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Structure, growth and growing space efficiency of *Pinus radiata* (D. Don) trees as affected by their social position

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Currently, silvicultural prescriptions such as thinning monospecific stands from above and transitioning from monospecific to mixed-species stands are scrutinised regarding their ability to reduce stress and damage. That the quantity and quality of the trees harvested by intermediate and final cuts will vary depending on the chosen prescription is likely but more or less neglected so far. Here we analyse 60 *Pinus radiata* (D. Don) trees earmarked for removal from the Jonkershoek thinning experiment at the West Cape, South Africa. The experiment comprises both thinning from above and below allowing for comparison of the structure and growth of dominant and subdominant trees removed at 11 years old. Thinning from above removed mainly dominant trees which were on average 44.3% larger in tree diameter, only 8.5% larger in tree height, but 83% larger in crown projection area and more than 25% tapering than subdominant trees extracted by thinning from below. The courses of diameter growth over age of the dominant trees were degressively asymptotic; those of subdominant trees were S-shaped, due to competitive pressure. The volume growth was exponential in both groups. However, the dominant trees achieved 2–3 times higher stem volumes at 10 years of age. Tree structure and growth were highly correlated: the mean annual volume increment showed a Pearson correlation of $r = 0.64$ with crown length, $r = -0.76$ with the current ratio of stem slenderness, and $r = -0.70$ with the competition index by Hegyi. Thus, crown length, slenderness and the competition index were most relevant in explaining tree growth. The analysis of the mode of competition indicated in both groups and in total a sub-proportional increase of stem growth with increasing size. Interestingly, growing space efficiency in terms of mean annual volume growth per crown projection area was similar in both groups.

Keywords: crown characteristics, growth trajectory, size-asymmetry of competition, structure–growth relationship, tree allometry

Introduction

Many works have been published about the course of tree growth depending on tree age or size (Bertalanffy 1951; Zeide 1993; Pretzsch et al. 2014). More recent studies have focused on tree allometry (Mäkelä and Valentine 2006; Pretzsch and Dieler 2012; Duursma et al. 2010), especially with respect to crown shape and its relevance for wood quality (Rais et al. 2020a; Rais et al. 2020b). Very few studies have combined tree structure and growth (Niklas 1994; West et al. 1997). Some older works did combine both to better understand tree growth per growing area (Mayer 1958; Pretzsch and Schütze 2015; Uhl et al. 2015). However, the relevance of the structural traits for the past and future growth course of trees was hardly ever considered. As the main variable for characterising the state of a tree, most approaches so far used mainly the stem diameter or tree mass, neglecting that crown and stem characteristics may have a strong additional effect on the growth behaviour as shown by Nicholson et al. (1975) and Roderick and Berry (2001). This becomes considerably important in case of suppressed trees and more heterogeneous stands (Wenk et al. 1990).

Pinus radiata (D. DON) is a commonly used tree species for plantations in South Africa (Bues 1985), South America, Australia and New Zealand. Growers can increase the growth rate of single trees and shorten the rotation length by lowering stand density (initial spacing or thinning). However, high growth rates affect wood quality of *P. radiata* negatively causing larger year rings, lower density, thicker branches and higher percentage of juvenile wood. A relevant issue for fast growing softwood is the juvenile wood, which includes the inner 10-year rings surrounding the pith of *P. radiata* (Cown 1992). Juvenile wood is generally characterised by low density (Cown et al. 2004), an abundance of knots and high microfibril angles (Donaldson and Burdon 1995; Watt et al. 2011). Finally, it results in structural timber grades of low stiffness and strength (Downes et al. 2002; Lasserre et al. 2005; Poschenrieder et al. 2016). In addition to space regulation, pruning is a direct silvicultural measure to reduce knottiness and improve timber properties (Rais et al. 2020c). To mitigate drought stress, stand density might be reduced in favour of the water supply and

growth of the remaining individuals (Aussenac and Granier 1988; Sohn et al. 2013; Steckel et al. 2020). Depending on the chosen kind of thinning either dominant or subdominant trees will be removed and harvested intermediately. So far, there is hardly any knowledge of the difference between the stem and crown characteristics and the growth and growing space efficiency of subdominant versus dominant trees.

Intermediate thinning also raises the question of how different thinning prescriptions may mitigate any drought or other stress and how they modify the productivity. Thinning from below may remove the subdominant trees in order to reduce drought stress for the remaining trees but it may also remove the most efficient trees, reducing stand productivity as shown by (Vuokila (1977, 1980) and Sterba (1999, 2019). Conversely, thinning from above results in a more intense decrease in competition than other types at equal thinning intensity: harvested stems are bigger with lower operational costs, and it promotes development of the trees marked for final harvest; however, it indicates little reduction of future mortality and little improvement in stand sanitation (Serrada 2000). For this reason, it is of interest to study also the growth per growing area of trees in different social positions.

Our main hypothesis was that in addition to current tree size and competitive status the antecedent growth and structure of trees co-determine their growth and productivity. In order to analyse thinning from above versus thinning from below in *P. radiata* stands we used individual tree data from stem analyses for analysing the relationship and feedback between tree structure and the long-term growth course. Based on *P. radiata* trees, we first studied the impact of the current structure on their growth in order to reveal the relevance of different crown characteristics for tree growth. We addressed the memory effects of the tree history by analysing the relationship between the structure of trees and their past and future growth course. We analysed the size-symmetry of competition between the trees in differently thinned stands and finally translated the single tree growth to stand productivity by relating the tree growth to the growing area.

Based on 60 stem analyses with 458 discs in total and additional measurements of tree characteristics, we answered the following questions:

Q1: How does the social position affect the stem and crown structure of *P. radiata* trees?

Q2: How does the social position affect the trajectories of diameter, and volume growth?

Q3: How do the growth trajectories and stem and crown structure depend on each other?

Q4: To what degree does the stem growth depend on the stem size?

Q5: Is the mode of competition size-symmetric or size-asymmetric?

Q6: How does the social position affect growth per crown projection?

