

**Effects of biodiversity and abiotic environment on the growth  
rates of native tree species in subtropical plantations**

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Leuphana Universität Lüneburg

vorgelegt von

M.Sc. Ying Li  
geb. 01.04.1984 in Beijing

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Betreuer und Gutachter:

Prof. Dr. Goddert von Oheimb

Gutachter:

Prof. Dr. Werner Härdtle

Gutachter:

Prof. Dr. Alexandra Erfmeier

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## Summary

Biodiversity loss could jeopardize ecosystem functioning. Yet, the evidences that support this demonstration have been mostly obtained in aquatic and grassland ecosystems. How biodiversity affects ecosystem functioning still remain largely unanswered in forests, particularly in subtropical broad-leaved evergreen forests (EBLF). Tree productivity, among a wealth of forest ecosystem functioning, is of particular interest because it reflects the carbon sink capacity and wood productivity. Biodiversity-productivity relationships have been usually investigated at community level. However, tree-tree interactions occur at small scale. Thus, local neighborhood approach may allow a better understanding of tree-tree interactions and their contributions to the effects of biodiversity on tree productivity / growth rates. This thesis aims to analyze the effects of biodiversity and the abiotic environmental factors on the tree growth rates using both local neighborhood and community-based approaches. Furthermore, tree growth rates vary among different tree species. Functional traits have been related to the species-specific growth rates to understand the effects of species identity. Therefore, I also evaluated the crown- and leaf traits to predict the interspecific difference in growth rates. For a better understanding of the mechanisms that underline the relationships of biodiversity and tree growth rates, data of high resolution and long time series is required to scrutinize the tree-tree interactions. Thereupon, I evaluated the applicability of terrestrial laser scanning (TLS) in assessing the tree dendrometrics.

This thesis was conducted in the Biodiversity Ecosystem Functioning (BEF)–China experiment, which is located in a mountainous subtropical region in southeast China. A total of 40 native broad-leaved tree species were planted. In the first study, I used the local neighborhood approach to analyze how local abiotic conditions (i.e. topographic and edaphic conditions) and local neighborhood (i.e. species diversity and competition by neighborhood) affect the annual growth rates of 6723 individual trees. The second study used the community approach to partition the effects of environmental factors (i.e. topographic and edaphic), functional diversity according to Rao's quadratic entropy ( $FD_Q$ ) and community weight mean (CWM) of 41 functional traits on community tree growth rates. The main question of the third study was how the species-specific growth rates are related to five crown- and 12 leaf traits.

In the fourth study, I investigated 438 tree individuals for the congruence between the conventional direct field measurements and TLS measurements.

It was found that tree growth rates were strongly influenced by the local topographic and edaphic conditions but not affected by the diversity of local neighborhood. In contrast, results obtained by using the community-based approach showed that  $FD_Q$  and CWMs of various leaf traits rather than abiotic environmental factors had significant impact on the community means of growth rates. Tree-tree interactions already occur in early life stages of trees, which were evidenced by the significant effect of competition by local neighborhood. These findings imply that the effects of abiotic environmental factors may be more evident at local scale and biodiversity effects may vary at different spatial scales. The species-specific growth rates were found to be related to specific leaf traits but not to crown traits and were best explained by both types of traits in combination. This finding supports the niche theory and provides the evidence for using functional diversity to examine the BEF relationships. The TLS-retrieved total tree height, stem diameter at 5 cm above ground, and length and height of the longest branch were highly congruent with those obtained from direct measurements. It indicates that TLS is a promising tool for high resolution, non-destructive analyses of tree structures in young tree plantations.

Being one of very few studies to incorporate the individual tree scale in examining the biodiversity-productivity relationships within the BEF researches, this thesis stresses the importance of using individual-tree based approach, functional diversity and TLS to find the evidences of explanatory mechanisms of the observed biodiversity and ecosystem functioning (e.g. tree growth rates) relationships. Biodiversity effects may evolve along the successional stages. Therefore, incorporating the interaction between biodiversity and time in analyzing BEF relationship is also encouraged.

## **Zusammenfassung**

Der Verlust der biologischen Vielfalt kann Ökosystemfunktionen nachhaltig stören. Bisher haben sich die Beweise, die diese Aussage untermauern, vor allem auf Gewässer- und Graslandökosysteme bezogen. Wie sich die biologische Vielfalt auf die Ökosystemfunktionen von Wäldern auswirkt, ist besonders für immergrüne Laubwälder weitgehend unbeantwortet. Die Baumproduktivität, eine von vielen Waldökosystemfunktionen, ist von besonderem Interesse, weil sie die Kohlenstoffspeicherkapazität und Holzproduktivität widerspiegelt. Die Beziehung zwischen Biodiversität und Baumproduktivität werden in der Regel auf Gemeinschafts- oder Plotebene untersucht. Jedoch treten Baum-Baum Interaktion in kleineren Maßstäben, unterhalb der Plotebene, auf. Dementsprechend können Untersuchungen der lokalen Nachbarschaften ein Ansatz zu einem besseren Verständnis von Interaktionen zwischen Bäumen und den Auswirkungen der Biodiversität auf die Baumproduktivität sein. Diese Arbeit zielt darauf ab, die Auswirkungen der biologischen Vielfalt und der abiotischen Umweltfaktoren auf die Baumwachstumsraten sowohl mit lokalen Nachbarschaften als auch mit gemeinschaftsgetragenen Ansätzen zu analysieren. Außerdem variieren zwischen den verschiedenen Baumarten die Baumwachstumsraten. Funktionale Merkmale wurden mit artspezifischen Wachstumsraten verbunden, um die Effekte der Identität der Arten zu verstehen. Hierbei wurden Kronen- und Blattmerkmale einbezogen, um die interspezifischen Unterschiede in den Wachstumsraten vorhersagen zu können. Für ein besseres Verständnis der Mechanismen, die die Beziehung zwischen der biologische Vielfalt und der Baumwachstumsraten unterstreichen, sind Daten von hoher Auflösung und einer langen Zeitspanne erforderlich, um die Baum-Baum Interaktionen zu untersuchen. Zusätzlich wurde die Anwendbarkeit von terrestrischem Laserscanning (TLS) bei der Messung der Baumdendrometrie evaluiert.

Diese Arbeit wurde im Rahmen des DFG Projekts „Biodiversity Ecosystem Functioning (BEF)–China“ (DFG FOR 891) durchgeführt. Das Untersuchungsgebiet befindet sich in einem gebirgigen Gebiet im subtropischen Südosten von China. Insgesamt wurden hierzu 40 einheimische Laubbaumarten gepflanzt. In der ersten Studie verwendete ich den lokalen Nachbarschaftsansatz zur Analyse der Einflüsse der lokalen abiotischen Umweltfaktoren (d.h. Topographie und Böden) und lokalen Nachbarschaft (d.h. Artenvielfalt, Konkurrenz durch Nachbarbäume) auf die jährlichen Wachstumsraten von 6723 Baumindividuen. In der zweiten Studie verwendete ich einen gemeinschaftsbezogenen Ansatz. Die Effekte der

topographischen und edaphischen Umweltfaktoren, die funktionale Diversität nach Rao's quadratic entropy ( $FD_Q$ ) und den gewichteten Gemeinschaftsmittel (CWM) von 41 funktionalen Merkmalen auf die Mittel des gemeinschaftlichen Baumwachstums wurden untersucht. Die Hauptfragestellung der dritten Studie war, wie das Baumwachstum im Zusammenhang mit fünf Kronen- und 12 Blattmerkmalen steht. In der vierten Studie untersuchte ich 438 Baumindividuen auf die Übereinstimmung zwischen der konventionellen (direkten) Feldvermessung und der TLS Vermessung.

Es konnte gezeigt werden, dass das Baumwachstum stark von den lokalen topographischen und edaphischen Zuständen beeinflusst ist, aber nicht von der Artenvielfalt der lokalen Nachbarschaft. Gegensätzlich dazu waren die Ergebnisse der zweiten Studie. Der gemeinschaftsgetragene Ansatz zeigt, dass  $FD_Q$  und CWMs von verschiedenen Blattmerkmalen eine Auswirkung auf die Mittel des gemeinschaftlichen Baumwachstums haben, wohin gegen abiotische Umweltfaktoren einen geringen Erklärungswert haben. Der signifikante Effekt von der Konkurrenz der Nachbarschaft auf das Wachstum der Baumindividuen weist darauf hin, dass bereits während der frühen Altersstufen Interaktionen zwischen Bäumen vorhanden sind. Diese Befunde implizieren, dass die Effekte der abiotischen Umweltfaktoren eher in kleinen Maßstäben wirken und die Effekte der Biodiversität in den verschiedenen räumlichen Maßstäben variieren. Das artspezifische Baumwachstum steht im Zusammenhang mit Blattmerkmalen aber nicht mit Kronenmerkmalen und wurde am Besten durch die Kombination der beiden Merkmalstypen erklärt. Das Ergebnis unterstützt die Nischentheorie und weist darauf hin, dass die Benutzung der funktionale Diversität zur Untersuchung der BEF Beziehungen angemessen ist. Die mittels TLS erfassten Baumhöhen, Baumstammdurchmesser sowie Länge und Höhe der längsten Ästen sind kongruent mit den Werten aus der konventionellen Feldmessung. Es konnte gezeigt werden, dass TLS ein vielversprechendes Instrument zu einer hochauflösenden und zerstörungsfreien Analyse der Baumstrukturen in jungen Baumbeständen ist.

Die Arbeit ist eine von wenigen BEF-Studien, die die Beziehung zwischen Biodiversität und Produktivität auf der Ebene von Baumindividuen untersucht. Die Arbeit unterstreicht die Bedeutung der Nutzung von individuen-basierten Ansätzen, funktionaler Diversität und TLS, um die Nachweise der Mechanismen der beobachteten BEF Beziehungen sichtbar zu machen. Biodiversitätseffekte könnten sich aber erst mit zunehmendem Alter stärker ausprägen. Daher wird der Ansatz der Interaktion zwischen Biodiversität und Zeit in der Untersuchung von BEF Beziehungen empfohlen.



## **Chapter 1**

### **Biodiversity effects on growth rates of native tree species in subtropical plantations**

## **1.1 General introduction**

### **1.1.1 Background**

The contemporarily extensive anthropogenic activities have been causing a large range of habitat modification, fragmentation and destruction, overexploitation of resources and increased rates of invasions. These are deemed as the main causes of the ongoing biodiversity loss at an alarming rate (Isbell 2010). Biodiversity loss does not only refer to the increased rates of species extinction, but also to the eliminations in functional and genetic diversity (Naeem et al. 1999). The dramatic biodiversity loss raises one central question that is “Does biodiversity matter for the ecosystem functioning?” Ecosystem functioning refers to the magnitudes and dynamics of ecosystem processes, for example, primary production, nutrient cycling and decomposition (e.g. Cardinale et al. 2012, Naeem et al. 1999). Ecosystems provide a wealth of ecosystem services that are essential for humans such as food, fresh water, regulating local climate and air quality, erosion prevention and pollination. For now, it is widely agreed that biodiversity loss could jeopardize ecosystem functioning and consequently cease the provision of ecosystem services (Cardinale et al. 2012, Loreau et al. 2002, MEA 2005, Schmid et al. 2009).

Among different types of ecosystems, forests harbor 80% of the terrestrial biodiversity, are essential for life on earth and supply a wide set of goods and services for human well-being (FAO 2014). However, forests, and in particular natural forests are severely threatened by the increasing demands for forest and agricultural products. In order to meet these demands, natural forest area was / is converted into forest plantation (Bauhus et al. 2010) or into agricultural land. Yet, how biodiversity affects functioning of forest ecosystem still remains largely unanswered due to the difficulty of conducting experiments in ecosystems with slow dynamics (Caspersen and Pacala 2001). However, the role of species diversity for the forest ecosystem functioning has been received more attentions and is increasingly recognized in recent years (Scherer-Lorenzen et al. 2005). It has been found that tree diversity promotes tree productivity, improves the nutrient cycling and enhances the stability and resistance of forest communities in the face of environmental change (Thompson et al. 2009). Among the major forest biomes of the world, tropical and subtropical forests are well known for their high biodiversity and provision of significant local, regional and global human benefits (Gardner et al. 2009). However, they have a high rate of deforestation and degradation, which may be attributed to over-harvesting, land use change, invasive species and global environmental

change (Bradshaw et al. 2009, FAO 2010, Lindquist et al. 2012). The future of tropical and subtropical forests species and ecosystems becomes more uncertain in the face of global change (Gardner et al. 2009). Nevertheless, in the last years, several studies that seek to understand how biodiversity affects the ecosystem functioning have emerged and devoted to tropical forests (Bruelheide et al. 2014). Subtropical forests, however, are less intensively studied with respect to the role of biodiversity for the ecosystem functioning. It is particularly true for subtropical evergreen broad-leaved forests (EBLF) in China (cf. Wang et al. 2007), which are the most widely distributed and representative forest type in the subtropical climatic zone of China (Dai et al. 2011). The forests are highly diverse and accommodate a high number of Chinese and East Asian endemic species (Wang et al. 2007). However, most of them were degraded and deforested during the Cultural Revolution (1966–1976), where no harvesting limits were in place (Dai et al. 2011). The majority of subtropical forests particularly EBLF in China exists as secondary degraded forests and are still under the high land-use pressure (Wang et al. 2007). Consequently, the EBLF with less anthropogenic disturbances are now restricted to sloping terrain (López-Pujol et al. 2006, Wang et al. 2007).

### **1.1.2 Biodiversity and tree productivity**

#### *Definition and measure of biodiversity*

The term “biodiversity” is firstly coined by Walter G. Rosen in 1985. The recognition and the use of “biological diversity” however could be dated back to 1955 (Magurran 2004). According to Convention on Biological Diversity (CBD), “biodiversity” is defined and mostly cited as: “*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*”. This definition explicitly dissects biodiversity into three organizational levels: genetic diversity, species (organismal) diversity and ecosystem diversity (Harper and Hawksworth, 1994).

