

Seasonal characteristics and determinants of tree growth in a Chinese subtropical forest

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Abstract

Aims

To quantify the seasonal differences in effects of leaf habit, species identity, initial diameter, neighborhood interaction and stand environment on tree absolute diameter growth rates in a subtropical forest in China.

Methods

We used man-made dendrometer bands to record radial increments of all trees with diameter at breast height (DBH) ≥ 5 cm and height ≥ 3 m within 25 comparative study plots (30 \times 30 m for each) of the 'Biodiversity–Ecosystem Functioning Experiment China' (BEF-China) in the Gutianshan National Nature Reserve, Zhejiang Province, China. We measured stem circumferences twice a year from 2011 to 2014 to calculate absolute diameter growth rate of a warm and wet season (WWS, April to September) and a dry and cold season (DCS, October to the next March) for each individual tree: annual growth (GR_{year}), growth during the WWS (GR_{WWS}) and growth during the DCS (GR_{DCS}). We firstly tested the differences in growth rates between different seasons using paired *t*-tests with Bonferroni correction. Then we applied linear mixed models to explore the effects of leaf habit, species identity, initial diameter, neighborhood interaction (indicated by richness, density and total basal area of all neighboring trees within a radius of 5 m around

target trees), stand age and topography (elevation, slope and aspect) on tree growth rates of the two different seasons in three deciduous and 14 evergreen species.

Important Findings

GR_{year} , GR_{WWS} and GR_{DCS} varied between 0.04–0.50 cm year⁻¹ (mean = 0.21), 0.03–0.46 cm season⁻¹ (mean = 0.18) and 0.01–0.05 cm season⁻¹ (mean = 0.03) across the 17 species, respectively. GR_{WWS} was significantly higher than GR_{DCS} for all species. Growth rates of faster growing species tended to have larger absolute differences between the WWS and DCS. Tree growth rates of both seasons and of the year (GR_{year} , GR_{WWS} and GR_{DCS}) varied significantly among leaf habit and species, and increased allometrically with initial diameter, decreased with stand age, but were not significantly related to topography and neighborhood richness or density. GR_{WWS} decreased with neighborhood total basal area, while GR_{DCS} did not. In conclusion, species might be temporally complementary, contributing to plot growth at different times of the year.

Keywords: BEF-China, deciduous trees, evergreen trees, neighborhood interaction, species richness

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INTRODUCTION

Tree growth is an important process in determining the carbon accumulation of forest ecosystems. Tree growth rates vary remarkably among species (Baker *et al.* 2003a; Hérault *et al.*

2011; Paine *et al.* 2015; Sánchez-Gómez *et al.* 2008), functional groups (Baker *et al.* 2003b; Chi *et al.* 2015; Kariuki *et al.* 2006) and forest types (Sardans and Peñuelas 2013) because of the independent or combined effects of different biotic and abiotic factors (e.g. Chi *et al.* 2015; Gómez-Aparicio *et al.*

2011; Li et al. 2017; Sardans and Peñuelas 2013; Scholten et al. 2017). Responses of tree growth rates to biotic and abiotic factors reflect differences in life-history strategies of species in resource utilization, defense mechanisms and reproductive allocation (Baker et al. 2003b; Rüger et al. 2011). In order to predict potential changes in forest structure, biomass, carbon storage and biodiversity under global environmental change (Binkley et al. 2002; Coomes and Allen 2007; Rüger et al. 2011), it is therefore important to understand the large variation in growth rates among trees within a forest.

Previous studies have examined the spatial patterns and controls of annual tree growth rates within a single forest (Baribault et al. 2012; Chi et al. 2015; Coomes and Allen 2007; Gómez-Aparicio et al. 2011; Uriarte et al. 2004), or among different forest types (Sardans and Peñuelas 2013). Although no general conclusion can be drawn for different species, different functional groups or different regions, it has been widely reported that tree size, light and nutrient availability shape annual tree growth rates (e.g. Baribault et al. 2012; Coomes and Allen 2007; Gómez-Aparicio et al. 2011; Paine et al. 2015). Compared to the spatial patterns, knowledge on the temporal patterns and controls of tree growth rates is still scarce. Among the few studies, solar irradiation, temperature and precipitation have been found regulating the inter-annual variation in tree growth rates (Clark et al. 2003; Dong et al. 2012; Feeley et al. 2007). There are also increasing numbers of studies that focus on the seasonal and diurnal variation in tree growth rates with improvements of the technology (such as widespread use of dendrometers (Biondi and Hartsough 2010; Deslauriers et al. 2007; Prior et al. 2004; Wagner et al. 2012, 2014).