Material and methods

Material and sampling

For this study we used sample trees from an experimental plot in Jonkershoek with a size of 1.64 ha, located in the south-west of South Africa, approximately 10 km south-east of Stellenbosch. The experiment was established in 2018 in a

10-year-old *P. radiata* stand encompassing nine plots. Variants of no treatment, thinning from below and thinning from above were established in triple repetition. Thinning was conducted in 2019 (age 11 years). Here, we selected 60 removed trees (10 per plot) from dominant (n = 29) and subdominant (n = 31) trees to compare their structure and growth. Table 1 summarises relevant site and plot characteristics.

At the last survey in 2019, the arithmetic mean stem diameter (standard deviation), minimum and maximum diameters were 19.6 (4.4), min = 5.9 and max = 31.2 cm on the non-treated plots. The respective values were 22.6 (2.7), min = 11.1 and max = 33.5 cm on the plots with thinning from below and 18.6 (4.9), min = 6.8 and max = 29.0 cm on the plots with thinning from above.

Figure 1 combines temperature and precipitation information for Jonkershoek from 2011 to 2019 and indicates water availability (Walter and Lieth 1967). Monthly water availability is graphically displayed as precipitation sum (in mm) divided by two, minus average monthly temperature (in °C). Negative values indicate water deficit illustrated by dots, and positive values indicate water surplus illustrated by vertical lines. The water deficit (after Thorntwaite and Mather 1955) averages 258 mm per year. In the context of plantation forest sites of the Western Cape, this value represents a high annual water deficit (Scheepers and du Toit 2020).

Characteristics of a tree's stem and crown structure
Description and analysis of tree structure and growth were mainly based on the tree variables, diameter at breast height (DHB, 1.3 m), height (h), crown diameter (CD), and crown projection area (CPA). The CPA results from the mean crown radius of eight crown radius measurements

$$\bar{r} = \sqrt{\frac{r_1^2 + r_2^2 + \dots + r_8^2}{8}}$$

as follows

$$\text{CPA} = \bar{r}^2 \times \pi$$

Based on the CPA, the crown volume and surface area can be computed. To compare the structure of dominant and subdominant *P. radiata* trees, the following ratios between tree organ sizes are frequently used: The slenderness (h/d), using h (m) and DBH (cm), addresses tree stability and the crown projection area (cd/d), using the crown diameter (cd, m) and stem diameter (d, cm), addresses the crown extension.

Competition index
To quantify the competitive status of the sample trees, we calculated their competition index according to Hegyi (1974) (CI) in 2019, before thinning was carried out. We used this commonly applied index

$$\text{CI}_j = \sum_{\substack{i \neq j \\ i=j}}^{n} \left(\frac{d_i}{d_j} \times \frac{1}{\text{DST}_{ij}} \right)$$

as it is mainly based on tree diameter, which was essential and measured in this study. This index quantifies the competition of central tree j based on the stem diameter of tree j, d_j, the DBH of its n neighbours $d_{i=1 \dots n}$ and the distance, DST$_{ij}$ between

Table 1: Site and plot characteristics of the experimental site in Jonkershoek, South Africa

Characteristics	Unit	Value
Location		
Altitude above sea level	m	300
Coordinates		18°55′42″E, 33°57′37″S
Climate[a]		
Average and range in mean annual temperature	°C	17.4 [16.3–18.2]
Average and range in mean annual precipitation	mm y⁻¹	1060 [800–1634]
Average and range in mean annual ETP	mm y⁻¹	835 [744–910]
Average and range in annual water deficit[b]	mm y⁻¹	258 [65–373]
Soil		
Soil parent material		Granite & colluvial sandstone
Soil type (WRB system)		Dystric Cambisol (humic)
Soil family (South African Taxonomic system)		Sweetwater 1110
Texture and depth of A horizon	cm	Sandy clay loam; 40
Texture and depth of the B horizon	cm	Sandy clay loam; 130
Plot		
Number		9
Establishment		2007
Trial size	ha	1.64
Tree		
Number		60
Age	y	11
Mean diameter under bark DBH	cm	19.3 (*4.1*)[c]
Mean height *h*	m	15.7 (*1.5*)
Mean crown proj. area *cpa*	m²	18.0 (*9.1*)
Mean distance of competitors *dist*	m	3.6 (*0.3*)
Mean DBH of the stand over bark *dmean*	cm	19.3 (*15.4*)
Mean stem volume under bark *v*	dm³	214 (*94*)

a Climate period between 2012–2019; figures in square brackets represent the range.
b After Thornthwaite and Mather (1955).
c Figures in round brackets represent the standard deviation.
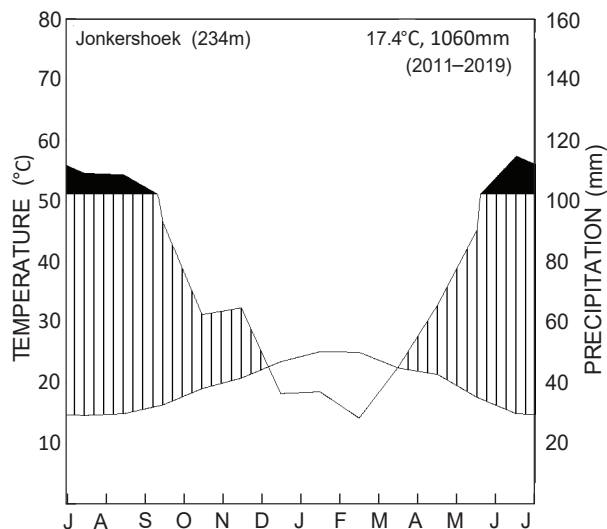
Figure 1: Jonkershoek climate chart (according to Walter and Lieth 1967)

central tree *j* and the respective neighbours. On average, 6.5 trees were selected as neighbour trees.

The technique of stem analysis
In total, we extracted 458 discs from the 60 removed trees. An analysis of diameter development and of the three-dimensional stem structure was possible by recording the height position of the collected stem disks and analysing year rings on them. The dashed lines in Figure 2 represent the analysis of year rings on stem disks, which delivered measurements for the reconstruction of diameter and stem form development. On average we sampled eight stem disks from each tree. If year rings were not sufficiently visible, the surface was additionally polished with sandpaper. Ring widths were measured in four rectangular directions. The annual volume was computed for each conical frustum in between neighbouring stem disks and finally summed up (Figure 2). Volume increment (*iv*) was derived by subtracting volume in year *n* from volume in year *n*+1.

