) as reported by Stape et al. (2006) can be a potential option to minimize time and cost for collecting data from a wide geographical or landscape level.

8 Future research opportunities

There are abundant future research opportunities to enhance the knowledge and understanding of forest resources and their contribution to the overall ecosystem in SWWA. Though growth of three species (jarrah, karri and marri) was analysed in chapters 2, 3 and 4, how each species affects the growth of another species was not analysed because of insufficient data, but this would be an interesting topic for future study. Evaluating the effect of thinning on habitat and food availability for avifauna species is one of the potential areas for future studies for conservation of avifauna in SWWA. Breeding of West Australian Cockatoos is linked to the spatiotemporal availability of its primary food (fruits of jarrah and marri) (Mastrantonis et al., 2019). Individual tree models that can predict and simulate the carbon sequestration and storage by West Australian forest could be a potential topic for future research, supporting efforts for climate change impact mitigation. Battaglia et al. (2004) developed a model called Carbon BALAnce (CABALA) to describe how carbon, nitrogen and water flow through the atmosphere, trees and soil and to provide the basis for a silvicultural decision support system. Developing plant functional structural models to understand the growth of tree species at organ level may be potential for future research opportunities to increase insight in growth-limiting factors, seasonal aspects of growth, and above- vs. below-ground competition. Another alternate option might be possible through the parametrization of previously existing models for major tree species. Several attempts have already been made to understand root growth in plant species. For example, Shanin et al. (2015) developed a spatially explicit and multi-layered discrete model of below-ground competition named RootInt (ROOTs INTake). This model describes the spatial distribution of below-ground biomass and allows simulation of competition between trees for below-ground soil nutrients. The model of Shanin et al. (2015) may be applicable to different tree species and stand structure. Salas et al. (2004) applied a fractal root model for estimating the root biomass and architecture in two legume tree species (*Erythrina lanceolata* and *Gliricidia sepium*). This study

also emphasized the usefulness of an architectural approach for the study of below-ground interactions in agroforestry systems. Yang et al. (2019) reported that a higher degree of competition reduced individual tree growth while lower degree of competition reduced stem quality in Liaodong oak (*Quercus liaotungensis*) in China. They recommended, considering the dual effect of competition, that future studies should be focused on determination of suitable competition intensity. Chapter 7 of this thesis used azimuthal effects of neighbouring competitors to understand above- vs. below-ground competition in jarrah, karri and marri forest of SWWA and concluded that these forests likely compete more for below-ground resources. Experimental studies are needed to further investigate above-ground and below-ground competition. This could include removing competitors specifically from the north, south, east and west direction of a plot and evaluating the growth of individual trees.

9 Conclusions

Data derived from field-based long-term experiments on forest trees are invaluable for providing a comprehensive insight on growth trend analysis and growth prediction. Using long-term datasets, this thesis has highlighted how stand density (manipulated through thinning operation) affects the growth of three endemic eucalypts (jarrah, karri and marri) growing in Mediterranean-climate forests of south-west Western Australia. This thesis further highlighted the value of individual tree-based models for explaining/predicting the growth of these species using size and competition from neighbouring trees.

Thinning enhanced diameter growth in all three species (jarrah, karri and marri), however, the response of tree growth to thinning was highly variable indicating that thinning effects are highly dependent on species and thinning intensity. Stand basal area growth was optimized at an intermediate level of thinning in jarrah and karri but was optimized in unthinned plots in marri,

indicating that stand-level basal area growth is highly dependent on thinning intensity and number of retained trees after thinning. A different response of thinning was observed in diameter and height growth for individual trees at different thinning intensities. This resulted in thinning having a significant effect on the allometry of DBH with each of height, height-DBH ratio and crown width.

Diameter growth of individual trees of all three species can be explained/predicted using size and/or age at the beginning of the growth period. This explanation/prediction was further improved by incorporating competition from neighbouring trees. The inter-tree competition that exists in these forests is partly azimuthal in nature, but the low explanatory power of azimuthal effects suggests that the greatest competition is for below-ground resources, although non-azimuthal competition for above-ground resources cannot be excluded.

This thesis provides important information that may be useful for the sustainable management, monitoring and growth explanation/prediction of jarrah, karri and marri forest of SWWA. It also demonstrates how thinning can help to improve the growth of retained trees. As competition from neighbours was a significant predictor with a negative effect on growth, it is recommended that neighbourhood competition be included when explaining/predicting growth and considering thinning treatments to minimize the effect of competition on growth. The optimum number and distance to competitors described in chapters 5 and 6 of this thesis will be useful for deciding which trees to remove in a thinning operation and determining the appropriate plot size for studying the effect of neighbouring trees' competition on the growth of subject tree. The modelling approaches developed in Chapters 5, 6 and 7 of this thesis are likely to be useful methods for understanding, explaining/predicting and managing individual tree growth of any species in the world where competition among trees restricts individual tree growth.

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