However, there are mainly two limitations for the studies on the seasonal changes of tree growth rates. Firstly, most of the existing studies have been conducted in tropical forests (Prior et al. 2004; Wagner et al. 2012, 2014) or boreal forests (Deslauriers et al. 2007; Duchesne et al. 2012). In comparison, subtropical forest has received much less attention. Secondly, most of the existing studies only focus on the effects of either some biotic factors such as functional traits (Li et al. 2017; Prior et al. 2004) or some abiotic factors such as climate (Biondi and Hartsough 2010; Wagner et al. 2012, 2014). Few explored the relative importance of different factors in driving seasonality of tree growth. For example, Prior et al. (2004) pointed out the importance of leaf attributes in determining seasonal patterns of tree growth rates in northern Australian. Biondi and Hartsough (2010) found that the relative effects of soil temperature and moisture on growth rates of *Pinus hartwegii* differed during different growth periods. It is reasonable that the drivers of tree growth rates may vary among seasons. Here, we take the advantage of a Chinese subtropical forest, which is composed of both evergreen and deciduous species, to explore the characteristic and drivers of tree growth in different seasons. We evaluate the degree to which tree growth rates are related to leaf habit, species identity, initial diameter, neighborhood interaction, stand age and topography between different seasons. Specifically, we ask the following questions:

- 1) How much do trees in the subtropical forest grow in different seasons?
- 2) How do leaf habit, species identity, initial size, neighborhood interaction, stand age and topography affect tree growth in different seasons; do these drivers of tree growth differ between seasons?

MATERIALS AND METHODS

Site description and plot survey

The study was conducted in the comparative study plots of the 'Biodiversity–Ecosystem Functioning Experiment China' (BEF-China) in the subtropical evergreen forest. The plots were located in the Gutianshan National Nature Reserve (GNNR), Zhejiang Province, China. The mean annual temperature and precipitation from 2005 to 2010 are 17.3°C and 1652.3 mm, respectively (see online supplementary Fig. S1, showed the climate diagram). Twenty-seven plots were randomly, but stratified by successional age resulting from the last logging events by local farmers, established across the subtropical evergreen forest in 2008. The dominant tree species in this region are *Pinus massoniana* and *Quercus serrata*, and *Castanopsis eyrei* and *Schima superba* in younger and older stands, respectively (Lang et al. 2012). More information about the reserve are also described by Hahn et al. 2017 and Wang et al. 2017. Our 30×30 m plots were located between 250 and 900 m in altitude, and each plot was further divided into nine subplots of 10×10 m (for details see Bruelheide et al. 2011). Two plots have been excluded from analyses due to disturbance by timber cutting in 2010. On average, richness and stem density of trees with diameter at breast height (DBH) ≥5 cm for these 25 plots ranged from 10 to 31, and 84 to 347 per 900 m², respectively. And the degree of deciduousness in terms of number of species and individuals ranged from 0 to 68.0%, and 0 to 50.6%, respectively, with the zero only occurred in one plot (CSP13).

Tree growth measurements

In September 2010, we tagged, mapped and installed man-made dendrometer bands on all 4375 trees with DBH ≥5 cm and height ≥3 m. Changes in tree circumference (ΔC) were measured with digital calipers (precision of ±0.01 mm) at ~6-month intervals in April and October of each year from 2011 to 2014. We defined the period from April to September as relatively wet and warm season (WWS), and the period from October to next March as relatively dry and cold season (DCS). During the period from 2005 to 2010, the mean temperature was 23.9 and 10.8°C, and the precipitation was 1087.1 and 565.2 mm in the WWS and DCS, respectively (see online supplementary Fig. S1). Changes in tree diameter (ΔD) for each WWS or DCS within a year were then calculated as changes in tree circumference (ΔC) divided by π (Vieira et al. 2005). To correct the effects of the possibly delayed measurement in some plots, we normalized the seasonal growth rates to a 183-day period, by adjusting the diameter growth per individual as $\Delta D \cdot 183 / \Delta T$ (ΔT is the number of days between two consecutive observation dates). Annual growth was calculated

as the sum of growth during two seasons. In the analysis, we excluded 207 trees that died and 13 trees that recruited into the 5-cm diameter class during the study period 2010–14.