How to measure diversity is an essential step for a sophisticated and comprehensive examination of diversity effects. Great efforts have been hitherto devoted to devising diversity measures (see Magurran 2004). There are a plethora of measures of diversity and an effective selection need to be oriented by the objective and purpose of studies. Diversity can be measured at different scales and levels of biological organization (Spellerberg and Fedor 2003). Counting the number of species usually termed as species richness is intuitively used as the simplest method to measure the diversity. However, this measure set the same weight to different species regardless of their abundances. Furthermore, species richness is highly

dependent on sampling effort / sampling area (Gaston 1996). The Shannon index is another commonly used diversity measure but takes both species richness and species evenness into account (Margalef 1972). Functional diversity was defined by Rosenfeld (2002) as the distribution of species in a functional space whose axes represent functional features. It is of ecological importance because it is the functional component of biodiversity that influences ecosystem functioning (Tilman 2001). There are also increasing recognitions of the attribution of the large number of functional groups to the positive relationships between species richness and ecosystem functioning (Díaz and Cabido 1997, Hector et al. 1999, Loreau et al. 2001, Tilman et al. 2001). Two assemblages with the same species richness may be dissimilar in functional diversity. Meanwhile, the more species included in an assemblage, the more likely the functional diversity of this assemblage increased (Hillebrand and Matthiessen 2009, Mouillot et al. 2005).

#### *Biodiversity-tree productivity relationship*

Among different forest ecosystem functions, productivity has been received particular interests because it reflects the carbon sink capacity and wood productivity (Bauhus and Schmerbeck 2010).

Biodiversity has been found to be positively, negatively, or not related to tree productivity in both experimental and observational studies (Huston et al. 2000). In Table 1 I summarized several studies to show the varied relationships between biodiversity and tree productivity / growth rates. The predominant direction of diversity-productivity relationships in forests was reportedly positive in a review by Forrester and Bauhus (2016). These ambiguous results may be due to different scales of the conducted studies, as suggested by Mittelbach et al. (2001) and Waide et al. (1999). They both found that the probability of a positive (hump-shaped) relationship increased with larger spatial scale. Chisholm et al. (2013) and Dimitrakopoulos and Schmid (2004) also strengthened the assumption of scale-dependent biodiversity effects. Furthermore, the biodiversity-productivity relationships were found varying with different site conditions (e.g. successional stage and environmental factors) (Healy et al. 2008, Vilà et al. 2003). Disentangling the effects of the site conditions from the biodiversity-productivity relationships can be very difficult in observational studies (Vilà et al. 2005). In the study from Vilà et al. (2003), the relationship between biodiversity and productivity became no longer significant when the environmental conditions were included in the analysis. In order to keep environmental conditions as constant as possible, the experimental approaches that randomly allocate diversity treatments were initiated during the early 1990s (Scherer-Lorenzen et al.

2005). The impact of biodiversity on tree productivity can also be species-specific (Grant et al. 2006). Redondo-Brenes and Montagnini (2006) found that productivity of some tree species responded positively in mixtures as compared to monoculture, while one species was suppressed when growing with other tree species and therefore less productive than in monocultures. The number of species studied can also influence the outcome of diversity effects (Firn et al. 2007).

Researchers have been seeking the mechanisms that underline the positive effect of biodiversity on tree productivity. There are three postulated mechanisms: niche complementarity, facilitation and selection effects (also usually referred as sampling effects) (Fridley 2001). Niche complementarity and facilitation reflect the positive interactions between species, which generate the positive relationship between biodiversity and ecosystem processes. Niche complementarity proposes that a combination of species different in requirements for different resources could lead to a higher and more efficient exploitation of resources (Hooper 1998, Tilman 1999). The interspecific niche differentiations allow the species to exploit resources in their own niche and thus reduce conspecific competition (Cardinale et al. 2007). This niche complementarity can occur in space or in time (Tilman 1999). With respect to space, when tree species with markedly divergent crown or root architectures grow together, the space of aboveground or belowground could be more thoroughly occupied. With respect to time, when combining the evergreens with deciduous species, evergreens could receive more light during the leafless period of deciduous species than they are grown with conspecific species. Facilitation refers to the beneficial effects of neighbors through improvement of the abiotic and biotic environment (Callaway 1995). The effect of facilitation has been shown more pronounced under stressful or unfavorable environmental conditions (Lin et al. 2012, Maestre et al. 2009). A classical case of facilitation is that the inclusion of species that are able to symbiotically fix atmospheric nitrogen (e.g. legumes) enhances the availability of nitrogen. Facilitative interactions can be asymmetric where the plant receives all the benefits but the benefactor does not profit, and symmetric analogous to mutualism where all plants benefit from each other (Vellend 2008). Selection effects recognize that positive biodiversity effects arise from the increased probability of having species with particular important traits (e.g. fast-growing) with increasing species richness (Huston 1997, van der Heijden et al. 1999). Loreau and Hector (2001) introduced a method to partition the selection effects and positive interactions (i.e. complementarity and facilitation) between species in biodiversity experiments.

**Table 1** Summary of some findings of the effects of biodiversity on tree productivity or tree growth rates; (+) refers to positive diversity effect, (•) no diversity effect, (-) negative diversity effect.

Diversity effects	Forest type and location	Diversity indices used	Reference
(+)	Experimental plantation in submontano in northern Portugal	Two species mixture (replacement series)	Nunes et al. (2014)
(+)	Tropical evergreen broadleaf and dry deciduous dipterocarp forests in Vietnam	Species richness Shannon diversity index Shannon evenness Biomass-species diversity Abundance-biomass-species diversity	Con et al. (2013)
(+)	Mixed stands of European beech and Norway spruce in pre-alpine South Bavaria, Germany	Pure vs. mixed stands	Pretzsch and Schütze (2009)
(+)	Experimental tropical plantations in Sardinilla, Panama	Species richness	Potvin and Gotelli (2008)
(+)	Douglas-fir / western hemlock and the mixed-conifer forest in western coast of USA	Shannon diversity index	Liang et al. (2007)
(•) (+)	Plantations in humid tropical lowlands of Costa Rica	Monoculture vs. mixed plantations	Redondo-Brenes and Montagnini (2006)
(+)	Plantation of mostly native rainforest and eucalypt species in the humid tropics of north-eastern Australia	Species richness Shannon diversity index	Erskine et al. (2006)
(+)	Plantation of <i>Acacia mearnsii</i> and <i>Eucalyptus globulus</i> ssp. <i>pseudoglobulus</i> in East Gippsland Australia	Tree species mixture (replacement series)	Bauhus et al. (2004)
(•)	Temperate broad-leaved forest, Thuringia, Germany	Species richness	Seidel et al. (2013)
(•)	Mediterranean forests, Iberian Peninsula	Species richness	Vilà et al. (2003)
(•)	Experimental plantation on a heavily degrade site in the moist semi-deciduous forest zone, Ghana	Two species mixture (replacement series)	Addo-Danso et al. (2012)
(-) (•)	Old-growth deciduous forest stands in Thuringia, Germany	Shannon diversity index	Jacob et al. (2010)
(-)	Old plantation and natural secondary forest in the wet tropics region of Queensland, Australia	Species richness Simpson's diversity index	Firn et al. (2007)

Biodiversity effects could all be ascribed to the differentiation of functional traits (Scherer-Lorenzen 2005), and were evidenced to be driven by the complementarity between species (Morin et al. 2011). Differences in functional traits can be associated with various growth rates, distinct crown or root architectures, and different physiological and ontogenetic strategies, to name just a few of the manifold possibilities. These are the cornerstones for niche differentiations and divergent performances. Biodiversity effects observed from a mixture of a number of species within a functional group could be less pronounced than a mixture of species from different functional groups (Díaz and Cabido 1997). Intercropping shade tolerant species and light demanding species induces canopy stratification and efficient use of light (Pretzsch and Schütze 2009). Increased soil exploitation and resources capture can be achieved by mixing tree species with different root depths / architectures (Bolte and Villanueva 2006, Lei et al. 2012). Likewise, tree species with contrasting crown architecture can explore the space in different niche and thus, reduce the interspecific competition for light compared to the intraspecific competition. It is therefore suggested that diversity of functional traits and species interactions determine the outcome of the biodiversity effects and consequently ecosystem processes (Walker et al. 1999).

### **1.1.3 Methods to study the effects of biodiversity on tree productivity**

#### *Community level versus individual level*

Ecosystem processes have been usually investigated at community levels, or following the approach by relating the averaged value of individuals to the “mean” environment of the same community (Pacala 1997). However, plants (e.g. trees) owing to their immobility are more strongly influenced by the immediate local environmental conditions (Stoll and Weiner 2000). Tree-tree interactions, thus, occur at small scale (Stoll and Weiner 2000, von Oheimb et al. 2011). Given the fact of intraspecific and interspecific variation of tree species, as well as different environmental conditions at mosaic scale, no individual would perform and interact with local environment identically (Grimm and Railsback 2005). Local neighborhood approach linking the performance of an individual plant to the properties of its immediate neighbors allows to understanding the tree-tree interactions (Coomes et al. 2002, Potvin and Dutilleul 2009, Srivastava and Vellend 2005). It is of particular implication for discovering and evidencing the mechanisms responsible for the effects of biodiversity on tree performance (e.g. growth rate).

### Conventional measurements versus terrestrial laser scanning

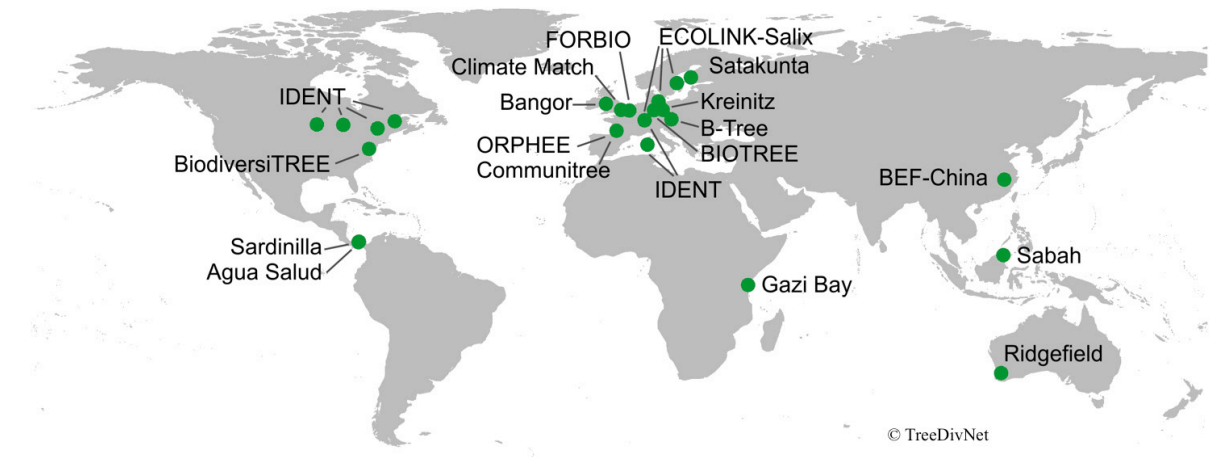
Conventionally, tree status and aboveground structures are determined with common instruments: hypsometer for the height parameters, measuring tape for length determination, caliper for diameters, compass for the azimuths as well as angle finder for the angles. These tools are easily accessible and operated and usually provide satisfying measuring results, which make them still widely used. On the other hand, the measurements using conventional method vary with different operators and are therefore susceptible to man-made errors. For a huge survey area, applying the conventional measurements to collect the data is very time-consuming, expensive, and sometimes not feasible. The conventional method also meets its threshold in collecting data of high resolution, e.g. the arrangement of branches. Airborne laser scanning (ALS) techniques have been successfully applied in measuring forest structures at both community and individual-plant levels, particularly for large survey areas (Jung et al. 2011, Vehmas et al. 2011). However, ALS usually fails to capture the elements at fine-scale spatial resolution (in the order of millimeters or a few centimeters). In the last few years, terrestrial laser scanning (TLS) has been deployed as an alternative approach to obtain three-dimensional (3D) structural elements of trees (Fleck et al. 2011, Jung et al. 2011, Schilling et al. 2012). The detailed quantification of crown structures of individual trees in a 3D environment by TLS provides an opportunity to understand how tree individuals interact with neighboring trees (Seidel et al. 2011, Seidel et al. 2015). Hence, TLS may be an innovative approach for understanding the mechanisms of the relationships between biodiversity and tree productivity. However, the applicability of TLS has never been evaluated either in biodiversity and ecosystem functioning experiments or in very young forest stands.

#### **1.1.4 Biodiversity Ecosystem Functioning (BEF)-China experiment**

Experimental studies allow the manipulation of different levels of tree species richness. They enable the determination of the direction of the causal relationship between biodiversity and ecosystem functioning, as well as the control over the stand age and density which are deemed as common co-varying factors in observational studies (Bruehlheide et al. 2014, Naeem et al. 1999). Most of BEF experiments have employed fast-growing and short-lived primary producers (e.g., bacteria, algae, herbaceous plants) (Cardinale et al. 2011, Hooper et al. 2005). The largest and longest-lived plants in territorial ecosystems, trees, have not been intensively studied as regards to how they benefit from biodiversity and how the biodiversity of plants provide benefits to the ecosystem functioning. The first forest BEF experiment worldwide is the Satakunta experiment established in Finland in 1999. According to



TreeDivNet, a platform for ecosystem researches in tree diversity experiments, there are 17 forest BEF experiments worldwide (Fig. 1). Most of them are located in the temperate biome. Four were established in tropical regions and only one in subtropical regions.