Figure 3 shows the graphical results of the stem analysis for a dominant and a subdominant tree (No. 52, plot 3 and No. 70, plot 7). The horizontal lines represent the collected stem disks and their height position along the stem axis.

Table 2 summarises the variables derived from measurements and used for further analyses.

Statistical analyses
To detect possible differences in the social status among tree attributes (Question 1), we applied the Student's *t*-test. The normality and variance equality assumptions were visually verified based on diagnostic plots and variance equality tests. For verification of normality we applied Q-Q-plots of the residuals and for the variance homogeneity the Levene test. The results of the *t*-tests are shown in Table 3.
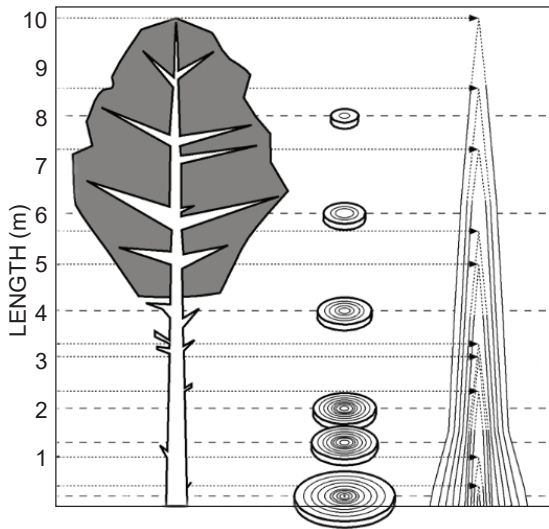
Figure 2: Schematic representation of the analysis of stem development by retracing tree ring width on stem disks. Length indicates the length of the stem. Variable n represents the number of annual leading shoots and the age of the tree at the time of the sampling. The numbers n-1, n-2...n-9 represent the number of annual leading shoots and stem age 1, 2...n years ago. The analyses of stem disks from different positions along the stem axis enable the reconstruction of the stem diameter, height and volume growth

To answer Question 2, we fitted the models $\ln(\text{DBH}) = d_0 + d_1 \times \ln(\text{age})$ and $\ln(\text{stem volume}) = v_0 + v_1 \times \ln(\text{age})$ to each of the stem diameter–age and stem volume–age courses individually by regression analyses. In the formulas, d_0 and v_0 represent the intercept of the age-site relationship, and d_1 and v_1 the respective slopes. We do not report the statistical characteristics of all 120 individual regression analyses, however, we visualise the resulting regression coefficients (Figure 4a and b). The resulting regresion coefficients were used for testing any differences between the trajectories of dominant and subdominant trees by pairwise t-test (Table 4). We further fitted general mixed models $\ln(\text{dbh}_{\text{all}}) = dd_0 + dd_1 \times \ln(\text{age}_{\text{all}})$ and $\ln(\text{stem volume}_{\text{all}}) = vv_0 + vv_1 \times \ln(\text{age}_{\text{all}})$ to all the data simultaneously in order to get mean courses for stem diameter and stem volume development for both groups dominant and subdominant trees (Figure 4c and d).

Question 3 was answered using correlation analysis. The coefficients d_o and d_1 of the model $\ln(\text{DBH}) = d_0 + d_1 \times \ln(\text{age})$ and the coefficients v_o and v_1 of the model $\ln(\text{stem volume}) = v_0 + v_1 \times \ln(\text{age})$ as well as social tree position, stem and crown characteristics were used to analyse relationships between tree structure and growth.

To analyse how stem growth depended on the stem size (Question 4) we fitted the models $iv = a_0 + a_1 \times v + a_2 \times v^2$ and $iv = a_0 + a_1 \times v$ to the data. By the first model we tested the presence of quadratic trend in the iv-v-relationship. However, parameter a_2 in model $iv = a_0 + a_1 \times v + a_2 \times v^2$ was not significant, so that the relation was supposed to be linear.

The model $iv = a_0 + a_1 \times v$ was then applied to reveal any size-symmetric or size-asymmetric relationships between

tree size and growth (Question 5). The closer a_0 to zero, the more size-symmetric is the mode of competition. In case of size-proportional growth rates the observations should follow $iv = a_1 \times v$. In this case the coefficient a_1 indicates the constant growth rate $a_1 = iv/v$.

Finally, we used the model $iv/v = a_0 + a_1 \times 1/v$ for quantifying the hyperbolically decreasing relative growth rate with increasing tree size, represented by stem volume (Question 6). The ratio iv/v multiplied by 100 is also called the growth percentage (Prodan 1965). For answering Question 6 we used the ratio of tree growth and crown projection area as an indicator of growing area and resource use efficiency of trees (Römisch 1995; Sterba and Amateis1998; Webster and Lorimer 2003; Pretzsch and Schütze 2005,). Here, we used the crown projection area (CPA) as substitute for the area occupied by a tree. The mean annual volume increment (MAIV) at age of 9 years (MAIV $= v_{t=9}/9$) was used as growth variable. The ratio MAIV/CPA indicates the mean growth in terms of volume per area and year at the tree level. Consequently, this ratio translates the tree growth to the stand level productivity. We chose the model $\ln(\text{MAIV}/\text{CPA}) = a_0 + a_1 \times \ln(\text{CPA})$ to analyse this relation at the group level and for the dominant and subdominant trees together (statistical characteristics Table 5, line 7 and subsequent).

All models addressed the relationship between the initial stem volume, v, at the beginning of the growing season 2017 and the mean annual stem growth, iv, in the subsequent three years 2017–2019. We parameterised this model for the dominant trees, the subdominant trees and the total number of trees (for statistical characteristics see Table 5, lines 1–6).

The results of the regressions analyses are summarised in Tables 4 and 5. For all models, we show only the fixed effects. In the models we applied random effects at the tree and plot level in order to consider temporal and spatial autocorrelation. In case of group comparison, the fixed effect variable group was categorical (dominant, subdominant).

The statistical software R 3.4.1 was used for all calculations, in particular the function lme from the package nlme (Pinheiro et al. 2019).