Stand age determination and topography measurements

Stand age was estimated based on the age of the fifth largest tree of each plot, which was determined from a stem core taken at breast height (Bruehlheide *et al.* 2011). The stand age of the plots ranged from 20 to 120 years. Topographic variables including elevation, slope and aspect were measured for each plot. The circular variable of aspect (in degrees) was sine- and cosine-transformed into the continuous variables northness and eastness:

$$\text{northness} = \sin(\text{aspect in degrees} \times \pi / 180)$$

$$\text{eastness} = \cos(\text{aspect in degrees} \times \pi / 180)$$

Definition and calculation of neighborhood interaction indices

Species richness, individual numbers and relative size of trees neighboring the target trees are important parameters indicating neighborhood interaction (Papaik and Canham 2006; Sánchez-Gómez *et al.* 2008). In general, high species richness of neighbors (neighborhood richness) may reduce competition between trees due to niche complementarity or facilitation (Tilman 1996), and thus may increase tree growth rates and forest productivity (Barrufol *et al.* 2013; Paquette and Messier 2011; Zhang *et al.* 2012). Whereas high individual numbers of neighbors (neighborhood density) may increase the competition for resources between trees and therefore reduce tree growth rates. And increasing size of neighbors may increase asymmetric competition for resources, as larger neighbors may depress growth of focal trees.

For each individual target tree, we calculated richness, number of stems and total basal area (neighborhood total basal area) of all trees within a radius of 5 m around it. These data were only available for trees that were >5 m away from the plot margin and thus trees closer to the margin were excluded in the further analysis. We only analyzed species with >30 surviving trees at the end of the study period. Finally, we included 1995 trees, belonging to 17 species (three deciduous and 14 evergreens), 12 genera and seven families in the analysis (Table 1). Species richness within a radius of 5 m around these studied trees ranged from 0 to 14.

Statistic analysis

Paired *t*-tests with Bonferroni correction were firstly used to test for the differences in growth rates between seasons (WWS versus DCS). Linear mixed models were then used to test the possible drivers of tree growth rate of full year (GR_{year} , cm year⁻¹), WWS (GR_{WWS} , cm season⁻¹) and DCS (GR_{DCS} , cm season⁻¹). Leaf habit (evergreen versus deciduous), species identity, initial diameter, neighborhood richness, neighborhood density, neighborhood total basal area, stand age and

topographic variables were included as fixed effects in these models. The interaction between leaf habit or species identity and initial diameter was also considered as fixed terms. Year, plot and tree individual were used as random effects, with tree individual nested in the plot and then crossed with year. Simple linear regressions were also used to display the relationship between growth rates and initial diameter.

Before data analysis, we excluded strongly negative (with annual diameter shrinkage of >25% of initial DBH) growth rates because they were unlikely but represented erroneous data (Dong *et al.* 2012; Rieger *et al.* 2011). Moderately negative growth data were not excluded because they originated from measurement error and removing only negative values would bias the results. When carrying out the simple linear regression and linear mixed model analysis, we added 0.1 to the growth rates and then log-transformed them as well as initial diameters to homogenize and normalize residuals.

All analyses were conducted within R 3.0.3 (<http://www.R-project.org/>). Paired *t*-tests and simple linear regressions were carried out with base packages. Linear mixed models were applied separately to the two seasonal growth rates as dependent variables using the package 'asreml' for R (Gilmour *et al.* 2009).

RESULTS

Characteristic of tree growth rates

For all species, yearly growth rate (GR_{year}) varied from 0.04 (*Eurya muricata*) to 0.50 cm year⁻¹ (*Castanopsis fargesii*), with an average of 0.21 cm year⁻¹ (Figs 1 and 2). The growth rate varied from 0.03 (*E. muricata*) to 0.46 cm season⁻¹ (*C. fargesii*) (mean 0.18 cm season⁻¹) during the WWS (GR_{WWS}) and from 0.01 (e.g. *Toxicodendron succedaneum* and *E. muricata*) to 0.05 cm season⁻¹ (*Castanopsis carlesii*) (mean 0.03 cm season⁻¹) during the DCS (GR_{DCS}) (Figs 1 and 2). Paired *t*-tests showed that GR_{WWS} was significantly larger than GR_{DCS} for all species (Fig. 1). GR_{WWS} accounted for >80% of GR_{year} (Table 2). Faster growing species generally exhibited larger differences than slower growing species between GR_{WWS} and GR_{DCS} in absolute value but not in relative value (Fig. 1; Table 2).