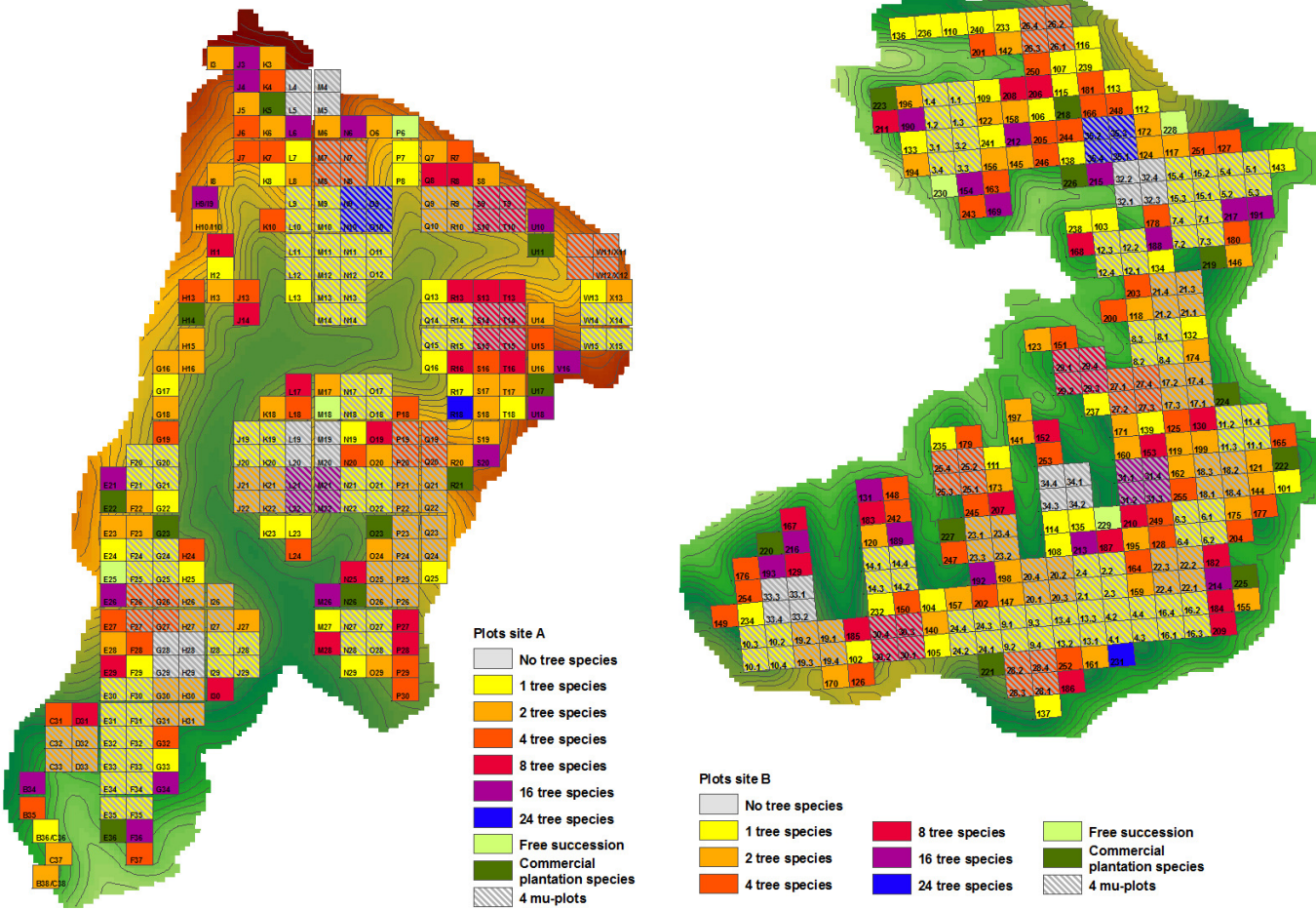
**Fig. 1** Distribution of the tree diversity experiments for researches on the relationships between tree species diversity and ecosystem functioning worldwide. Source: TreeDivNet.

The BEF-China experiment is the first forest BEF experiment established in highly species-rich subtropical regions, and currently the largest-scale forest BEF experiment in the world. BEF-China provides a perfect platform to ascertain the effects of biodiversity on a variety of ecosystem functioning in subtropical forests. It is located in a mountainous subtropical region near to Xingangshan Township, Jiangxi Province, China (N29°08′-11′, E117°90′-93′). The mean annual temperature is 16.7°C and the mean annual precipitation 1821mm (Yang et al. 2013). The wet season lasts mainly from April to August. The natural vegetation of this region is characterized by subtropical broad-leaved forests with evergreen species dominating in abundance (Bruelheide et al. 2011).

BEF-China comprises two experimental sites (A and B), each covering about 26.6 ha. Site A and Site B were planted in 2009 and 2010, respectively. Prior to the experiment, the sites were covered with a plantation of two economically important timber species *Pinus massoniana* and *Cunninghamia lanceolata*. At both experimental sites, the soils are Cambisols and Cambisol derivatives, interspersed with Regosols on ridges and crests, and Anthrosols from Colluvial deposits on foot slopes and valley floors. The relief is highly variable, with slopes ranging from 0 to 45° (Bruelheide et al. 2014, Yang et al. 2013).

A total of 271 plots and 295 plots are included in Site A and Site B, respectively. Each plot has the size of 25.82 m × 25.82 m (horizontally projected area), which is corresponding to the traditionally used Chinese area unit 1 mu. With a planting distance of 1.29 m, a total of

400 trees were planted in each plot, resulting in a planting density of 0.6 trees m<sup>-2</sup>. Three different random extinction scenarios, one replicate of one of these scenarios and two non-random extinction scenarios (rarity and specific leaf area (SLA)) were used to create a gradient of tree species richness treatments. In total, seven richness levels of 0, 1, 2, 4, 8, 16 and 24 tree species were assigned to 15, 88, 68, 40, 26, 19 and 5 plots at each site, respectively (Fig. 2). The species pool used in the tree species richness treatments is composed of 24 native broad-leaved tree species at each site. In addition, two commercially important species *Pinus massoniana* and *Cunninghamia lanceolata* were also included but were planted only as monoculture, because it is a common practice to cultivate these species in monocultures. Different species richness levels were randomly assigned to plots, as were the positions of individual trees within plots. For detailed explanation on the design and establishment of BEF-China see Bruelheide et al. (2014) and Yang et al. (2013).



**Fig. 2** Richness treatments and spatial arrangement of plots at Site A and Site B, respectively. Different color represents different richness treatments (0, 1, 2, 4, 8, 16, 24). Source: www.bef-china.de.

### 1.1.5 Main approaches and hypotheses

Tree growth rates are usually used to indicate the tree productivity and growth performance, and are often determined by using tree height, stem diameter and wood volume. Since tree crowns determine the proportion of light captured (Sterck et al. 2001), they are also used to indicate tree productivity. Furthermore, tree crowns are highly sensitive to local neighborhood and have the ability to shade neighboring trees (Lang et al. 2010, Simard and Zimonick 2005). However, measuring crown variables is more difficult and more time consuming, which makes them not so widely used in calculating growth rates compared to simpler measures such as tree height and stem diameter. In this thesis growth rates of height, stem diameter at 5 cm above ground, crown diameter and wood volume were used to quantify the growth responses.

Irrespectively of tree species identity, tree growth rates vary with different abiotic environmental conditions (e.g. topographic and soil conditions), as well as with different biotic environmental conditions (e.g. biodiversity, competition by neighboring trees). Moreover, tree species of different life stages respond differently to environmental factors, resulting in ontogenetic changes in growth responses (Pretzsch and Dieler 2012). The early successional stage of forest stands is often featured by intensive and complex tree-tree interactions as well as high dynamics. This is also typical for forest ecosystems that develop after stand-replacing or partial disturbances and diverse in species, progresses and structures (Swanson et al. 2011). The development of trees at early stages strongly determines their vitality and competitiveness, and the ability of trees to reach the canopy (Günter et al. 2009, Kobe 2006). The survival rate and fitness of tree individuals in the early life stage have also implications on their success in reproduction, thus the ability to transfer their genes to the next generations. Therefore, the early successional stage was paid particular attention in this thesis. Under identical environmental conditions growth rates among tree species differ widely. Tree-tree interactions along environmental gradients were also found to vary among different tree species (Lintunen and Kaitaniemi 2010, Uemura et al. 2006). This species-specific differences arise from the differences in resource use efficiency, allocation patterns and adaptive strategies (Forrester et al. 2006, Riedel et al. 2013). A number of functional traits have been used to relate the species-specific growth rates to understand the effects of species identity (Díaz et al. 2007). Hence, in this thesis I evaluated the different functional traits (i.e. crown- and leaf traits) to predict the species-specific tree growth rates.

By taking the opportunity of the BEF-China experiment, this thesis aims to analyze the effects of biodiversity and the abiotic environmental factors on the tree growth rates in the early stage of BEF plantations using both local neighborhood (Chapter 2) and community-based (Chapter 3) approaches. Furthermore, the functional traits were related to predict the growth rates at the community level (Chapter 3) and at the species level (Chapter 4). Specific hypotheses were stated as following:

In this early stage of tree development,

[H1] Environmental factors (i.e. site topography and edaphic conditions) are the strongest predictors for the growth performance.

[H2]: Diversity effects on growth performance already occur in early successional stages.

[H3]: Functional traits are good predictors for tree growth rates.

Through Chapter 2 the local neighborhood approach was used to address H1 and H2. The goal of this study was to analyze how local abiotic site conditions (i.e. topographic and edaphic conditions) and local neighborhood (i.e. species diversity and competition by neighborhood) affect the annual growth rates of individual trees. Annual growth rates of total tree height, stem diameter at 5cm above ground and crown width for 6723 individuals of 24 tree species in the third year after establishment of the experiment were used as response variables. Aspect, slope, curvature and elevation were included to represent the local topography. Total nitrogen and carbon and nitrogen (C/N) ratio were included to reflect the local soil conditions. For characterizing local neighborhood the Shannon diversity index of neighboring tree species and the competition index of neighborhood were used. In line with [H1], the tree growth rates were strongly influenced by the local topographic and edaphic conditions. Contrary to the [H2], the growth rates of tree individuals were not affected by the Shannon index of their local neighborhoods. However, tree individuals already interacted with each other, evidenced by the significantly reduced growth rates of focal trees with increasing size of neighboring trees. Using the local neighborhood approach, tree individuals in the early stage of this experiment were more strongly influenced by the abiotic local conditions than by the local neighborhoods. Tree-tree interactions at local scales already occurred but the diversity effects of local neighborhood was not yet significant to explain the growth variations. In addition, this study also found that tree growth rates were markedly species-specific, which will be further explored in relation to functional traits in Chapter 4.

Chapter 3 used the community-based approach rather than the local neighborhood approach applied in Chapter 2 to examine (H1) and (H2). This study aimed to partition the effects of environmental factors (i.e. topographic and edaphic), functional diversity according to Rao's quadratic entropy ( $FD_Q$ ) and community weighted mean (CWM) of a set of functional traits (i.e. leaf traits) on community tree growth rates. Annual growth rates of crown width of 23 tree species calculated at plot level were used as response variables. Environmental factors included elevation, aspect, slope, solar insolation, profile curvature and plane curvature, as well as soil carbon content and nitrogen content calculated as plot mean values. A total of 41 plant functional traits were used to calculate FD and CWMs. They included traits connected to the leaf economics spectrum (LES) (e.g. specific leaf area (SLA) and leaf nitrogen content (LNC)), traits related to stomatal conductance, traits related to xylem properties and leaf microscopic traits (e.g. stomata density, thickness of the palisade parenchyma). Contrary to [H1], environmental factors did not significantly affect the plot means of annual crown width growth rates and explained only a small fraction of the total variation in growth rates. FDs and CWMs of various leaf traits, however, had significant impact on the community means of crown width growth rates. Specifically, functional diversities of leaf water potential, leaf vein length and extrafloral nectaries were positively related to the community mean crown growth rates, which confirmed the [H2]. But CWMs were stronger predictors for the community growth rates than FDs.

Based on the findings of the species-specific growth rates and the significant impact of CWMs of various leaf traits in Chapter 2 and 3, Chapter 4 aimed to study how the growth rates are driven by a variety of key functional traits to test [H3]. They can provide explanations for the strong effects of species identity and CWMs of certain functional traits on the variations in growth rates. Growth rates of wood volume were calculated across 39 broad-leaved tree species grown in the experiment. Five crown and six physiological and six morphological leaf traits that are related to light harvesting and photosynthesis strategy were related to the species-specific growth rates. Leaf traits but not crown traits were able to significantly explain the variations of growth rates among different tree species. The combination of both crown and leaf traits better explained the species-specific differences in growth rates better than each type of traits alone.

Moreover, finding the evidences for the mechanisms that drive the patterns of tree-tree interactions and underlie the biodiversity effects is one ultimate goal of the BEF researches. More systematically collected data of higher resolution might assist to understand the mechanisms in a more fundamental way. Therefore I explored the performance of TLS in

assessing the tree dendrometrics in a young tree plantation with highly variable topography and evaluated the applicability of TLS in the early stage of forest BEF experiment (Chapter 5). I investigated 438 young tree individuals for the congruence between the conventional direct field measurements and TLS measurements. Total tree height, stem diameter at 5 cm above ground, and length and height of the longest branch were used to test if TLS was a promising tool for high-resolution, non-destructive analyses of tree dendrometrics in the early stage of a forest BEF experiment. Values of variables retrieved from TLS were highly congruent with those obtained from direct measurements, despite the poor descriptions of some individuals of very small-sized and leaf-on tree species. Furthermore, TLS allows for a more accurate and objective identification of the longest branch than is possible in the field. TLS proved to be a promising tool for high resolution, non-destructive analyses of tree structures in young tree plantations and forest BEF experiments.

## **1.2 General discussion and outlook**

To my knowledge this thesis is one of very few studies to incorporate the individual-plant scale in examining the relationship between biodiversity and productivity in the framework of BEF experiments. The analyses of biodiversity and tree productivity relationships by using the individual-tree approach and the community-based approach provide different perspectives about how growth performances of trees were governed by various factors. For the first time, the species-specific growth performance was related to both crown- and leaf traits. I found that the tree growth performance was better explained by crown traits than by leaf traits and best explained by the combination of crown and leaf traits. This thesis is also the first to test the determination of tree parameters by using TLS in BEF experiments. The non-destructive and highly accurate measurement technique makes TLS a promising tool in forest BEF studies to scrutinize the tree-tree interactions.

### **1.2.1 Effects of environmental factors on tree growth rates**

The first hypothesis was confirmed at local neighborhood level with results of Chapter 2 and was rejected at the plot level with results of Chapter 3. Light and nutrient availability are widely recognized as key factors determining plant growth rates. Topography affected light availability (Ishii and Higashi 1997) and soil properties affected nutrient availability. Therefore, topographic and edaphic factors have often been found to influence growth rates

across life stages (Chen et al. 1999, Grier et al. 1989). The diameter growth of mountain beech individuals growing in New Zealand decreased with elevation ranging from 600 m a.s.l. to 2000 m a.s.l. (Coomes and Allen 2007). In Chapter 2 individual-tree growth was not affected by the elevation, which only varied by 170 m. In the northern hemisphere, south-facing slopes receive more solar irradiation than north-facing slopes (Warren 2010). In this thesis tree individuals growing on the south-facing slopes had better growth performance than those on the north-facing slopes, as also found by Fralish (1994) in 47 undisturbed and mature forest stands. Slope inclination may be correlated with soil conditions, mechanical exposure and frequency of disturbances (Nagamatsu and Miura 1997). For biomechanical reasons, morphologies of stem and crown of trees vary with slope inclination (e.g. Getzin and Wiegand 2007, Ishii and Higashi 1997, Lang et al. 2010). I found a negative relationship between slope inclination and individual-tree growth rates, which is in agreement with the results of von Oheimb et al. (2011) obtained in the same region. Topography played an important role in determining individual-tree growth rates in this thesis. Nevertheless, the impact of topography was not universal on different types of growth rates (i.e. height growth rate, diameter growth rate and crown width growth rate). Diameter growth of trees was responsive to most of the topographic factors, while growth of height and crown width was affected by fewer topographic factors. This indicated that maintaining the capacity of light harvesting had the highest priority for trees at this early successional stage. Regarding soil conditions, increasing soil nitrogen content enhanced tree growth performance, which is in accordance with results of Canham et al. (1996), Ceccon et al. (2004) and Unger et al. (2012). N availability to plants is regulated by C/N ratio reflecting the rates of N immobilization, mineralization and nitrification. I found that the C/N ratio negatively influenced tree growth rates, which was also observed by Yamakura and Sahunalu (1990) in Southeast Asian forests. Contrary to the significant impacts of topographic and edaphic factors on individual-tree growth rates, the environmental conditions played only a marginal role in explaining the tree growth rates at the community level (Chapter 3). The BEF-China experimental sites are of high environmental heterogeneity and the within-plot variability of environmental factors is also considerably high (Ying Li, unpublished data). The aggregated growth rates of crown width and the mean environmental conditions at the plot level might level out the impact of the local environmental conditions on each individual tree. Furthermore, tree growth was found to respond to environmental conditions in species-specific ways (Babst et al. 2012, Drobyshev et al. 2013). The analyses using an individual-tree approach in this thesis considered tree species as a random factor, while analysis at the community level accounted

for the species-specific differences in CWM of functional traits. This might also contribute to the contrasting results between individual-tree level and community level.