Results

Effect of the social position of a tree on its stem and crown characteristics (Q1)
Almost all the investigated stem and crown attributes were significantly influenced by the social status of the tree (Table 3). The tree size of dominant trees was significantly larger than of subdominant ones. The DBH was 70 mm larger, which means an average superiority of 44.3% compared to subdominant trees. The height of dominant trees was 13 dm larger, that is, 8.5%. Crown projection area of dominant trees was 83% larger than for subdominant trees. Subdominant trees indicated an average slenderness of 1.0 m cm^{-1} and dominant trees had an average of 0.7 m cm^{-1}; this reflects a decrease of 25%. The crown projection area was the only variable with no significant difference between dominant and subdominant trees ($p = 0.13$). The Hegyi index was lower (by 38%) for dominant than for subdominant trees.
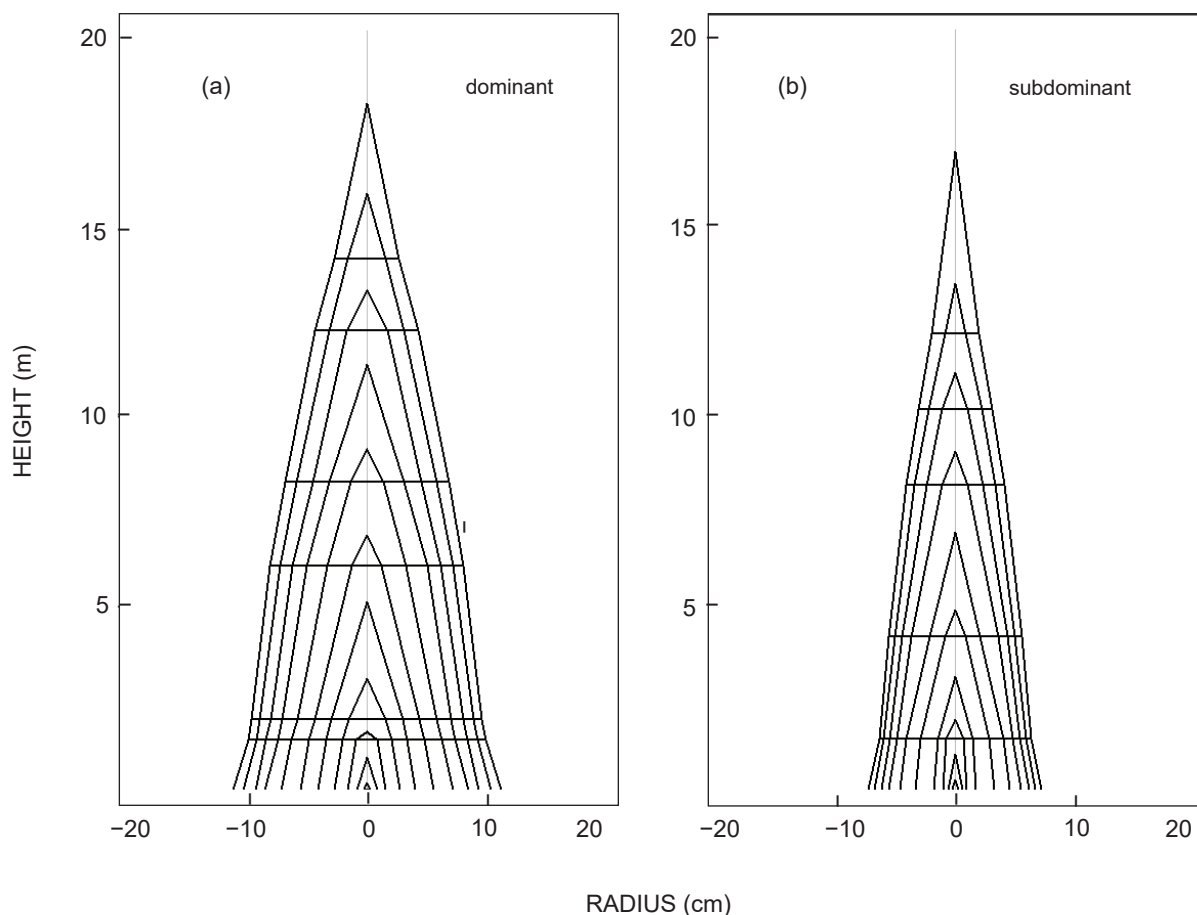
Figure 3: Stem of (a) dominant and (b) subdominant trees by example. All stem diameter, height, and volume growth variables in this study were derived from stem analyses

Table 2: List of variables, units and explanations

Variable	Unit	Name and explanation
cdd	m cm^{-1}	Crown projection ratio, ratio between mean crown diameter and diameter at breast height *d* according to Assmann (1970: p 112)
CI	./.	Competition index according to Hegyi (1974)
cl	m	Crown length
cpa	m^2	Crown projection area based on eight radii
DBH	cm	Stem diameter at breast height of 1.3 m
dist	m	Mean distance of competitors
dmean	cm	Mean DBH of the stands
h	m	Tree height
hd	m cm^{-1}	Slenderness ratio, ratio between height *h* and diameter dbh
v	dm^3	Stem volume derived by several stem disks along stem
iv	dm^3 a^{-1}	Mean stem growth rate per annum

The courses of stem growth depending on the social position of the trees (Q2)

The courses of stem diameter plotted over age (Figure 4a) had a logarithmic shape in case of the dominant trees, whereas the subdominant trees were obviously slowed down by competition and reflected S-shaped trajectories. The stem volume (Figure 4b) developed exponentially. At 9 years old,

the dominant trees already had three to fourfold larger stem volumes than their subdominant neighbours.

Table 4 reflects that the courses of stem diameter and stem volume growth of dominant and subdominant trees differed significantly. The dominant trees generally showed superior development; the intercepts were mostly lower and the slopes higher than those of the subdominant trees. The characteristic

Table 3: Statistical differences of stem and crown characteristics between dominant (n = 29) and subdominant (n = 31) trees. Coefficient of determination, estimate and standard error (in round brackets) as well as results of the pairwise t-test

Variable	Unit	R^2-value	Dominant	Subdominant	Ratio dominant / subdominant	P-value
DBH under bark	mm	0.74	226.7 (3.8)	157.1 (5.4)	1.44	<0.001
Height	dm	0.19	163.6 (2.3)	150.8 (3.3)	1.09	<0.001
Crown proj. area	m^2	0.31	22.7 (1.4)	12.4 (2.0)	1.83	<0.001
Slenderness	m cm^{-1}	0.61	0.73 (0.02)	0.98 (0.03)	0.75	<0.001
Crown proj. ratio	m cm^{-1}	0.02	0.23 (0.01)	0.25 (0.01)	0.92	0.13
Hegyi index	m^{-1}	0.51	1.60 (0.09)	2.57 (0.13)	0.62	<0.001

differences between both groups are shown in Figure 4c and d. The respective model parameters are visualised in Figure 4e and f and the tests of group differences are shown in Table 4.