Considering different leaf habit, the GR_{year} was higher in evergreen trees than deciduous trees (0.21 versus 0.19 cm year⁻¹). However, the evergreen and deciduous trees had similar growth rates during the WWS (GR_{WWS}), each with an average of 0.18 cm season⁻¹, but with different growth rates during the DCS (GR_{DCS}), with GR_{DCS} of 0.03 cm season⁻¹ for evergreen and 0.02 cm season⁻¹ for deciduous trees, respectively (Fig. 2). However, when incorporating the effects of plots, the difference in growth rates between evergreen and deciduous was significant over the year and in both seasons (Table 3). Paired *t*-tests showed that GR_{WWS} was significantly larger than GR_{DCS} for both evergreen and deciduous trees (Fig. 2).

Drivers of tree growth rates in different seasons

The linear mixed model showed that leaf habit, species identity, initial diameter, neighborhood total basal area, stand age and

Table 1: basic information and abbreviations of 17 species in Gutianshan, Zhejiang Province, China

Species	Abbreviation	Family	Num	DBH ₀ (cm)			
				Mean	Min	Max	SD
<i>Castanea henryi</i>	CASHEN	Fagaceae	51	10.7	5.0	32.0	6.4
<i>Castanopsis carlesii</i>	CASCAR	Fagaceae	30	18.0	5.0	58.1	14.8
<i>Castanopsis eyrei</i>	CASEYR	Fagaceae	282	15.5	5.0	65.2	9.8
<i>Castanopsis fargesii</i>	CASFAR	Fagaceae	33	17.4	5.2	47.1	10.2
<i>Cyclobalanopsis glauca</i>	CYCGLA	Fagaceae	42	7.6	5.0	16.7	2.8
<i>Cyclobalanopsis myrsinifolia</i>	CYCMYR	Fagaceae	41	14.0	5.0	56.2	11.2
<i>Cyclobalanopsis stewardiana</i>	CYCSTE	Fagaceae	60	6.8	5.0	12.9	1.7
<i>Daphniphyllum oldhamii</i>	DAPOLD	Daphniphyllaceae	50	13.6	5.3	27.3	5.9
<i>Eurya muricata</i>	EURMUR	Theaceae	62	6.0	5.0	9.4	0.9
<i>Lithocarpus glaber</i>	LITGLA	Fagaceae	219	8.5	5.0	21.8	3.7
<i>Myrica rubra</i>	MYRRUB	Myricaceae	39	11.1	5.1	25.2	5.5
<i>Pinus massoniana</i>	PINMAS	Pinaceae	150	16.6	5.0	61.9	9.6
<i>Quercus serrata</i>	QUESER	Fagaceae	48	10.6	5.1	18.7	4.0
<i>Rhododendron latoucheae</i>	RHOLAT	Ericaceae	55	6.5	5.0	10.5	1.4
<i>Rhododendron ovatum</i>	RHOOVA	Ericaceae	33	6.3	5.0	13.3	1.6
<i>Schima superba</i>	SCHSUP	Theaceae	332	13.6	5.0	69.8	9.8
<i>Toxicodendron succedaneum</i>	TOXSUC	Anacardiaceae	31	8.7	5.0	23.5	4.2

Abbreviations: DBH₀ = initial diameter at breast height (cm), Num = the number of individuals. Species names in bold font indicate deciduous species.

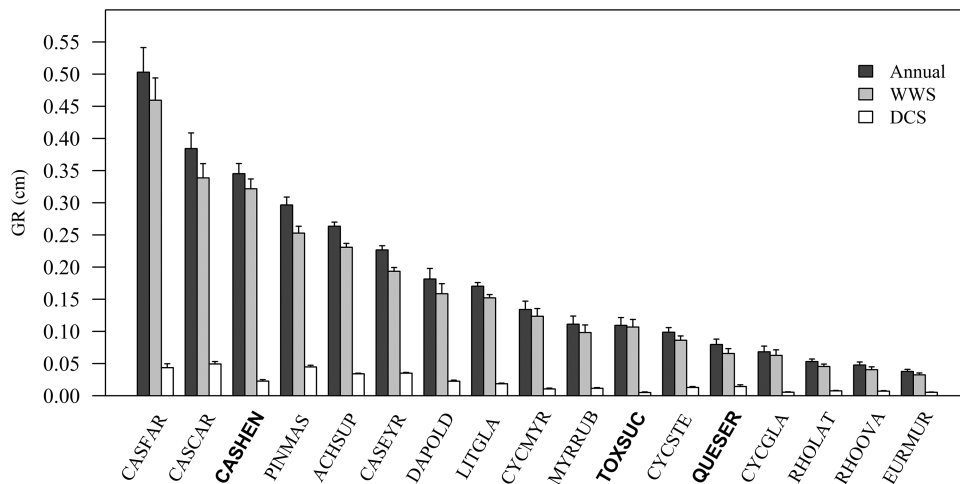


Fig. 1: annual and seasonal growth rates of trees of 17 species. Abbreviation: GR = growth rate. Species are presented by decreasing mean annual growth rate. The abbreviations of species are given in Table 1. Species names in bold font indicate deciduous species. The error bars showed the standard errors. Paired *t*-tests showed that GR_{WWS} was significantly different from GR_{DCS} at $P < 0.05$ for all species.