### **1.2.2 Effects of biodiversity on tree growth rates**

The second hypothesis was rejected at individual-tree level by using the Shannon index of neighborhood species, but was confirmed at the community level by using the  $FD_Q$ . Processes governing tree-tree interactions are competition resulting in negative tree-tree interactions, and complementarity and facilitation resulting in positive interactions. Positive effects of biodiversity on tree growth rates are the result of positive tree-tree interactions. In Chapter 2, I found that larger-size neighboring trees significantly enhanced the height growth, but reduced stem and crown diameter growth of focal trees. The size of neighboring trees indicated the pressure of competition by local neighbors on the individual trees. The competition by the local neighborhood was also found to be a great source of variation in individual-tree growth in a young secondary subtropical forest near the experimental site (von Oheimb et al. 2011) and in the tropical tree biodiversity plantation in Sardinilla (Potvin and Dutilleul, 2009). The significant impact of competition by local neighborhood indicated that the tree-tree interactions already occurred in early life stages of trees. Regarding the positive tree-tree interactions, the individual trees analyzed in this thesis were not affected by the species diversity of neighboring trees (Chapter 2). In contrast, relative growth rate in the basal diameter of individual trees increased with species diversity in the Sardinilla experiment five years after establishment (Potvin and Gotelli 2008). I propose four explanations for the non-significant effect of local neighborhood diversity: 1) species diversity effects on tree growth rates might only become apparent at higher levels of diversity that resulted in increased occupied niche space, both spatially and temporally (Papaik and Canham 2006); 2) the relationship between species diversity and ecosystem functioning could be non-linear due to the redundancy in the ecosystem functioning (Ehrlich and Ehrlich 1981, Walker 1992, Schmid 2002). Thus, using a linear model could not capture the pattern of growth rate with increasing level of diversity; 3) the diversity effects might become more apparent with time, because the magnitude of complementarity increases as experiments are running longer and trees are growing (Cardinale et al. 2007, Pacala and Tilman 2002); 4) responses of tree growth rates to the diversity are affected by species identity (e.g. Grant et al. 2006, Redon-Brenes and Montagnini 2006, Seidel et al. 2013). Tree species studied in this thesis might react differently to diversity levels. On-going research shows that in particular the tree species *Choerospondias axillaris* benefits from more diverse neighborhoods. *C. axillaris* is a fast



growing deciduous tree species with the highest mean value of growth rates in the BEF-China experiment.

The examination of the relationships between biodiversity and tree growth rates or productivity has been mostly confined to the community level and few studies adopted the individual-tree based approach. Contrary to the non-significant local diversity effects found at individual-tree level,  $FD_Q$  at plot level was found to be significantly related to plot-level crown growth rates. Likewise, Lang et al. (2010) found a higher crown overlap in species-rich plots than species-poor plots. In a small-scale diversity experiment with subtropical tree species close to the experimental site used for this thesis, nitrogen acquisition and retention were promoted in mixed stands (Lang et al. 2014). Functional groups based on niche differentiation among species provide a method to examine the effects of functional diversity on ecosystem functioning (Hooper et al. 2002). In this thesis functional groups were delineated by a multitude of leaf traits related to the leaf economics spectrum (Wright et al. 2004, Díaz et al. 2004) and wood economics spectrum (Baraloto et al. 2010, Freschet et al. 2010, Martínez-Cabrera et al. 2011), which imply the fundamental trade-off between rapid resource acquisition and resource conservation. Wood density reflects the stratification of canopy layers (Poorter et al. 2012) and leaf area the strategy of light capture (Osnas et al. 2013). The positive response of crown diameter increments to the  $FD_Q$  of wood density and leaf area found in Chapter 3 indicated that the spatial complementarity already occurred at plot level. Meanwhile, the positive effects of  $FD_Q$  of leaf area and plant water related traits indicated the occurrence of temporal complementarity (Kröber et al. 2015, Zhou et al. 2011). Furthermore, facilitation might also occur, as evidenced by the increased crown width increment by presence of extrafloral nectaries. Plants produce extrafloral nectaries to attract ants to reduce damages from herbivores (Agrawal and Rutter 1998, Kessler and Baldwin 2002). The ant visitation to extrafloral nectaries has been found to increase plant fitness (Smiley 1985, Oliveira 1997).

Why was diversity effect found at the community level but not at the individual-tree level? I will discuss this mainly from two perspectives: different scales of analysis and different measures of diversity. Commonly the mean productivity estimated at plot / community levels was linked to the biodiversity gradients, particularly in aquatic and grassland ecosystems. The outcome of the relationship can be generated not only by positive interactions via complementarity and facilitation, but also by sampling effects (Loreau and Hector 2001). Individual-tree based approach can potentially exclude the sampling effects (Coomes et al. 2002, Potvin and Dutilleul 2009). At individual-tree level the number of different species of the local neighborhood ranged from 1 to 8, while at plot level the number different species

ranged from 1 to 24. The probability to combine species with contrasting niches might be higher in more diverse plots than in a more diverse local neighborhood. Species identity of the focal tree was not accounted for the calculation of the local neighborhood diversity, thus if the presence of neighbors of specific species would result in a positive interactions with the focal tree it is also dependent on the species identity of the focal tree (i.e. diversity-productivity relations vary with species).

Regarding the measures of biodiversity, species diversity was mostly used probably due to the common perception that biodiversity equals variety at the species level of organization (Spellerberg and Fedor 2003). However, species diversity does not capture the functional characteristics of organisms involved, which can be quantified by functional diversity (FD) (Hooper et al. 2002). Although higher species richness is typically related to greater levels of ecosystem functioning (Cardinale et al. 2006), species diversity does not explicitly incorporate the traits responsible for these processes (Clark et al. 2012). Grime (1988) and Odum (1969) demonstrated that ecosystem level processes are affected by the functional characteristics of organisms involved. Therefore, FD is considered as the main driver of changes in ecosystem functions (Reiss et al. 2009). Hooper et al. (2002) discussed the relationships between species diversity and functional diversity and summarized that the pattern of these relationships depends on the level of taxonomic resolution. Therefore, increasing the number of tree species that share similar functional traits (e.g. different genotypes of a given species) may not increase complementarity of resources use (Hooper et al. 2002). However, the lack of a priori demonstrations of the specific traits that are relevant to particular ecosystem processes (Tilman 2001) resulted in no universal functional classification (Hooper et al. 2002).

### **1.2.3 Functional traits in determining tree growth rates**

The growth rates of tree species planted in BEF-China at this early stage were considerably species-specific, and an important question is which factors drive tree growth rates to be different among species. According to the Production Ecology Equation (e.g. Richards et al. 2010), the proportion of resources captured and the efficiency of the conversion of resources into biomass affect growth rates of plants. Tree species that have contrasting growth rates should be different in these two aspects, which is explicitly reflected by specific functional traits (e.g. Poorter and Garnier 1999, Reich et al. 1997, Wright et al. 2004). For example, stomatal conductance regulates the carbon uptake and transpiration (Graham and Sharkey 1982, Wright et al. 2004) and assimilation rates (Kröber and Bruelheide 2014). Furthermore,

CWMs of a set of functional traits explained 42% of variation in plot-level growth rates (Chapter 3). As such I hypothesized that differences in functional traits were responsible for the species-specific growth rates. By confirming the third hypothesis, the results of Chapter 4 showed that leaf traits (i.e. stomatal conductance, water potential and leaf toughness) significantly affected the species-specific mean growth rates. The positive relationship between stomatal conductance and tree growth rates was also reported by Chaturvedi et al. (2011) and Poorter and Bongers (2006). Ehleringer and Cook (1984) reported that photosynthetic rate of *Encelia farinosa* decreased with declining water potential, which is in agreement with the positive relationship between leaf water potential and tree growth rates found in Chapter 4. The negative relationship between leaf toughness and growth rates, which was also reported by Coley (1988), implies a trade-off between persistence and growth. In contrast, Westbrook et al. (2011) found growth rates to be unrelated to leaf toughness in the understory of a neotropical forest. The CWMs and  $FD_Q$  of the leaf traits that significantly explained the species-specific growth rates also affected the tree growth rate at plot level. Besides leaf traits that more generally reflect the efficiency of resource use, crown traits, particularly those characterizing the crown dimensions, determine the fraction of light resources captured. It has been also found that crown length and crown projection area were good single predictors for tree growth rates (Fichtner et al. 2013, Sterck et al. 2003, Xiao et al. 2003). In contrary, none of the crown traits were able to significantly predict growth rates. This result suggests that under the well-lit conditions the initial crown characteristics alone of tree saplings of the same age and size seem to have no clear ecological implications for species-specific growth rates. The effects of crown dimensions became significant when combined with leaf traits. This finding indicates that crown dimensions might further explain the interspecific difference in growth rates trees that have similar photosynthetic efficiency. Finally, the combination of crown- and leaf traits was the best model to predict the growth rates. I concluded that sets of traits related to carbon assimilation at the leaf-level and to overall amount of leaves exposed at the crown-level jointly explained species-specific growth rates better than either set of traits alone.

#### **1.2.4 Terrestrial laser scanning (TLS) as a promising tool in BEF research**

TLS has been used to more precisely estimate the characteristics of individual trees, for example, common inventory variables such as total tree height, diameter at breast height, and basal area (e.g. Moskal and Zheng 2012). Unsatisfactory tree height estimation with TLS has been often reported for larger trees and in stands of high density (Maas et al. 2008, Tansey et

al. 2009). In this thesis the young trees sampled for examining the applicability of TLS had a mean height of 238.4 cm ( $\pm$  112.6 cm). The TLS-retrieved height was highly congruent with the data obtained from direct measurements but showed a slight underestimation, which was also reported by Maas et al. (2008). Direct field and TLS measurements for GD were also highly correlated. In particular in the case of non-circular stem cross-sections TLS data could provide more accurate estimations (cf. Poeschel et al. 2013). Nowadays, extracting crown characteristics by using TLS has been intensively studied to obtain the spatiotemporal development of crowns for a fundamental understanding of tree-tree interactions and their ecological outcomes. It is because tree-tree interactions lead primarily to morphological response of the crown (Grams and Anderson 2007). Crown variables such as crown base height, crown area and crown volume have been successfully retrieved by using TLS data (e.g. Metz et al. 2013, Moorthy et al. 2011). The aggregate effect of the differential spatial development of single branches shapes the crown development (Stoll and Schmid 1998, Sumida et al. 2002). TLS was able to more accurately identify the longest branch of the young trees by taking advantage of the 3D environment of the point clouds and the convenient navigation in the software Pointools. Based on the reliable determination of tree structural parameters in young trees achieved by TLS data, TLS could gain more insight of tree-tree interactions through accurately documentation with high-resolution and along time series. The clear pictures of the complex tree-tree interactions help to understand the effects of biodiversity on ecosystem functioning and the underlying mechanisms. Recently, Seidel et al. (2015) applied the TLS-retrieved characteristics of neighboring trees to examine how the neighborhood affected tree diameter increments in an even-aged and mono-specific stand and found that space fillings from the neighborhood is the most suitable estimator.

### **1.2.5 Future research needs**

Huge efforts have been invested to answer the question “what is the consequence of losing biodiversity on ecosystem functioning?” The controversial results challenged the drawing of general BEF relationships (Giller et al. 2004, Thompson and Starzomski 2007). Particularly in forest ecosystems, the mechanisms of biodiversity effects have not been thoroughly investigated and the reliable evidence was rare. More focus should be given to BEF research in forest ecosystems. The central role of local neighborhood played in determining tree productivity (Potvin and Dutilleul 2009, Weigelt et al. 2007) suggested that the evidences of explanatory mechanisms of the observed relations between biodiversity and ecosystem functioning (e.g. tree growth rate) could be more apparent and rather detected at an

individual-tree scale (cf. Potvin and Dutilleul 2009). Therefore, future research about the relations between biodiversity and tree growth rates should incorporate individual-plant scale. Species diversity rather than functional diversity and structural diversity has very often been used to examine the effects of diversity on tree growth rates. Niche differentiation is the basis for complementary use of resources. The assumption that species diversity increases the divergence in niches has, however, rarely been tested with empirical data. Functional and structural diversity and size inequality explicitly reflect the spatial and temporal heterogeneity of forest community or local neighborhood. Neumann and Starlinger (2001) found only few and weak correlations between plant species diversity and stand structure diversity. I suggest that species diversity needs to be related to the functional and structural diversity for a deeper understanding of the ecological meaning of species diversity. Furthermore, spatial and temporal heterogeneity should be given more attention in BEF researches in order to find more concrete evidences for the underlying mechanisms. Biodiversity effects are not static but evolving with time (Cardinale et al. 2007). Interspecific interactions tend to change with stand development (Cavard et al. 2011). Most studies used one-year productivity or mean annual productivity spanning over several years, while few looked at how time changes the biodiversity effects on tree growth rate. At the same experimental sites, the negative effects of herbivory on tree growth rates with increasing tree species richness become more pronounced with time as trees grow larger (Schuldt et al. 2015). Therefore, incorporating the interactions between biodiversity and time in analyzing the BEF relations may be another promising approach.

Although TLS has been successfully in retrieval of tree parameters, no study except Seidel et al. (2013) applied TLS data to study the relationships between tree diversity and tree productivity. TLS allows more accurate estimation of tree parameters, particularly crown characteristics (Metz et al. 2013). This could help researches to quantify the aboveground tree-tree interactions with a much higher resolution to monitor how the trees find their own niche and what is the implications of different niche occupations. Therefore, I strongly emphasize using TLS in exploring the mechanisms of the relations between tree diversity and tree productivity.