Structure and growth (Q3)

We found that tree structure and growth were highly correlated; the mean annual volume increment showed a Pearson correlation of r = 0.64 with crown length, r = −0.76 with the current ratio of stem slenderness, and r = −0.70 with the competition index by Hegyi. Thus, crown length, slenderness and the competition index were most relevant in explaining tree growth (Figure 5c).

High competition indices strongly reduced d and v, but less so for h (Figure 5a). The stem shape in terms of hd, was increased by competition. Most crown size variables were reduced by increasing CI. Despite this tendency crown volume slightly increased with CI as the crown length cl stayed more or less constant and the crown of subdominant trees expanded laterally and developed a shade habitus. Interestingly, the relationship between stem size and crown characteristics were not very closely correlated, suggesting a high plasticity of tree crowns: cl, hd and CI were most relevant in explaining tree growth (Figure 5c).

Stem growth depending on stem size (Q4)

We found a significantly positive intercept, a_0, of $iv = a_0 + a_1 \times v$ in most cases, which indicated a linear but sub-proportional relationship between stem volume increment and growth (Figure 6a). This sub-proportional relationship iv-v means that the relative growth rates iv/v were not constant but hyperbolically decreasing (as $iv = a_0 + a_1 \times v$ for iv/v resulted $iv/v = c/v$). The grey lines in Figure 6b represent constant relative growth rates of 0.2, 0.4 and 0.6, that is, growth percentages of 20%, 40% and 60%.

Symmetry and asymmetry of growth (Q5)

The relationship between the absolute growth rate from 2017 to 2019, iv, and the stem volume at the beginning of this growth period, v, shown in Figure 6a, represents the mode of competition in terms of size-symmetry of competition (Schwinning and Weiner 1998; Pretzsch and Biber 2010). In case of size-proportional growth rates the observations should follow the trend of the straight grey lines starting in the origin and proceeding with $iv = a_1 \times v$, e.g. with a_1 = 0.2, 0.4 and 0.6 respectively.

Trees in both groups and in total represented a shallower iv-v-relationship than described by the grey lines for size-proportional growth (Figure 6a). Certainly, size is beneficial

for growth. Nevertheless, in our stands tree growth did not increase over-proportional with size as in light-limited systems.

Growth per growing area of dominant versus subdominant trees (Q6)

In terms of the MAIV, we observed a clear superiority of dominant over subdominant trees (Figure 7a and Table 5). We tested the mean $maiv$ values of dominant versus subdominant trees by a linear mixed model [lme(MAIV ~ social tree class, random= ~1|plot)] with the plot number as random effect. The fixed effect mean values (standard errors) were 47.4 (±3.8) cdm yr^{-1} for dominant and 32.1 (±2.4) cdm yr^{-1} for subdominant trees. The means of the two groups were significantly different (n = 60, p < 0.001).

The relationship between MAIV/CPA and CPA was continuously decreasing with CPA. We also tested the mean MAIV/CPA values of dominant versus subdominant trees by a linear mixed model with the plot number as random effect. The fixed effect mean values (standard errors) were 1.90 (±0.41) cdm m^{-2} yr^{-1} for dominant and 1.78 (±0.26) cdm m^{-2} yr^{-1} for subdominant trees; the mean of the two groups did not differ significantly (n = 60, p < 0.398).

The overall mean was 1.50 (± 0.10) cdm m^{-2} yr^{-1}, that is, a productivity of 15 m^3 ha^{-1} yr^{-1} for dominant and subdominant trees on average if up-scaled to one ha.

Discussion

The basic reaction patterns of crown allometry under competition

Under ample water supply and light limitation within the canopy the relationships between the vertical and lateral expansion of stem and crown of dominant and subdominant trees would indicate a tree allometry characteristic for light competition (Bonser and Aarssenc1994; Niklas 1994). The dominant trees would use their privileged height for expanding their crowns, and interception of light at the expense of the subdominant trees. This would result in much higher crown projection areas, but lower slenderness ratios than subdominant trees. In addition, the dominant trees would achieve an over-proportional growth rate and size-asymmetric competition due to their social status. The analysed trees on our plots followed this pattern only partially.