the interaction between species and initial diameter (Table 3; Fig. 3) significantly influenced GR_{year}, while the effects of neighborhood richness, neighborhood density and topographic variables were not significant (Table 3). The significant factors influencing GR_{WWS} were similar to those for GR_{year}. Both GR_{year} and GR_{WWS} were positively related to initial diameter, but negatively related to neighborhood basal area and stand age (Table 3). Compared to GR_{WWS}, the interaction between leaf habit and initial diameter did while neighborhood total basal area did not significantly influence GR_{DCS} (Table 3).

DISCUSSION

Seasonal differences in tree growth rates

Consistent with previous studies (e.g. Prior et al. 2004; Wagner et al. 2012, 2014), we found that growth rates fluctuated within year. Trees grow much faster at the relative wet and warm season (WWS) than the relative dry and cold season (DCS) for all trees with different leaf habits. In addition, tree growth rates in this subtropical forest differed significantly among different leaf habits and species. It is noteworthy that growth rates of evergreen

species were higher than those of deciduous species during both seasons. It is easy to understand the lower growth rates of deciduous species at DCS, because few leaves were left to photosynthesis for tree growth. But the reason of higher growth rates for evergreen than deciduous species at WWS remains unclear. Further studies are needed to explore why deciduous species did not have a compensatory growth advantage at both seasons but still coexist with the evergreen species in the studied forest.

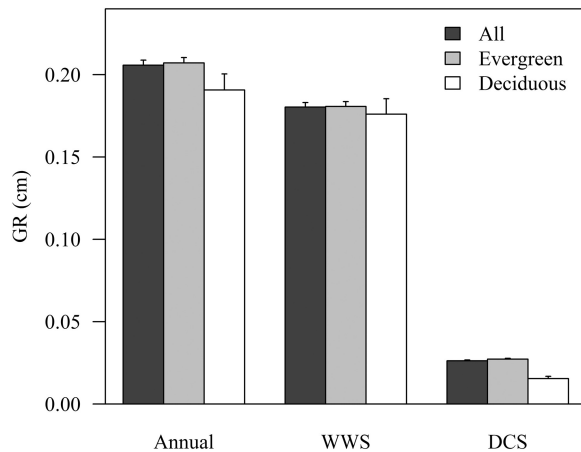


Fig. 2: annual and seasonal growth rates of all, deciduous and evergreen trees. Abbreviation: GR = growth rate. The error bars showed the standard error. Paired t -tests showed that GR_{WWS} was significantly different from GR_{DCS} at $P < 0.05$ for both evergreen and deciduous species.

However, the decreasing proportion of deciduous tree individuals and species with succession did occur in this subtropical forest (Bruehlheide *et al.* 2011). The growth disadvantage of deciduous species may to some extent relate with their decreasing importance in the community with succession.

Seasonal differences in factors influencing tree growth rates

Results of linear mixed models showed that neighborhood total basal area was significantly negatively correlated with GR_{WWS} but not with GR_{DCS} . This reflects that trees may experience stronger asymmetric resources competition in growth at WWS than DCS. One possible reason lies in that trees need more resources to support their faster growth at WWS, and therefore become more sensitive to the neighborhood asymmetric competition in resources. While in the DCS, trees grow much slower (4.5–22.0% of that in the WWS), resource availability may become less limiting and the importance of neighborhood asymmetric competition may reduce. In contrast, compared to WWS, DCS has lower temperature and water availability, the competition between trees may be weakened and facilitation may even occur under stressful conditions (Bertness and Callaway 1994).