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#### **1.4 Article overview and authorship declaration**

(according to §12b of the guideline for cumulative dissertations in sustainability science [January 2012], in the following termed “the guideline”)

##### **Overview of articles included in this PhD thesis:**

[1] Li Y, Härdtle W, Bruelheide H, Nadrowski K, Scholten T, von Wehrden H, von Oheimb G (2014) Site and neighborhood effects on growth of tree saplings in subtropical plantations (China). *Forest Ecology and Management* 327: 118–127.

[2] Kröber W, Li Y, Härdtle W, Ma K-P, Schmid B, Schmidt K, Scholten T, Seidler G, von Oheimb G, Welk E, Wirth C, Bruelheide H (2015) Early subtropical forest growth is driven by community mean trait values and functional diversity rather than the abiotic environment. *Ecology and Evolution*, doi: 10.1002/ece3.1604.

[3] Li Y, Kröber W, Bruelheide H, Härdtle W, von Oheimb G (in press) Crown and leaf traits as predictors for species-specific growth rates of trees in a subtropical biodiversity-ecosystem functioning experiment. *Journal of Plant Ecology*, in press.

[4] Li Y, Hess C, von Wehrden H, Härdtle W, von Oheimb G (2014) Assessing tree dendrometrics in young regenerating plantations using terrestrial laser scanning. *Annals of Forest Science* 71: 453–462.

**Declaration of authorship:**

Article #	Short title	Specific contributions of all authors	Author status	WF	Publication status
[1]	Early growth response of native species in a subtropical plantation	GvO, WH, <b>YL</b> : conceptual design; <b>YL</b> : data collection and preparation; HB, <b>YL</b> , HvW, KN: data analysis; <b>YL</b> , GvO: writing of manuscript; GvO, WH, HB, HvW, KN, TS, <b>YL</b> : internal revision of manuscript	Co-author with predominant contribution	1.0	Published in Forest Ecology and Management (IF = 2.660)
[2]	Functional traits drive tree productivity	WK, <b>YL</b> : data collection and preparation; WK, HB, <b>YL</b> : data analysis; WK, HB: writing of manuscript; <b>YL</b> , WH, KM, BS, KS, TS, GS, GvO, EW, CW, HB: internal revision of manuscript	Co-author with important contribution	0.5	Published in Ecology and Evolution (IF = 1.658)
[3]	Relating crown and leaf traits to tree growth	HB, <b>YL</b> : conceptual design; <b>YL</b> , WK: data collection and preparation; <b>YL</b> , HB: data analysis; <b>YL</b> : writing of manuscript; GvO, WH, HB, WK, <b>YL</b> : internal revision of manuscript	Co-author with predominant contribution	1.0	Accepted by Journal of Plant Ecology (IF = 2.646)
[4]	TLS application in long-term tree experiments	GvO, <b>YL</b> : conceptual design; CH, <b>YL</b> : data collection and preparation; <b>YL</b> , HvW: data analysis; <b>YL</b> : writing of manuscript; GvO, WH, CH, HvW, <b>YL</b> : internal revision of manuscript	Co-author with predominant contribution	1.0	Published in Annals of Forest Science (IF = 1.981)

WF = Weighting Factor; IF = ISI Web of Science Impact Factor 2014

*Specific contributions of all authors:*

Ying Li (YL)<sup>1</sup>

Goddert von Oheimb (GvO)<sup>2</sup>

Werner Härdtle (WH)<sup>1</sup>

Helge Bruelheide (HB)<sup>3,8</sup>

Carsten Hess (CH)<sup>1</sup>

Wenzel Kröber (WK)<sup>3</sup>

Keping Ma (KM)<sup>4</sup>

Karin Nadrowski (KN)<sup>5</sup>

Bernhard Schmid (BS)<sup>6</sup>

Gunnar Seidler (GS)<sup>3</sup>

Karsten Schmidt (KS)<sup>7</sup>

Thomas Scholten (TS)<sup>7</sup>

Henrik von Wehrden (HvW)<sup>1,9,10</sup>

Christian Wirth (CW)<sup>5,8</sup>

Erik Welk (EW)<sup>3</sup>

Affiliations:

<sup>1</sup>Leuphana University Lüneburg, Faculty of Sustainability, Institute of Ecology,  
Scharnhorststraße 1, D-21335 Lüneburg, Germany

<sup>2</sup>Technische Universität Dresden, Faculty of Environmental Sciences, Institute of General  
Ecology and Environmental Protection, Piennner Straße 7, D-01735 Tharandt, Germany

<sup>3</sup>Martin Luther University Halle Wittenberg, Institute of Biology / Geobotany and Botanical  
Garden, Am Kirchtor 1, D-06108 Halle, Germany

<sup>4</sup>Institute of Botany, CAS, 20 Nanxincun, Xiangshan, Beijing, 100093, China

<sup>5</sup>University of Leipzig, Special Botany and Functional Ecology, Johannisallee 21-23, D-  
04103 Leipzig, Germany

<sup>6</sup>University of Zurich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

<sup>7</sup>Eberhard Karls University Tübingen, Physical Geography and Soil Science, Rümelinstraße  
19-23, D-72070 Tübingen, Germany

<sup>8</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher  
Platz 5e, D-04103 Leipzig, Germany

<sup>9</sup>Centre for Methods, Leuphana University Lüneburg, Germany

<sup>10</sup>Research Institute of Wildlife Ecology, Savoyen Strasse 1, Vienna 1160, Austria

*Author status:*

Single author [Allein-Autorschaft] = Own contribution amounts to 100%.

Co-author with predominant contribution [Überwiegender Anteil] = Own contribution is greater than the individual share of all other co-authors and is at least 35%.

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Co-author with small contribution [Geringer Anteil] = own contribution is less than 20%.

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(according to §14 of the guideline)

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Co-author with small contribution [Geringer Anteil]	0.0

Ich versichere, dass alle in diesem Anhang gemachten Angaben jeweils einzeln und insgesamt vollständig der Wahrheit entsprechen.

Lüneburg, August 2015

## **Chapter 2**

### **Site and neighborhood effects on growth of tree saplings in subtropical plantations (China)**

Ying Li, Werner Härdtle, Helge Bruelheide, Karin Nadrowski, Thomas Scholten, Henrik von Wehrden and Goddert von Oheimb

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## Site and neighborhood effects on growth of tree saplings in subtropical plantations (China)

Ying Li<sup>a,\*</sup>, Werner Härdtle<sup>a</sup>, Helge Bruelheide<sup>b,g</sup>, Karin Nadrowski<sup>c</sup>, Thomas Scholten<sup>d</sup>, Henrik von Wehrden<sup>a,e,f</sup>, Goddert von Oheimb<sup>a</sup><sup>a</sup>Leuphana University Lüneburg, Faculty of Sustainability, Institute of Ecology, Scharnhorststr. 1, D-21335 Lüneburg, Germany<sup>b</sup>Martin Luther University Halle Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, D-06108 Halle, Germany<sup>c</sup>University of Leipzig, Special Botany and Functional Ecology, Johannisallee 21–23, D-04103 Leipzig, Germany<sup>d</sup>Eberhard Karls University Tübingen, Physical Geography and Soil Science, Rümelinstraße 19–23, D-72070 Tübingen, Germany<sup>e</sup>Centre for Methods, Leuphana University Lüneburg, Germany<sup>f</sup>Research Institute of Wildlife Ecology, Savoyen Strasse 1, Vienna 1160, Austria<sup>g</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany

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## ABSTRACT

Reforestation and afforestation often takes place in the form of monocultures. These have increasingly come under criticism due to their greater susceptibility to adverse environmental conditions and pathogens and because of the negative long-term impacts they have on soil fertility. Moreover, reservations have frequently been expressed as to whether monoculture is the only way to maximize biomass productivity. Subtropical forests in China are not only rich in tree species but are also diverse in terms of topography. However, historical clear-cutting and the high demand for wood have meant that considerable areas of these forests have been degraded or lost entirely. In recent years, great efforts have been made in subtropical China to restore and afforest vast areas. Nonetheless, conifer monoculture plantations are still prevalent owing to the lack of data on the relationship between diversity and ecosystem functioning and the limited knowledge of the growth performance of native broad-leaved tree species in plantations in this region. In this study, we investigated the growth response of individual tree saplings in a large-scale forest biodiversity and ecosystem functioning (BEF) experiment established in a highly heterogeneous environment in subtropical China (BEF-China). The experiment was established during the period November 2008 to April 2009 and incorporates a species pool of 24 tree species across 261 plots (0.067 ha each) and a broad richness gradient with 1–24 species per plot. Annual growth rates of tree height, stem diameter and crown width for 6723 saplings of 24 species in the third year after establishment were used as response variables. We analyzed the effects of initial size, local abiotic site conditions and local neighborhood on growth performance using mixed effects models. Initial size, local topographic (aspect, slope, curvature, elevation) and edaphic variables (total nitrogen, C/N ratio) as well as local neighborhood variables (competition index, Shannon index) were included as fixed effects. Random effects were plot and species identity. The results showed that growth performance of tree saplings was markedly species-specific and strongly affected by initial size and local site conditions. In this early stage of the experiment, local Shannon diversity did not yet explain a significant amount of variation in sapling growth. However, the significant effect of the increasing size of neighboring trees indicated that tree–tree interactions had already occurred. A greater investment in height growth at the expense of diameter growth suggested that light intercept is the priority for tree sapling growth. This study stresses the importance of better understanding the effects of local site conditions on initial growth in mixed-species plantations.

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\* Corresponding author. Address: Institute of Ecology, Faculty of Sustainability, Leuphana University Lüneburg, Scharnhorststr.1, D-21335 Lüneburg, Germany. Tel.: +49 4131 677 2847; fax: +49 4131 677 2808.

E-mail addresses: [ying.li@uni.leuphana.de](mailto:ying.li@uni.leuphana.de) (Y. Li), [haerdtle@uni.leuphana.de](mailto:haerdtle@uni.leuphana.de) (W. Härdtle), [helge.bruelheide@botanik.uni-halle.de](mailto:helge.bruelheide@botanik.uni-halle.de) (H. Bruelheide), [nadrowski@uni-leipzig.de](mailto:nadrowski@uni-leipzig.de) (K. Nadrowski), [thomas.scholten@uni-tuebingen.de](mailto:thomas.scholten@uni-tuebingen.de) (T. Scholten), [henrik.vonwehrden@uni.leuphana.de](mailto:henrik.vonwehrden@uni.leuphana.de) (H. von Wehrden), [vonoheimb@uni.leuphana.de](mailto:vonoheimb@uni.leuphana.de) (G. von Oheimb).

## 1. Introduction

Forests are complex ecosystems with high spatial heterogeneity in terms of structure and resources. In managed forests, however, stands have often been manipulated to maximize homogeneity. As more natural forest management approaches gain in importance, the paradigm “managing for complexity” has emerged (Bauhus et al., 2009; Boyden et al., 2012; Puettmann et al., 2009; Pretzsch, 2009). In particular, an increasing number of studies have discussed the potential benefits of tree species mixtures to various ecosystem functions and services (Bauhus and Schmerbeck, 2010; Kelty, 2006; Scherer-Lorenzen, 2013), while monocultures have increasingly come under criticism due to their greater susceptibility to adverse environmental conditions, pathogens (Hantsch et al., 2013) or herbivores (Jactel and Brockerhoff, 2007), and their negative long-term impacts on soil fertility (Puettmann et al., 2008). Arguments in favor of more structurally complex and diverse forests are relevant for the management of both established forests and re- and afforestations. In many regions of the world huge efforts are made to restore degraded forests and to increase the area covered by forests in order to increase the production of timber, fuel and pulp wood, to reduce atmospheric CO<sub>2</sub> levels by carbon sequestration, to stabilize regional climate conditions or to improve erosion control (Dixon and Wisniewski, 1995; Houghton et al., 2012). However, re- and afforestation often takes the form of easily manageable monocultures, despite growing evidence of the beneficial effects of mixed-species stands on ecosystem functions and services (e.g., growth rates, biomass production, nutrient cycling, light harvesting, plant nutrition; Forrester et al., 2006a; Forrester, 2014; Gamfeldt et al., 2013; Kelty, 1992; Richards et al., 2010). In recent years, a small number of large-scale forest diversity and ecosystem functioning (BEF) experiments have been established in different biomes in order to improve our understanding of the underlying mechanisms (for an overview see Bruelheide et al., 2014).

Subtropical evergreen broad-leaved forests (EBLF) once covered about one quarter of China’s land area (Wang et al., 2007). Due to a long history of intensive land use, the majority of this area was converted to agricultural land, and monospecific conifer stands occupy a large proportion of the present forest area. EBLF ecosystems are almost as rich in woody species as tropical forests (Bruelheide et al., 2011), and they are characterized by a highly diverse topography. In recent years, great efforts have been made in subtropical China to restore and afforest vast areas (Lei et al., 2009, 2010; Wang et al., 2007). However, the choice of monocultures or species mixtures for restoration and afforestation is still under debate owing to the lack of data on the relationship between diversity and ecosystem functioning in this region (He et al., 2013; Lang et al., 2014; Zhang and Wang, 2012). More critically, because little is known about the growth performance of native broad-leaved tree species in plantations, particularly in mountainous plantations, the current re- and afforestation efforts are mainly coniferous monoculture. For the first time, we analyze the initial growth response of individual trees of a high number of native broad-leaved tree species in the only forest BEF experiment that is located in the species-rich subtropical region (BEF-China) and that incorporates not only a broad richness gradient, but also great environmental heterogeneity.

Working with the view that heterogeneity in forest ecosystems is of great importance necessitates the use of individual-tree approaches rather than stand-based approaches to explain and model tree growth (Pretzsch, 2009). Individual-tree approaches are based on the assumption that resource supply and individual tree performance are spatially explicit processes on a local neighborhood scale (Boyden et al., 2012; Stoll and Weiner, 2000), and

that local conditions within the vicinity of a tree are, thus, more important for its growth than average stand conditions (Puettmann et al., 2009). Individual-tree growth is, thus, a function of tree species identity, tree age/size, local abiotic conditions and local neighborhood interactions (Pretzsch, 2009). The growth variation between different species can be explained by species-specific differences in resource use efficiency and allocation patterns (Forrester et al., 2006b; Riedel et al., 2013). Trees of different dimensions may react differently to exogenous factors, resulting in ontogenetic changes in growth responses (Pretzsch and Dieler, 2011). For example, it has been found that light harvesting efficiency decreases with tree age and size due to modifications in leaf structure and fractional biomass allocation to foliage (Niinemets, 2010). We focused on sapling growth in our study, because the regeneration phase is often characterized by a mixture of various tree species, and, thus, intensive and complex tree–tree interactions. Furthermore the sapling stage largely determines a tree’s ability to reach the canopy, and thus affects the forest structure (Günter et al., 2009; Kobe, 2006).