Dominant trees were on average 44.3% larger in tree diameter, only 8.5% larger in tree height, but 83% larger in crown projection area and 25% more tapering than subdominant trees extracted by thinning from below. Despite the significantly larger stem and crown diameters or lower
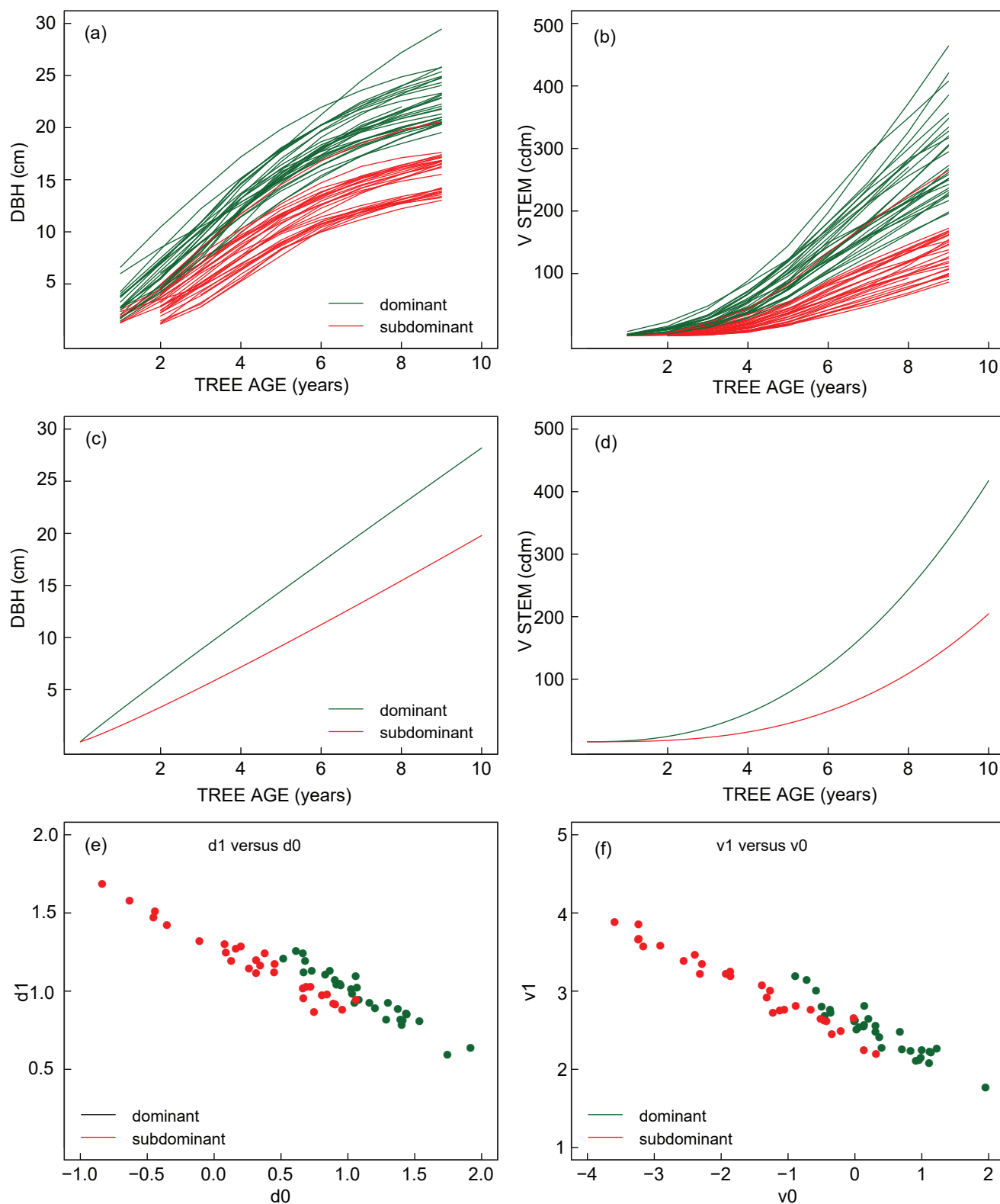
Figure 4: Courses of growth of diameter at breast height (a) and stem volume (b) over tree age. Mean courses of modelled diameter at breast height growth (c) by ln(DBH) = d_0 + d_1 × ln(age) and stem volume (d) by ln(stem volume)=v_0 + v_1 × ln(age). Scatterplot of the allometric exponents (d1) over the allometric factors (d0) of the models (e) ln(DBH) = d_0 + d_1 × ln(age) and (f) ln(stem volume)=v_0 + v_1 × ln(age) respectively

stem slenderness, the relative growth rates and the growth per occupied unit area were amazingly similar. This suggests a high morphological plasticity and acclimation to different social layers of the stand.

The size-growth relationship
The analysis of the mode of competition indicated in both groups and in total a sub-proportional increase of stem growth with increasing size (Figure 6a). This means a size-asymmetric competition according to Schwinning and Weiner (1998). It shows that size is beneficiary for growth in our stand, however, growth does not increase over-proportional with size as in light limited systems (Pretzsch and Biber 2010). The sub-proportional increase of stem growth with increasing size rather indicates a dominance of water limitation Schwinning and Weiner (1998).

The sub-proportional *iv-v* relationship reflects that the relative growth rates *iv/v* decrease with increasing tree size (Figure 6b). This is in line with the growing area efficiency results, which was not significantly different (but was higher for subdominant trees in the shade than for dominant trees with full sunlight).

Growing area efficiency
Different thinning concepts can strongly modify the stand productivity (Zeide 2001, 2002; Pretzsch 2020). In temperate forests removal of subdominant trees can strongly increase

stand growth as they use resources and growing area inefficiently compared with their dominant neighbours. Thus, the removal of subdominant trees can improve the resource supply of the larger trees which use the additional resources more efficiently for growth than their smaller trees. Therefore the relationship between stand density and growth may be unimodally shaped with highest productivity under medium stand density (Assmann 1961).

Here, interestingly, we found similar growing area use efficiency for small and tall trees. The similar productivity of small and tall trees suggested a high flexibility in thinning approaches. Thinning from above and below may have similar consequences for the stand growth, as the productivity of both dominant and subdominant trees was similar. The cause behind the high efficiency of small trees may be the sufficient light supply even in the understorey in the South African conditions compared to the more light-limited conditions in Europe, where most of the comparison between thinning from above and below where generated so far (Sterba 1999; Zeide 2001; del Río et al. 2008; Sterba 2019; Pretzsch 2020). It may also partially be a consequence of the lower evapotranspirational demand experienced by subdominant trees in slightly lower strata of the canopy.

The relevance for forest management and wood utilisation
The analyses of the *iv-v* relationships revealed that in our stands tree growth does not increase over-proportionally with size as common in light limited systems (Schwinning and Weiner 1998; Wichmann 2001), where large trees can make use of their preferential access to light. Tree growth in the analysed stands rather seems to be water limited, indicated by the proportional to even sub-proportional *iv-v* relationship (Pretzsch and Dieler 2011). Subdominant trees are inferior in terms of absolute growth but superior in growth rates. This indicates hardly any light limitation, over-proportional share of water and their strong contribution to stand growth.