Seasonal similarity in factors influencing tree growth rates

According to the results of linear mixed models, tree growth rates increased with increasing initial diameter and decreased with increasing stand age, but did not correlate with topography and neighborhood richness or density at both WWS and

Table 2: absolute and relative differences between two seasons in tree growth rates for 17 species in Gutianshan, Zhejiang Province, China

Species	Contribution of GR_{WWS} to GR_{year} (%)	Absolute difference (cm season ⁻¹)	Relative difference (GR_{WWS}/GR_{DCS} , %)	Rank of relative difference
<i>Castanopsis fargesii</i>	91.34	0.42	11.64	4
<i>Castanea henryi</i>	93.17	0.30	9.22	6
<i>Castanopsis carlesii</i>	88.15	0.29	6.95	10
<i>Pinus massoniana</i>	85.26	0.21	7.04	9
<i>Schima superba</i>	87.56	0.20	6.86	11
<i>Castanopsis eyrei</i>	85.32	0.15	4.57	17
<i>Lithocarpus glaber</i>	89.33	0.13	8.38	8
<i>Daphniphyllum oldhamii</i>	87.42	0.13	4.75	16
<i>Cyclobalanopsis myrsinifolia</i>	92.11	0.11	14.29	3
<i>Toxicodendron succedaneum</i>	97.60	0.10	20.56	1
<i>Myrica rubra</i>	88.28	0.09	5.33	14
<i>Cyclobalanopsis stewardiana</i>	87.32	0.07	18.85	2
<i>Cyclobalanopsis glauca</i>	92.01	0.06	5.88	13
<i>Quercus serrata</i>	82.44	0.05	4.91	15
<i>Rhododendron latoucheae</i>	85.53	0.04	8.63	7
<i>Rhododendron ovatum</i>	84.93	0.03	9.48	5
<i>Eurya muricata</i>	85.98	0.03	6.41	12

Species was listed in order to the absolute differences between two seasons in tree growth rates. Species names in bold font indicate deciduous species.

Table 3: results of mixed model analyses for annual and seasonal absolute tree growth rates in Gutianshan, Zhejiang Province, China

Fixed factors	Annual						Summer						Winter					
	DF	Coef	denDF	F	P		Coef	denDF	F	P		Coef	denDF	F	P			
Intercept	1	-2.509	18.3	452.60	<0.001		-2.418	20.0	548.00	<0.001		-2.859	3.0	5568.00	<0.001			
DE	1	1.008	1505.1	58.15	<0.001		0.948	1503.4	49.17	<0.001		0.658	1510.7	129.80	<0.001			
Species	15	—	1528.1	31.63	<0.001		—	1526.8	27.75	<0.001		—	1496.3	48.80	<0.001			
ln(DBH ₀)	1	0.610	1579.2	220.40	<0.001		0.577	1583.7	207.70	<0.001		0.283	1298.3	288.40	<0.001			
DE: ln(DBH ₀)	1	-0.188	1734.3	1.05	0.305		-0.184	1724.3	0.70	0.402		-0.170	1537.0	11.10	<0.001			
Species: ln(DBH ₀)	15	—	1684.2	3.72	<0.001		—	1675.5	3.44	<0.001		—	1538.6	6.80	<0.001			
Rich_5m	1	0.005	1499.7	0.21	0.649		0.005	1502.4	0.23	0.631		-4.59E-04	1350.2	1.40	0.236			
Den_5m	1	-0.001	1186.9	0.29	0.592		-0.002	1237.6	0.45	0.501		-0.001	852.6	0.60	0.442			
TBA_5m	1	-0.389	1487.9	14.89	<0.001		-0.356	1491.4	13.07	<0.001		-0.039	1335.2	3.50	0.063			
Stand_age	1	-0.009	22.2	13.25	0.001		-0.009	22.0	14.66	<0.001		-0.002	24.6	6.80	0.015			
Elevation	1	4.06E-05	18.9	0.02	0.896		-5.18E-05	18.8	0.13	0.720		1.73E-04	19.3	3.50	0.076			
Inclination	1	-0.001	18.9	0.20	0.658		-4.31E-04	18.9	0.22	0.642		-0.001	19.3	0.10	0.722			
Eastness	1	0.099	18.7	1.18	0.291		0.098	18.7	1.13	0.301		0.023	19.1	1.30	0.264			
Northness	1	0.073	18.4	0.67	0.424		0.075	18.4	0.68	0.420		0.007	18.6	0.10	0.726			

Variance component of random factors					
	comp	SE	z ratio	SE	z ratio
Year	0.002	0.003	0.990	0.001	0.980
Plot	0.084	0.029	2.847	0.086	2.855
ID	0.224	0.009	25.653	0.218	25.595
Residuals	0.039	0.001	39.011	0.039	39.064

Abbreviations: Coef = coefficient of fixed variable, comp = variance component, DE = leaf habit (evergreen and deciduous), denDF = denominator degree of freedom, DF = nominator degree of freedom, ID = individual tag, ln (DBH₀) = log-transform initial diameter, neighborhood density (Den_5m) = number of individuals within a radius of 5 m around the focal tree, neighborhood richness (Rich_5m) = richness within a radius of 5 m around the focal tree, neighborhood total basal area (TBA_5m) = total basal area of trees within a radius of 5 m around the focal tree, SE = standard error of variance component, z ratio = comp/SE. z ratio >2 can be considered significant. The coefficients of DE and DE:ln (DBH₀) indicate the differences in regression coefficient between evergreen and deciduous trees. Deciduous trees are baseline group.