Resource availability and competition are generally assumed to be primary drivers of sapling growth (Coates et al., 2003; Kobe, 2006). Many resources, such as soil nutrients and water availability are inherently patchy at small spatial scales (Boyden et al., 2012). On sloped terrain, topography is considered to be the major abiotic factor influencing the direction and the intensity of incoming sunlight (Ishii and Higashi, 1997) as well as the spatial distribution of soil resources. Local neighborhood interactions may result in aboveground competition for light and belowground competition for water and nutrients, but also in complementarity (also known as competitive reduction) and facilitation (Cavard et al., 2011; Vandermeer, 1989). While complementarity occurs when two or more species show reduced competition in mixed compared to pure stands, facilitation occurs when one species has a positive effect on the growth of another species in a mixed stand. Tree growth will be positively related to diversity when the positive interactions (i.e., complementarity and facilitation) dominate the competitive interactions (Forrester et al., 2006b). Furthermore, neighborhood interactions intensify with increased soil resources (Baribault and Kobe, 2011).

The growth response of trees has most often been determined using tree height and stem diameter growth. Crown dimensions such as the crown width have also been used; however, these are more difficult and more time consuming to determine than height or stem diameter. Height growth is generally assumed to have the highest priority in carbon allocation in trees (Collet and Chenost, 2006). On the other hand, crown dimensions are highly sensitive to local neighborhood interactions as they strongly determine the individual’s ability to intercept light and to shade neighboring trees (Lang et al., 2010; Longuetaud et al., 2008, 2013; Schröter et al., 2012; Simard and Zimonick, 2005), and morphological responses of the tree crown are the most important effect of competition for light (Grams and Anderson, 2007). Furthermore, crown elements are the very first parts of the aboveground constituents of a tree to have contact with neighbors, and adjustments immediately occur to optimize carbon gain (Fichtner et al., 2013). Finally, plant costs for optimizing light harvesting are lower for branch than for stem construction and support (Küppers, 1989). We, therefore, expect a sensitivity ranking of growth response variables to neighborhood interactions of height growth < diameter growth < crown dimensions (Simard and Zimonick, 2005).

The aim of our study is to analyze how local abiotic site conditions and local neighborhood affect the annual growth rate of individual saplings in the early stage of a subtropical plantation with heterogeneous site conditions and a large species pool. Three specific hypotheses will be tested: (1) Variations in sapling growth are



species-specific and strongly determined by initial size; (2) edaphic conditions and site topography are more important predictors than neighborhood interactions of the growth performance of individual trees in this early stage of tree development; (3) diversity effects of the local neighborhood already occur, but will vary with the growth response variable (height < diameter < crown width). This paper reports the first study on initial tree growth in BEF-China. Tree growth is one of the key ecosystem functions addressed in this largest forest BEF experiment worldwide.

## 2. Materials and methods

### 2.1. Study site

The BEF-China experiment is located in a hilly subtropical region near Xingangshan Township, Jiangxi Province (N29° 08–11, E117° 09–93), China. The mean annual temperature is 16.7 °C and the mean annual precipitation 1821 mm. The natural vegetation of this region is a subtropical broad-leaved forest with evergreen species dominating in abundance (Bruehlheide et al., 2011). The BEF-China project encompasses two experimental sites (site A and site B), which were planted in 2009 and 2010, respectively. Because it was established earlier, we focus on site A in this study. This site covers a total area of 26.6 ha, ranging in altitude from 105 to 275 m a.s.l. The relief is highly variable, with slopes ranging from 0 to 45°. The soils are Cambisols and Cambisol derivatives, interspersed with Regosols on ridges and crests, and Anthrosols from colluvial deposits on foot slopes and valley floors. Due to the mountainous topography, erosion is a typical feature and results in a mixing of parent material and soil components from crest to valley positions.

### 2.2. Experimental design

Prior to the experiment, the site was covered with a plantation of *Pinus massoniana* Lamb. and *Cunninghamia lanceolata* (Lamb.) Hook. After clearing, a total of 261 plots, each with a projected area of 666.7 m<sup>2</sup> (25.8 × 25.8 m), were established during the period November 2008 to April 2009. Three different random extinction scenarios, one replicate of one of these scenarios and two non-random extinction scenarios were used to create a gradient of species richness levels (see Bruehlheide et al., 2014 for detailed explanations). In total, seven richness levels of 0, 1, 2, 4, 8, 16 and 24 tree species were assigned to 15, 88, 68, 40, 26, 19 and 5 plots, respectively. In the 246 plots with a richness level > 1, 400 (20 × 20) individual tree saplings were planted at equal projected distances of 1.29 m in March 2009, resulting in a total of 98,400 trees (Bruehlheide et al., 2014). Each tree is tagged with a unique numeric code. Replanting of tree individuals that died during the first growing season was conducted for deciduous species in November 2009 and for evergreen species in March 2010. Treatments (i.e., tree species richness level) were randomly assigned to plots, as were the positions of individual tree saplings within plots. The species pool is composed of 24 native broad-leaved tree species (Table 1). Further details on the general design and establishment of the BEF-China experiment are given in Bruehlheide et al. (2014) and Yang et al. (2013).

Due to the large number of trees planted in the experiment, the growth measurements focused on trees within the central part of every plot (Li et al., 2014). In the monocultures and 2-species mixtures the central 6 × 6 planting positions (i.e., 36 trees per plot) and in the 4-, 8-, 16- or 24-species mixtures the central 12 × 12 planting positions (i.e., 144 trees per plot) were analyzed (Fig. 1), resulting in a total of 18,930 planting positions. On the two sampling dates (September–October 2010 and September–October

2011) 10,938 living tree individuals were present in these positions. The analyses refer to individual trees (the “focal trees”) and their local abiotic and biotic site conditions. Due to the schematic planting scheme each focal tree has eight proximate neighbor trees, four neighbors to the main compass directions at a distance of 1.29 m and four neighbors in the diagonal at a distance of 1.82 m. For these analyses only those trees were included as focal trees for which information on the eight neighbor trees was available. Trees of the outermost row could, therefore, only act as neighbors, but not as focal trees (Fig. 1). Thus, in monocultures and 2-species mixtures 16 focal trees and in the 4-, 8-, 16- and 24-species mixtures 100 focal trees per plot were used (Fig. 1). Finally, 10 plots had to be removed from the analysis due to missing tree labels and 5 plots due to a very low number of focal trees (<2), resulting in a total number analyzed of 6723 focal trees and 4179 neighbor-only trees across 231 plots (the final number of plots per richness level (i.e., 1, 2, 4, 8, 16, 24) were 83, 65, 37, 25, 17, 4, respectively).

### 2.3. Data sampling

For each tree individual, the total tree height, the stem diameter at 5 cm above ground (hereafter ground diameter/GD), and the crown diameter along two directions (north–south and east–west) were measured in September–October 2010 and re-measured in September–October 2011 (i.e., in the second and third year after the planting of seedlings). Total height was measured with a measuring pole as the length from stem base to the apical meristem. GD was measured with a caliper to the nearest millimeter, and the position of the diameter measurement was permanently marked on the stem with white paint. Crown diameters were determined with a linear tape.

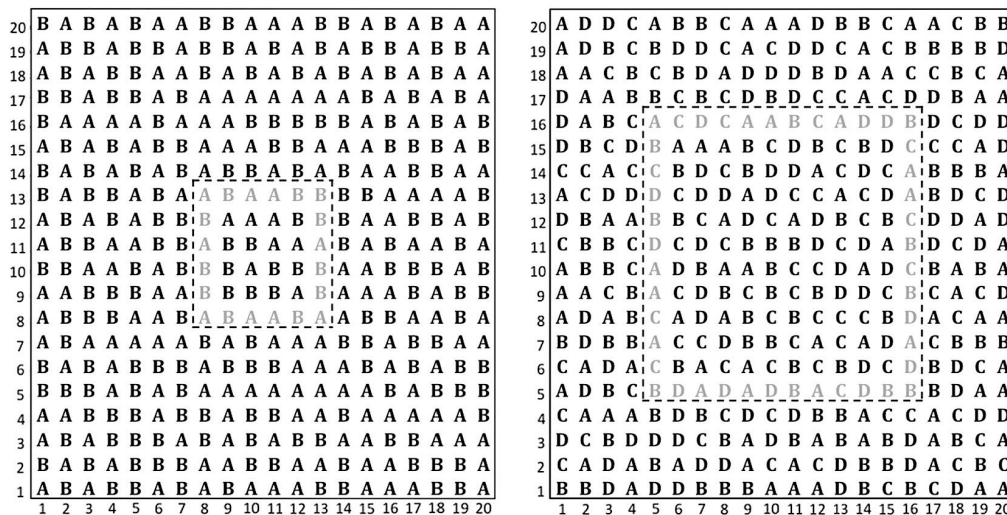
Topographic variables, i.e. aspect, slope, curvature and elevation, were extracted from a 5 m digital elevation model (DEM), calculated by ordinary kriging with a nested variogram (Webster and Oliver, 2001) based on a field campaign dataset (with differential GPS measurements). Each tree has a unique position consisting of plot, row and column number. Therefore, the obtained topographic variables could be assigned to each tree position. The overall quality of the DEM was high, with an explained variance of 98% and a root mean square error (RMSE) of 1.9 m (10-fold cross validation) in an elevation range of 112 m. All topographical calculations were made using ArcGIS 9.0 (ESRI Corp., Redlands, California, USA).

Nine soil samples per plot were collected in 2010 by taking soil cores at a depth of 0–5 cm. The soil was sampled at the center of nine systematically distributed subplots. The nine soil samples per plot were thoroughly mixed so that one mixed sample per plot was obtained. Thus, soil characteristics only vary at the plot level and all trees in a plot were assigned the same values. The soil chemical variables total carbon (C) and total nitrogen (N) content were determined. Prior to the chemical analyses, soil samples were air-dried and sieved (<2 mm). For the C and N analyses, dry soil samples were ground with a ball mill and subsequently weighed (determination of oven dry weight). Total C and N were determined with a C/N analyzer (Vario EL, Elementar, Hanau, Germany). Besides N, phosphorus (P) as one of the major plant nutrients may also limit tree growth and ecosystem productivity (Baribault et al., 2012; Elser et al., 2007; Vitousek et al., 2010). To date, P data are only available at the plot level for a low number of plots ( $n = 30$ ). However, total soil P was measured for key soil profiles of the experimental site (Scholten, unpubl. data). Eight such pedons were distributed over the area at representative parts of the slopes (crest, top slope, mid slope, toe slope). Total P content was determined by X-ray fluorescence. Mean P content for all soil horizons was 434 mg kg<sup>-1</sup> (standard deviation 11 mg kg<sup>-1</sup>) which can be

**Table 1**

Tree species planted in experimental site A of BEF-China. Information is given on leaf habit (D = deciduous, E = evergreen) and successional stage (E = early, I = intermediate, L = late). Assessments are based on expert knowledge and on observations in the nearby Gutianshan National Nature Reserve (Yu et al., 2001; Bruehlheide et al., 2011, 2014).

Species name	Abbreviation of the species name	Leaf habit	Successional stage
<i>Acer davidii</i> Franch.	Acđ	D	E/I
<i>Castanea henryi</i> (Skan) Rehd. & Wils.	Cah	D	E
<i>Castanopsis carlesii</i> (Hemsl.) Hay.	Cac	E	L
<i>Castanopsis eyrei</i> (Champ.) Tutcher	Cae	E	L
<i>Castanopsis sclerophylla</i> (Lindl.) Schott.	Cas	E	E/I/L
<i>Choerospondias axillaris</i> (Roxb.) Burt & Hill	Cha	D	E
<i>Cinnamomum camphora</i> (Linn.) Presl	Cic	E	E/I/L
<i>Cyclobalanopsis glauca</i> (Thunb.) Oerst.	Cyg	E	I/L
<i>Cyclobalanopsis myrsinifolia</i> (Blume) Oerst.	Cym	E	I/L
<i>Daphniphyllum oldhamii</i> (Hemsl.) K. Rosenth.	Dao	E	L
<i>Diospyros japonica</i> Sieb. & Zucc.	Dij	D	E
<i>Koelreuteria bipinnata</i> Franch.	Kob	D	E
<i>Liquidambar formosana</i> Hance	Lif	D	I
<i>Lithocarpus glaber</i> (Thunb.) Nakai	Lig	E	I/L
<i>Melia azedarach</i> Linn.	Mea	D	E
<i>Nyssa sinensis</i> Oliver	Mys	D	E
<i>Quercus acutissima</i> Carruth.	Qua	D	E
<i>Quercus fabri</i> Hance	Quf	D	E
<i>Quercus serrata</i> Murray	Qus	D	E
<i>Rhus chinensis</i> Mill.	Rhc	D	E
<i>Sapindus saponaria</i> Linn.	Sas	D	E
<i>Schima superba</i> Gardner & Champion	Scs	E	E/I/L
<i>Triadica sebifera</i> (L.) Small	Trs	D	E
<i>Triadica cochinchinensis</i> Loureiro	Trc	D	E



**Fig. 1.** Exemplary illustrations of the sampling areas for plots with monoculture or 2-species mixtures (left) and for plots with 4-, 8-, 16-, and 24-species mixtures (right). The alphabetic characters indicate different tree species that were randomly assigned to the plots. Tree individuals located within the dashed lines were measured. Each tree has eight proximate neighbor trees. For the analyses only those trees were included as focal trees for which information on the eight neighbor trees was available (black letters within dashed lines). Trees of the outermost row could only act as neighbor trees (gray letters).

rated as medium P level for tropical soils according to Landon (1984). On selected plots ( $n = 30$ ), Hedley P-fractions (Hedley et al., 1982) were sequentially extracted and grouped in labile, moderately labile and stable P pools (i.e., Cross and Schlesinger, 1995). First results show P concentrations in the topsoil (0–5 cm) of 43, 138 and 236  $\text{mg kg}^{-1}$  for labile, moderately labile and stable P pools (Todt, unpubl. data), respectively, which matches well with the data for total P. Accordingly, at this stage, no significant response of tree growth to P limitation is likely at our study site.

**2.4. Data analyses**

Annual tree height and GD growth rates were calculated as the difference between total height and GD in 2011 and 2010,

respectively. Crown width (CW) was calculated as the average of the two crown diameter measures. Annual CW growth rate was determined as the difference between CW in 2011 and CW in 2010.