Many studies on thinning and growth of pines report an immediate stand growth reduction when stand density is reduced by thinning (Mäkinen and Isomäki 2004; del Río et al 2017). Whereas more shade tolerant tree species such as

Table 4: Statistical differences between the courses of growth of dominant (n = 29) and subdominant (n = 31) trees reflected by the regression coefficients d_0 and d_1 of the model $\ln(DBH) = d_0 + d_1 \times \ln(age)$ and the coefficients v_0 and v_1 of the model $\ln(stem\ volume) = v_0 + v_1 \times \ln(age)$. The table presents the means, standard errors, and the results of the pairwise t-test

Coefficients	Dominant trees		Subdominant trees		
	Mean	SE	Mean	SE	p-value
d_0	1.11	0.06	0.32	0.09	<0.001
d_1	0.97	0.03	1.17	0.04	<0.001
v_0	0.35	0.12	−1.55	0.22	<0.001
v_1	2.49	0.06	3.04	0.09	<0.001

Table 5: Statistical characteristics of the models for analysing the size-symmetry or asymmetry of competition ($iv = a_0 + a_1 \times v + a_2 \times v^2$), the dependency between relative growth rate and stem volume ($iv/v = a_0 + a_1 \times 1/v$) and the growing area efficiency ($\ln(MAIV/CPA) = a_0 + a_1 \times \ln(CPA)$). Finally, we tested for any differences between the groups regarding MAI or MAI/CPA. The group d refers to dominant, and s to subdominant trees

| Relationship	Group	n	a_0	SD (a_0)	P-value	a_1	Std (a_1)	P-value
iv~v	d	29	9.67	9.48	0.316	0.28	0.07	<0.001
iv~v	s	31	13.93	2.31	<0.001	0.17	0.04	<0.001
iv~v	d & s	29	7.66	2.68	<0.01	0.29	0.02	<0.001
iv/v~1/v	d	31	0.24	0.07	<0.01	15.20	9.12	0.106
iv/v~1/v	s	60	0.11	0.04	<0.01	17.45	1.88	<0.001
iv/v~1/v	d & s	60	0.24	0.02	<0.001	12.30	1.44	<0.001
MAI~CPA	D	29	3.05	0.28	<0.001	0.13	0.09	0.09
MAI~CPA	S	31	2.66	0.37	<0.001	0.01	0.15	0.94
MAI~CPA	D & s	60	1.64	0.29	<0.001	0.52	0.10	<0.001
MAI/CPA~CPA	D	29	3.05	0.28	<0.001	−0.87	0.09	<0.001
MAI/CPA~CPA	S	31	2.66	0.37	<0.001	−0.99	0.15	<0.001
MAI/CPA~CPA	D & s	60	1.64	0.29	<0.001	−0.48	0.10	<0.001
MAI~group	d vs. s	60	47.36	3.78	<0.001	−15.27	2.39	<0.001
MAI/CPA ~group	d vs. s	60	1.90	0.41	<0.001	−0.22	0.26	0.40
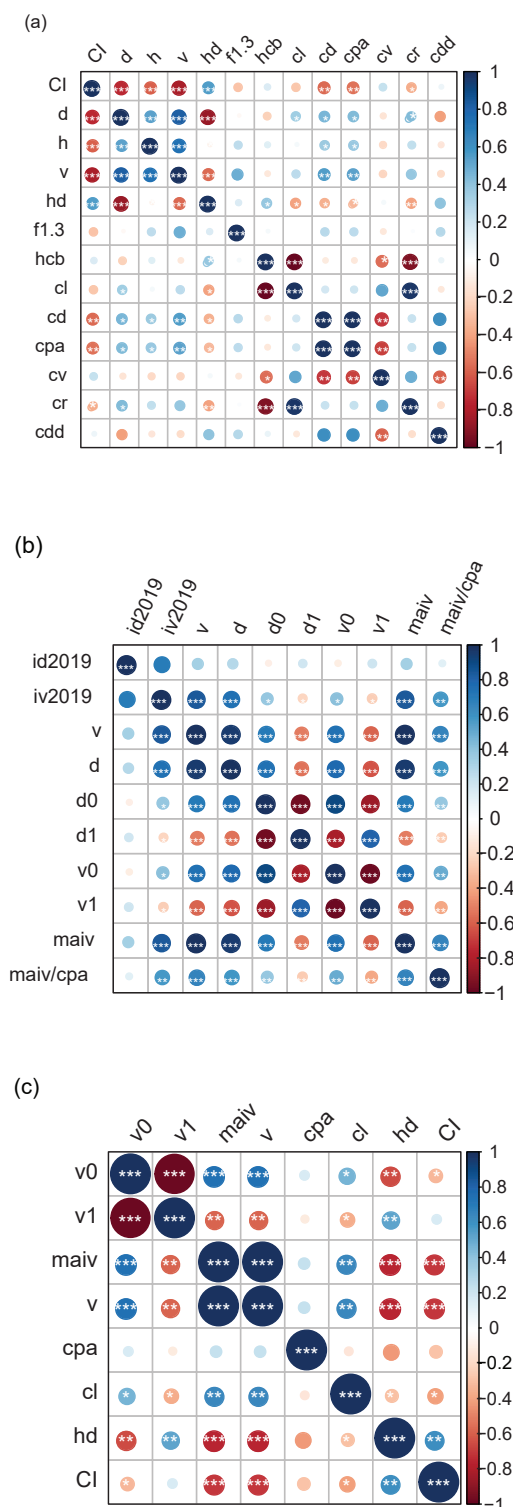
Figure 5: Correlation (a) between various stem and crown measures and ratios, (b) between growth and efficiency variables, and (c) between structure and growth variables. Significant Pearson correlation coefficients are reflected by *, ** or *** in case of significance levels of $p < 0.05$, $p < 0.01$ and $p < 0.001$ respectively. Blue symbols indicate positive correlations, red symbols negative correlations

Norway spruce or silver fir have a higher growth resilience to density reductions, pine is less resilient. Our findings that the growing space efficiency of dominant and subdominant trees is rather similar support these findings for pine. The subdominant trees were not less efficient than the dominant ones like for many species in temperate forests. Hence, it is unlikely that the removal of subdominant trees would increase the stand productivity. Both density reduction by thinning from above and below would probably cause similar growth reductions.

We hypothesise that under Mediterranean conditions where growth is mainly water limited (in contrast to the light limitation in more northern ecosystems) big trees do not over-proportionally benefit from their size. The size–growth relationship is proportional or degressive, indicating rather a size–symmetric competition for water (Schwinning and Weiner 1998; Wichmann 2001). The mode of competition may vary between rather light limited in moist years and water limited in dry years; however, the proportional or even degressive relationship between growth and size indicates prevalence of water limitation.