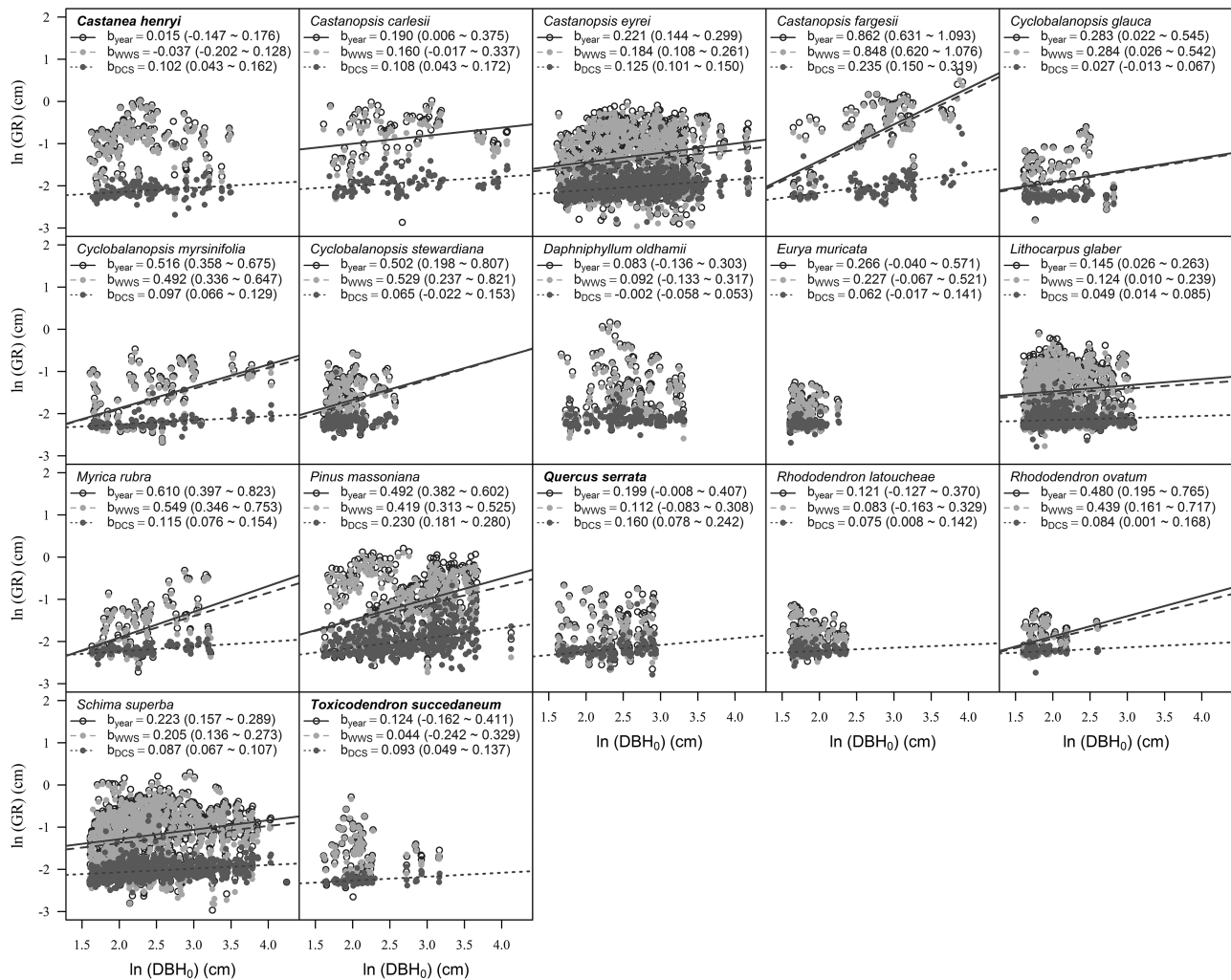


Fig. 3: the relationships between three periodic growth rates (annual: open circle with solid line, WWS: light grey solid circle with dashed line, DCS: dark grey solid circle with dotted line) and initial diameter for 17 species. Abbreviation: $\ln(\text{GR})$ = growth rate was added 0.1 and then log-transformed. b indicates the regression slope, numbers within parenthesis indicate 95% confidence intervals. Lines are plotted for significant relationships with significance set at $P < 0.05$. Species names in bold font indicate deciduous species.