The original values of aspect ranged from 0 to 360 degrees, corresponding to 0 to  $2\pi$  in radian units. The radian values were sine and cosine transformed into degrees of eastness and northness, respectively. The higher the degrees of eastness or northness the closer the slope is exposed to eastern or northern direction, respectively. Values for curvature range from  $-398$  to  $327$ . A negative value indicates that the surface is concave (local depression), and a positive value indicates that the surface is convex (local ridge). The C/N ratio was calculated from the soil C and N contents on a weight basis ( $\text{g g}^{-1}$ ).

For each focal tree a competition index (CI) was calculated as:

$$CI = \sum_{i=1}^N GD_i$$

where  $GD_i$  is the  $GD$  of the  $i$ -th neighbor.  $N$  is the total number of neighbors ranging from 1 to 8. The  $CI$  value of focal trees that have no immediate living neighbors is zero. A higher  $CI$  value corresponds to a higher competitive impact of the neighbors on the focal tree.

Local neighborhood species diversity of each focal tree was calculated as the Shannon index:

$$H = -\sum_{i=1}^N P_i \ln P_i$$

where  $P_i$  is the proportion of number of individuals of each species out of the overall number of neighbor trees ( $N$ ).

All independent variables are presented with their interquartile range and mean values ( $\pm$ standard deviation (SD)) in Table 2.

Statistical analyses were performed with mixed effects models conducted in R 3.0.2 (R Development Core Team, 2011) using the package lmerTest (Kuznetsova et al., 2013). At the level of individual trees, the fixed continuous effects of the topographic (slope, aspect, curvature, elevation) and edaphic (N content, C/N ratio) variables as well as the local neighborhood variables (CI, Shannon index) were assessed for the three response variables growth rates of height, GD and CW. The GD measured in 2010 was included as explanatory factor initial size in the three models in order to account for the differences in size at the beginning of the experiment. Correlation tests ensured that all fixed effects in the models were independent variables. Although the species composition of the local neighborhood may be an important factor influencing individual tree growth (Lang et al., 2012), we did not consider species composition in our analyses. As there were 4771 different species compositions with a total of 6723 focal trees, the variation in response variable explained by species composition was almost as high as by the residual error without taking species composition into account. Thus, we decided to pool the errors brought about by species compositions and the residual error term. We standardized all fixed predictor variables to allow for comparing the effect on the growth variables as a response of one SD change in predictors within one specific model. The species identity of the focal tree and plot were included as crossed random effects. The tested data were all normally distributed and no violations of homogeneity and normality of variance were detected from the models. The three models (height growth model, GD growth model and CW growth model) were optimized with a step-wise backward selection of fixed factors using the Maximum Likelihood (ML) approach comparing Akaike's Information Criterion (AICs) (Zuur et al., 2009). Thus, the final model only contained significant effects. To obtain

unbiased estimates of variances, the final models were recalculated using the Restricted Maximum Likelihood (REML) approach. As there were only continuous predictors in the model and no interactions included, the effects account for the variance after all other predictors were accounted for. In consequence, the effects do not depend on the order in which predictors were specified in the model.

### 3. Results

The mean total height per species ranged from 52 to 301 cm after the third growing season (i.e., in autumn 2011). The overall mean tree height was 120 cm  $\pm$  86 cm, and the mean GD and CW were 1.9 cm  $\pm$  1.4 cm and 84 cm  $\pm$  62 cm, respectively.

Growth performance was markedly species-specific and strongly related to initial size (Table 3, Fig. 2). Species identity explained 19% and 15% of the total random variance in the height and GD growth model, respectively. In the CW growth model, the variance component of species identity was 23%. Overall, species identity as a random factor explained a larger proportion of the random variance (15–23%) in all three growth response variables as compared to plot (8–16%). In all models, growth rates were highly significantly and positively related to initial size (Table 3). Moreover, initial tree size varied significantly between different species ( $F = 304.3^{***}$ ).

The three response variables responded similarly to most of the local abiotic variables, with the exception of slope and curvature (Table 3). Tree saplings located on south-facing slopes performed better than those growing on north-facing slopes. Slope had a significantly negative impact on GD growth rate, but did not affect height and CW growth rates. The individuals positioned in local depressions had higher increments in height than those on local ridges, whereas curvature did not impact CW growth rate and marginally influenced GD growth rate. No significant effect of elevation was found. Nitrogen content had a positive and C/N ratio a negative influence on sapling growth rate.

The CI was significantly positively related to height growth, but negatively related to GD and CW growth (Table 3), i.e. the focal tree had higher height growth rates at higher competitive impact levels of the local neighbors, whereas the opposite was found for GD and CW growth rates. Shannon diversity of the local neighborhood did not influence individual tree growth rates for any of the three response variables.

### 4. Discussion

#### 4.1. Species-specific growth variation

Our first hypothesis was confirmed by the large effect size of initial size in all three growth response models. Initial size was

**Table 2**

Summary of the characteristics of the topographic and edaphic conditions as well as local neighborhood of the focal trees (IQR = interquartile range; SD = standard deviation; N = nitrogen; C = carbon; CI = competition index).

		IQR	Mean ( $\pm$ SD)
Topographic conditions	Northness <sup>a</sup>	−0.82–0.30	−0.22 ( $\pm$ 0.64)
	Slope (°)	24.02–38.90	31.24 ( $\pm$ 9.90)
	Curvature (°) <sup>b</sup>	−22.36–55.09	16.67 ( $\pm$ 71.56)
	Elevation (m)	176.91–222.85	198.20 ( $\pm$ 34.03)
Edaphic conditions	N content (%)	0.23–0.28	0.26 ( $\pm$ 0.03)
	C/N ratio	14.1–17.0	15.58 ( $\pm$ 2.15)
Local neighborhood	CI	6.4–15.5	11.56 ( $\pm$ 6.79)
	Shannon index	0.64–1.33	0.93 ( $\pm$ 0.54)

<sup>a</sup> The higher the value, the closer the aspect is to north.

<sup>b</sup> Positive values are for convex surface (local ridge) and negative for concave surface (local depression).

**Table 3**

Results from the mixed effects models for sapling growth responses (annual increment in height, ground diameter (GD) and crown width (CW), respectively) to initial size, local neighborhood and environmental variables (N = nitrogen; C = carbon; CI = competition index).

		Response variables			
		Annual height growth rate Estimate (±SD)	Annual GD growth rate Estimate (±SD)	Annual CW growth rate Estimate (±SD)	
Fixed effects	Initial size	12.25 (±0.64)***	0.23 (±0.01)***	13.12 (±0.50)**	
	Aspect to north <sup>a</sup>	-2.35 (±0.83)**	-0.04 (±0.02)**	-2.15 (±0.78)**	
	Slope (°)	n.s.	-0.03 (±0.01) <sup>†</sup>	n.s.	
	Curvature (°) <sup>b</sup>	-3.27 (±0.61)***	-0.02 (±0.01) <sup>†</sup>	n.s.	
	Elevation (m)	n.s.	n.s.	n.s.	
	N content (%)	2.84 (±0.92)**	0.07 (±0.02)***	2.44 (±0.97) <sup>†</sup>	
	C/N ratio	-3.82 (±0.97)***	-0.05 (±0.02) <sup>†</sup>	-2.46 (±1.02) <sup>†</sup>	
	CI	1.16 (±0.59) <sup>†</sup>	-0.04 (±0.01)***	-2.30 (±0.50)***	
	Shannon index	n.s.	n.s.	n.s.	
	Variance components				
	Random effects	Species identity	19%	15%	23%
		Plot	8%	12%	16%

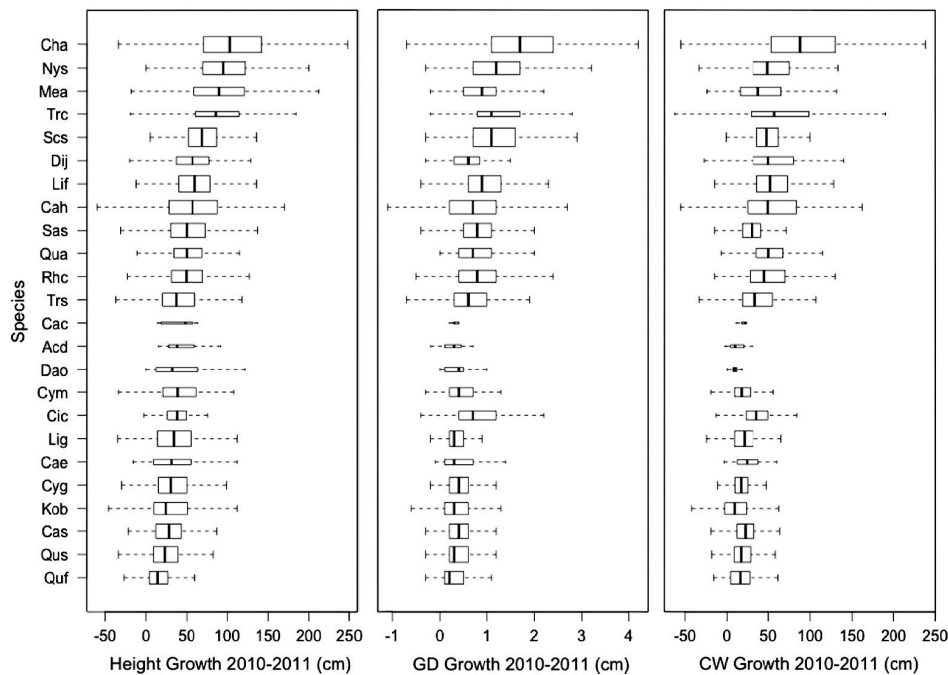
\*\*\*  $Pr < 0.001$ .

\*\*  $0.001 \leq Pr < 0.01$ .

<sup>†</sup>  $0.01 \leq Pr < 0.05$ , n.s.: not significant ( $Pr \geq 0.1$ ).

<sup>a</sup> The higher the value, the closer the aspect is to north.

<sup>b</sup> Positive values are for convex surface (local ridge) and negative for concave surface (local depression).



**Fig. 2.** Annual height, ground diameter (GD) and crown width (CW) growth rates of 24 species. Bold lines are the medians. The box widths are proportional to the square roots of the number of observations in each species. Outlier values are not plotted. Species are arranged in order of increasing annual height growth rates on the y-axis. For the abbreviations of species names see Table 1.

found to greatly affect tree growth, particularly in younger trees (MacFarlane and Kobe, 2006; Pacala et al., 1994). On the contrary, Lang et al. (2012) found no effect of initial size on both height and stem diameter growth in a field experiment close to our experimental area. Furthermore, sapling growth was markedly species-specific, indicating an interspecific variation in key functional traits. Generally it is suggested that trait-growth rate relationships are much stronger for saplings than for large trees (Poorter et al., 2008). Several key traits have been proposed to be universally important for plant growth; these are summarized in the leaf-height-stem-seed scheme (Poorter et al., 2008). In forests, classical life-history theory predicts that light-demanding tree species,

which are also termed early successional or pioneer species are characterized by small values of leaf mass per area, maximum adult height, wood density and seed mass, whereas the opposite trait values are characteristic for shade-tolerant species, which are also termed late successional or climax species (Poorter et al., 2008). The majority of species included in our study are classified as early successional (13 species). Only one species occurs mainly in the intermediate stage, and four species are classified as late successional. A further three species show no preference for any particular successional stage. Finally, one species occurs mainly in early/intermediate stages, and three species are characteristic for the intermediate/late stages. Because our experiment was

established after clear-cutting of the previous conifer plantation, the early phase of sapling establishment was characterized by full light supply. Under low-light conditions biomass accumulation has often been found to be similar between light-demanding and shade-tolerant species, whereas under high-light conditions biomass accumulation is much higher in light-demanding species (Niinemets, 2010; Poorter, 1999) resulting in a higher plasticity (Böhnke and Bruelheide, 2013). The growth rates of most of the species were consistent with these assumptions, i.e. early successional species were fast growing and intermediate/late successional species were slow growing under high irradiation. This is possibly explained by the fact that early successional species have lower wood construction costs as well as higher xylem hydraulic conductance and higher photosynthetic capacity (Chave et al., 2009). Low growth rates of late successional species in full sunlight might also be caused by a lower specific leaf area (Böhnke and Bruelheide, 2013) and morphological, chemical or physiological constraints, such as low root length/leaf area ratio, heat damage during summer or photoinhibition (Niinemets, 2010; Song et al., 2007). The tree species *Schima superba* and *Liquidambar formosana*, which are classified as indifferent or mid-successional, respectively, but showed high growth rates in our study represented remarkable exceptions to the general pattern of early successional/fast growing and late successional/slow growing. Further exceptions were the early successional species *Koelreuteria bipinnata*, *Quercus serrata* and *Quercus fabri*, which had very low growth rates. For single species, sapling growth rates have been analyzed in other studies, and the findings are in accordance with our results. High growth rates for saplings of *Schima superba* and *Melia azedarach* (Chen et al., 1999) and *Choerospondias axillaris* (Matsumura et al., 2007) have been observed in forest gaps, whereas *Quercus serrata* was shown to be very slow-growing (Xing et al., 2012).

#### 4.2. Local abiotic site conditions

The local abiotic site conditions strongly influenced individual-tree growth rates. Thus the high environmental heterogeneity of our study site is an important cause of the high intraspecific variability in growth rates. Light availability is broadly recognized as a key factor determining sapling growth (Finzi and Canham, 2000). In our experiment, clear-cutting of the previous stand meant there was no upper canopy which would have caused spatial variation in light availability for the saplings. Light conditions can, however, also be affected by abiotic factors. Topography is one of the major abiotic factors influencing the direction and intensity of incoming sunlight (Ishii and Higashi, 1997). In the northern hemisphere, south-facing slopes receive much more solar irradiation than north-facing slopes, creating strong gradients of light, temperature and soil moisture: higher light levels and temperatures as well as lower soil moisture are found on south-facing slopes (Warren, 2010). In our study, tree growth was positively related to aspect to south, indicating that higher irradiation benefitted tree growth. As the net effect is positive, potential water limitation seems to be of less importance for early growth.

GD growth rate was negatively related to slope inclination. This is consistent with the results of von Oheimb et al. (2011) obtained in the same region. Slope inclination may correlate with edaphic conditions, in particular soil depth, soil moisture and nutrient availability. Soils on steeper slopes and on crests are shallower, and therefore limit rooting space in one dimension. In addition, steeper slopes may be drier due to higher surface runoff, higher interflow rates and lower soil depth. Furthermore, slope inclination may also be positively correlated with mechanical exposure and frequency of disturbance (Nagamatsu and Miura, 1997). As a consequence, aboveground biomass growth may be reduced on

steeper slopes. In contrast to GD, sapling CW growth rate was not influenced by slope inclination in our study. This is in accordance with Lang et al. (2010) who concluded from a study in a nearby forest nature reserve, that the interplay of stem inclination and crown displacement allows for a plastic response of tree individuals on sloping terrain, resulting in similar CW along a gradient of slope inclination.