The analysed stands are still in an early development phase and they were not yet thinned. This, in the present state, our analyses suggest only some first hints for forest management. The finding that the productivity decreased with tree volume (Figure 6b) and with crown size (Figure 7b) means that stand density reduction may reduce the competition and increase the growing area and growth per tree. But as a consequence of the tree size growth acceleration it will also reduce the growth per unit area, that is, the tree and stand productivity. This suggests that stand density reductions may accelerate individual tree growth but at the expense of stand productivity.

The rather similar productivity of trees in different social classes (Figure 6b) suggests that density reductions by thinning from below or above will likely cause similar effects on stand productivity. Thinning from above will probably primarily promote the size growth of the dominant trees. As the subdominant trees are left in the stand this will result in rather vertically structured stands. Thinning from below may promote the dominant trees through improved water supply. However, thinning from below will homogenise the stand structure as the lower tree layer is continuously removed. Thinning from below may better adapt the stands to drought stress and avoid fire ladders. In any case, further survey of the different thinning variants is required for revision or substantiation of these first results about practical implications.

Conclusions

The results on *P. radiata* showed that the relative growth rates and the growth per occupied area are amazingly similar despite significantly larger stem and crown diameters as well as lower stem slenderness. This suggests a high morphological plasticity and acclimation to various levels of resource limitation in the different social layers of the stand. The similar relative growth rates and growing area efficiencies suggest a high growth resilience at the stand level to various silvicultural treatment options. Further ongoing studies on the Jonkershoek thinning will complete the overview of the effect of thinning from above versus below on stand stability, stand growth, and wood quality of the removed and remaining trees of *P. radiata*.
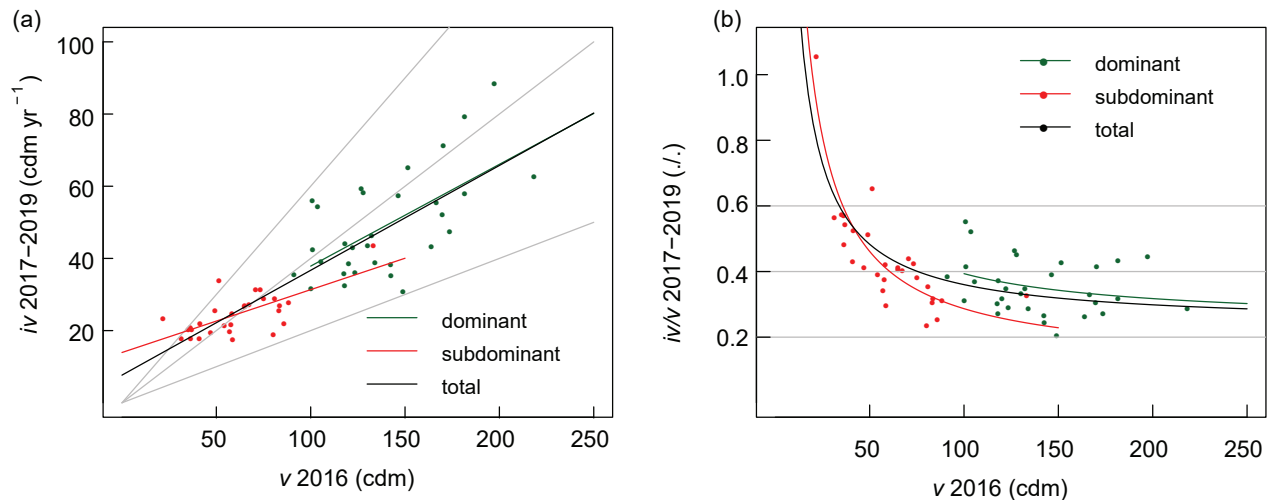
Figure 6: Mean absolute stem volume growth in 2017–2019 (a), and mean volume growth percentage (b), plotted over and modelled in dependence of the initial stem volume at the end of growing season 2016. Shown are the observed values, regression lines for dominant and subdominant trees separately and for both groups together
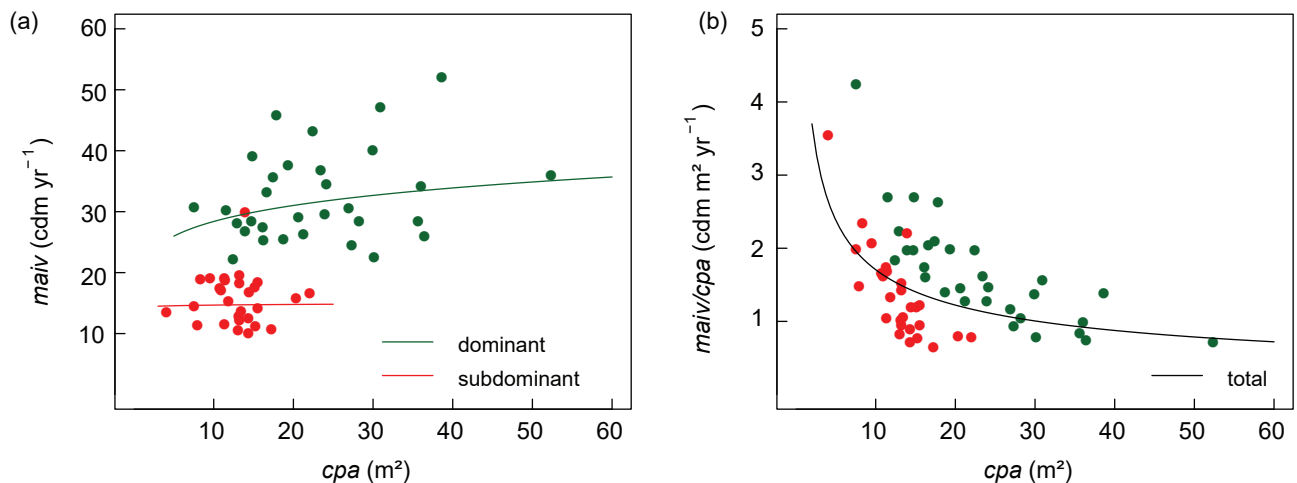

Figure 7: Mean annual stem volume growth, MAIV, and growing area efficiency, MAIV/CPA of dominant (green) tree versus subdominant trees (red). (a) Mean annual stem volume growth plotted over crown projection area. (b) Mean stem volume growth per crown projection area plotted over crown projection area. For the statistical characteristics of the models, see Table 5

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