DCS season. This indicates that the response of seasonality tree growth in this subtropical forest to initial diameter, stand age and neighborhood richness or density may follow the same principles as annual growth does. Firstly, we observed an allometric (linear on log–log scale) increase of growth rates (GR_{year} , GR_{WWS} and GR_{DCS}) with initial diameter, which was consistent with the results of previous studies reached (Coomes and Allen 2007; Enquist *et al.* 1999). For a given species, the increase of diameter, on one hand, may promote growth because of the increase of light availability and competition strength (Coomes *et al.* 2011; King *et al.* 2006; Sheil *et al.* 2006); on the other hand, it may suppress growth because of size limits (sigmoidal growth, Stoll *et al.* 1994), decreased vigor as a result of aging (Hervault *et al.* 2011), increased allocations to reproduction (Thomas 1996), and increased root and stem respiration (Ryan and Yoder 1997). The species-specific relationship between growth rates and diameter was

determined by the balance of these different factors. In this study, we observed differences in the relationships between growth rates (GR_{year} , GR_{WWS} and GR_{DCS}) and diameter among 17 species, while no significantly negative relationships were found. These resulted in positive effects of initial diameter on growth rates for overall trees and for individuals from both evergreen and deciduous trees.

Furthermore, we found that tree growth rates declined with stand age at all analysis. Two possible effects coupled with the stand age may result in the declining growth rates with stand age. Firstly, soil nutrients, especially nitrogen, become increasingly immobilized in the organic surface horizon, resulting in a decline of nutrient availability with stand age (Gower *et al.* 1996). Tree growth may thus decrease by nutrient shortage. This result suggests that individual tree growth may have the same relationship with stand age as forest growth does (Gower *et al.* 1996; Tang *et al.* 2014). In

addition, we speculate that stand age related decreasing nutrient supply may occur in both seasons. The possible fluctuations of nutrient supply within different seasons may exist in all different aged stands. Secondly, the larger plot-level basal area in the aging plot may to some extent result to stronger competition among trees and hence reduce tree growth rates.

However, the little effect of neighborhood richness was consistent with previous studies carried out to analyze sapling growth in response to manipulated biodiversity in a nearby area (Lang et al. 2012; Li et al. 2014). In another study at the same site, Lang et al. (2013) suggested that the local diversity effects on tree growth of four dominant species were reduced by the changes in complementary effects over time, local neighborhood species composition and snow break disturbance. These findings together indicate that neighborhood species composition and identity may play a more important role in tree growth than neighborhood species richness does (Lang et al. 2012). However, we did not test the effects of neighborhood species composition or identity due to the large number of possible combinations of species around the focal trees in the natural forest. Besides, neighborhood interactions may function at a distance of up to 20 m (Stoll and Newbery 2005). Thus, the 5 m radius may have weakened our chances to detect species richness effects, especially considering that individuals of different species may have different interaction radii (Stoll and Newbery 2005).

We did not find significant effects of topographic variables on both annual and seasonal growth, which was contrast to previous studies (e.g. Coomes and Allen 2007; Kariuki et al. 2006; Li et al. 2014). Within these studies, local topographic conditions, such as elevation, slope and aspect, were found to affect tree growth rates indirectly through their associations with light and nutrient availability (Coomes and Allen 2007; Kariuki et al. 2006; Li et al. 2014), as light and nutrient availability usually directly control tree growth rates (Baribault et al. 2012; Rüger et al. 2011; Rüger and Condit 2012). Therefore, we suspect that aging-related nutrient declination may play important roles in tree growth of this subtropical forest, which may weaken the indirect effects of topographic condition.

CONCLUSION

This study demonstrates that tree growth rates vary widely among seasons in the subtropical forest in the Gutianshan National Nature Reserve, China. Leaf habit, species identity, initial size, neighborhood competition and stand age together explained the observed seasonal patterns of tree growth. The growth disadvantages for deciduous species compared with evergreen species may be one of the explanations for the decreasing deciduousness degree in the community with succession. Species might be temporally complementary, contributing to plot growth at different times of the year.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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