Height growth rates were greater on concave than on convex slopes. This is not in agreement with other previous findings, which were explained by the fact that soil surface disturbance is more frequent on concave slopes than on convex slopes (Tsujino et al., 2006). Although this might be an important process in the long term, our study analyzed the short-term perspective, and here another factor may be paramount. Soil nutrient availability is probably much better in local depressions compared to ridges and convex slopes because of lateral translocation processes. Downslope transport of nutrients in soil water, sediments and litter influences growth rates positively. Remarkably, the effect size of curvature was the highest among topographic factors in the height growth model, presumably because of more intensive interactions between the focal tree and its local neighbors. For a tree on a concave slope, the crowns of neighboring trees in the uphill direction are positioned higher than those on convex slopes, and, thus, interact more strongly at a given height (Lang et al., 2010; Umeki, 1995). This was partly confirmed by the positive effect of the neighborhood competition in the height growth model (Table 3). In contrast, crown width was not affected by curvature. The crown expansion of trees growing on concave slopes could be more strongly constrained by neighbors growing on higher slope positions, which probably offsets the benefits from higher soil nutrient supply.

Individual-tree growth has often been found to be strongly related to soil fertility (e.g., Baribault and Kobe, 2011; Scowcroft et al., 2007; van Breugel et al., 2011; Zhang et al., 2010). Our current results show that growth rate is significantly determined by the total N content and the C/N ratio of the upper mineral soil. N is generally considered to be the principal limiting nutrient for plant growth in many terrestrial ecosystems, and a number of previous experiments conducted under controlled conditions have confirmed this for sapling growth (e.g., Canham et al., 1996; Ceccon et al., 2004). The soil C/N ratio is often used as an indicator for N immobilization, mineralization and nitrification rates, and thus for N availability to plants. This is based on the fact that soils with a high C/N ratio are characterized by a rapid immobilization of N by heterotrophic bacteria, and that the activity of these bacteria may be limited by N in these soils. As a result, the N nutrition and thus growth of plants may be negatively related to the soil C/N ratio. The negative influence of C/N on tree growth rates was also found in our study and is in agreement with the results reported by Yamakura and Sahunalu (1990).

#### 4.3. Effects of the local neighborhood

In our experiment the planting grid size was 1.29 m in horizontal projection. This distance is rather low compared to other forest BEF experiments, but was selected to more closely mimic naturally regenerating forests (Bruelheide et al., 2014). The mean size of the saplings was 120 cm in height and 84 cm in CW after three growing seasons. This means that only some of the trees were large enough to have direct contact with each other. However, in sloping terrain the size of neighbors positioned in an uphill direction is enlarged relative to a focal tree due to the rooting position at a higher elevation and may, thus, generate stronger interactions at a given stature than is the case for trees growing on level ground (Lang et al., 2010; Umeki, 1995). We, therefore, expected direct

interactions among neighboring trees to occur already in this early stage.

We found that increasing size of neighboring trees (expressed as CI) significantly enhanced height growth, but reduced stem and crown diameter growth, strongly supporting our expectation. This is consistent with the findings of Potvin and Dutilleul (2009) in an experimental tree plantation in Panama and von Oheimb et al. (2011) in a younger secondary subtropical forest near the experimental site, where competition by local neighbors was the overwhelming source of variation in individual-tree growth. In recent years, the understanding of tree–tree interactions has been considerably improved, and it appears that these interactions in mixed-species stands are more complex than predicted by existing theories. The outcome of tree–tree interactions may vary with species identity, local neighborhood species composition, the dominance of above- versus belowground processes and tree spatial patterning (Beyer et al., 2013; Coates et al., 2013; Fraver et al., 2014). This may be the reason why the effect sizes of CI were relatively small compared to those of the local abiotic variables, i.e. the relative importance of local neighborhood competition on sapling growth was lower than that of local abiotic factors. The fact that the opposite was true for the competition impact on height versus GD and CW growth can be explained by the fact that height growth has the highest priority for carbon allocation. At moderate levels of competition, height growth rates increase at the expense of diameter growth, and competition suppresses height growth only when it is very high (Pretzsch, 2009; Simard and Zimonick, 2005).

However, local neighborhood interactions may not only take place through competition, but also through complementarity and facilitation. The heterogeneous topographical and resource conditions as well as the great local species diversity in our experiment suggest that the effects of niche differentiation and facilitation might be expressed earlier than in experiments established in homogenous sites with small diversity gradients (Potvin and Gotelli, 2008; Tylianakis et al., 2008). We therefore expected diversity effects of the local neighborhood to occur in this early stage. However, our results did not support this hypothesis. In a small-scale diversity experiment with subtropical tree species, Lang et al. (2012) found species composition rather than species richness to influence sapling growth rate. This experiment, established under homogenous conditions on a former agricultural field, was conducted over two years and included a lower species richness gradient of the local neighborhood than our experiment (1, 2 and 4 tree species). Lang et al. (2012) provided two mutually non-exclusive explanations: species diversity effects on tree growth responses might become apparent only at higher levels of diversity (Papaik and Canham, 2006) and/or might evolve at a later stage of sapling development. The former explanation may be valid because the occupied niche space should increase with higher species number and thereby make niche complementarity more likely to occur. The latter explanation is substantiated by the assumption that various forms of environmental heterogeneity that regulate the performance of species co-vary with time and, in this way, modulate the magnitude of diversity effects (Cardinale et al., 2011). In the above-mentioned small-scale diversity experiment Lang et al. (2014) found that species richness effects on tree sapling nitrogen acquisition and system nitrogen retention strengthened over time. In our study, the complementarity and facilitation effects obviously have not yet been large enough to significantly contribute to sapling growth variation. However, future research will test our expectation of increasing BEF effects of the local neighborhood on individual-tree growth performance over time.

In conclusion, the most important impediment to the wide-scale successful re- and afforestation with native broad-leaved tree species is the lack of knowledge of the silvicultural requirements of

most of these species. Our results highlight the pronounced influence of local abiotic environment (i.e., topographic and edaphic conditions) on tree sapling growth. Tree–tree competitive interactions occurred already in this initial stage and were of lower importance compared to the local abiotic environment. Accordingly, we stress the importance of better understanding the impact of local abiotic and biotic conditions on initial growth of native species.

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## **Chapter 3**

### **Early subtropical forest growth is driven by community mean trait values and functional diversity rather than the abiotic environment**

Wenzel Kröber, Ying Li, Werner Härdtle, Keping Ma, Bernhard Schmid, Karsten Schmidt, Thomas Scholten, Gunner Seidler, Goddert von Oheimb, Erik Welk, Christian Wirth and Helge Bruelheide

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## Early subtropical forest growth is driven by community mean trait values and functional diversity rather than the abiotic environment

Wenzel Kröber<sup>1</sup>, Ying Li<sup>2</sup>, Werner Härdtle<sup>2</sup>, Keping Ma<sup>3</sup>, Bernhard Schmid<sup>4</sup>, Karsten Schmidt<sup>5</sup>, Thomas Scholten<sup>5</sup>, Gunnar Seidler<sup>1</sup>, Goddert von Oheimb<sup>6</sup>, Erik Welk<sup>1</sup>, Christian Wirth<sup>7,8</sup> & Helge Bruelheide<sup>1,8</sup>

<sup>1</sup>Martin Luther University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, D-06108 Halle (Saale), Germany

<sup>2</sup>Faculty of Sustainability, Institute of Ecology, Leuphana University Lüneburg, Scharnhorststr. 1, D-21335 Lüneburg, Germany

<sup>3</sup>Institute of Botany, CAS, 20 Nanxincun, Xiangshan, Beijing 100093, China

<sup>4</sup>University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

<sup>5</sup>Physical Geography and Soil Science, University of Tübingen, Rümelinstraße 19-23, D-72070 Tübingen, Germany

<sup>6</sup>Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Piennner Str. 7, 01737 Tharandt, Germany

<sup>7</sup>University of Leipzig, Johannisallee 21–23, D-04103 Leipzig, Germany

<sup>8</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany

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### Correspondence

Wenzel Kröber, Martin-Luther-University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, D-06108, Halle (Saale), Germany.  
Tel: +49-345-55-26222;  
Fax: +49-345-55-27228;  
E-mail: wenzel.kroeber@botanik.uni-halle.de

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### Introduction

One of the most important aims in functional biodiversity research is to predict the importance of different facets of biodiversity to ecosystem functions (EFs). It has been shown that many different EFs are positively related to producer diversity (Loreau et al. 2001; Hooper et al. 2005; Balvanera et al. 2014). A meta-analysis (Cardinale

### Abstract

While functional diversity (FD) has been shown to be positively related to a number of ecosystem functions including biomass production, it may have a much less pronounced effect than that of environmental factors or species-specific properties. Leaf and wood traits can be considered particularly relevant to tree growth, as they reflect a trade-off between resources invested into growth and persistence. Our study focussed on the degree to which early forest growth was driven by FD, the environment (11 variables characterizing abiotic habitat conditions), and community-weighted mean (CWM) values of species traits in the context of a large-scale tree diversity experiment (BEF-China). Growth rates of trees with respect to crown diameter were aggregated across 231 plots (hosting between one and 23 tree species) and related to environmental variables, FD, and CWM, the latter two of which were based on 41 plant functional traits. The effects of each of the three predictor groups were analyzed separately by mixed model optimization and jointly by variance partitioning. Numerous single traits predicted plot-level tree growth, both in the models based on CWMs and FD, but none of the environmental variables was able to predict tree growth. In the best models, environment and FD explained only 4 and 31% of variation in crown growth rates, respectively, while CWM trait values explained 42%. In total, the best models accounted for 51% of crown growth. The marginal role of the selected environmental variables was unexpected, given the high topographic heterogeneity and large size of the experiment, as was the significant impact of FD, demonstrating that positive diversity effects already occur during the early stages in tree plantations.

et al. 2011) revealed that 414 of the 574 independent experimental manipulations of species richness had a positive effect on producer biomass. This also applies to forests, which represent *the* most important ecosystems globally because of their broad geographical cover and the unique ecosystem services they provide (Quijas et al. 2012). A review of worldwide inventories demonstrated positive relationships between forest growth and standing

biomass and tree species richness in the majority of published studies (Scherer-Lorenzen 2013). For example, it was shown that biomass production in Swedish forests increases with tree species richness (Gamfeldt *et al.* 2013).

Such biodiversity-focused research has often tried to minimize environmental variation, which can lead to an underestimation of other major determinants of tree growth such as climate or soil conditions. An analysis of the pan-European tree-ring network showed that forest productivity in central and southern Europe is driven by temperature in high-elevation and high-latitude areas, and moisture at low elevations (Babst *et al.* 2013). Climate also determines tree growth at the microsite scale with respect to differences in slope, aspect, and inclination (Chen *et al.* 1999; Geiger *et al.* 2003). In the Northern Hemisphere, south-facing slopes receive more solar irradiation than north-facing slopes (Warren 2010), resulting in positive effects on individual tree growth (Fralish 1994; Li *et al.* 2014). As a consequence, each single variable, such as slope aspect, inclination, or altitude, has the potential to significantly affect tree growth (Sarimi *et al.* 2014). In addition, soil conditions have a strong impact on forest productivity (Grier *et al.* 1989), making soil type a key predictor in forest growth models (Landsberg and Waring 1997; Pinjuv *et al.* 2006). Such strong dependence of forest productivity on climate and soil conditions indicates that any attempt to detect biodiversity signals on tree growth needs to be separated from effects of the abiotic environmental setting. Accordingly, for the current study, we analyzed a large forest biodiversity experiment on the assumption that the biodiversity treatments only induced broad variation in functional diversities of tree communities across a heterogeneous landscape, and we ignored all other design aspects of the experiment. It is considered that analyzing a designed experiment as if it were a sample survey of plots across the landscape (Snedecor and Cochran 1989) is justified, when the aim is to maximize the environmental impact on ecosystem functioning.

The selected set of environmental variables were related to topography (slope, aspect, and elevation) and soil (pH value, carbon, and nitrogen content in the topsoil), both of which were considered to be relevant to tree growth when the experiment had been established. During the early stage of the experiment, we assumed that the environmental variables had not yet been, or had only been minimally, affected by the experimental biodiversity treatments. This assumption may clearly not apply over a longer term, in particular, given that as microclimate and soil conditions respond to biodiversity in feedback loops, and depending on plot productivity and tree richness, organisms modify their environment (Bruelheide *et al.* 2014).

Further key determinants of forest production include the particular tree species, as it is well documented that tree growth can vary by an order of magnitude among different tree species (Lieberman *et al.* 1985; Lambers and Poorter 1992). It is generally assumed that early successional species outperform late successional ones because of higher rates of photosynthesis (Bazzaz 1979). This applies to our study as deciduous species generally grow faster than evergreen ones, and early successional species are often deciduous (e.g., Budowski 1965); however, species growth rates can also differ within successional categories. One approach to better understanding such species identity effects is to relate species-specific differences in growth rates to the species' functional traits (Díaz *et al.* 2007). It has been shown that a few key traits that describe the leaf economics spectrum (LES) (Wright *et al.* 2004), such as specific leaf area (SLA) or leaf nitrogen content, can successfully predict tree growth of 53 rainforest species in Bolivia (Poorter and Bongers 2006). At the plot scale, productivity should depend on the mixture of species in the community. According to the mass ratio hypothesis (Grime 1998), the most abundant or dominant species are expected to exert the highest impact on EF. This hypothesis provides the basis for using community-weighted means (CWMs) of trait values, which are obtained from averaging traits at the community level by weighting the species' traits with the species' relative abundance in the given community (Ackerly *et al.* 2002). In grasslands, this approach has been successfully employed for predicting EF from CWM trait values (Garnier *et al.* 2004; Roscher *et al.* 2012). Thus, as one important EF indicator, tree growth may be predicted in relation to the CWM of a single key trait or from a combination of CWMs of different uncorrelated traits.

As CWM represents the overall plot mean, it does not account for trait variation within plots and it fails to capture the effect of functional diversity (FD), both in terms of selection and complementarity effects (Loreau and Hector 2001). In particular, functional diversity may increase resource complementarity and facilitation among species in species-rich plots and thus increase forest productivity (Spasojevic and Suding 2012; Dias *et al.* 2013). For example, in southern New Zealand, nutrient-rich forest sites were not only characterized by species with high relative growth rates, but also showed higher variation in growth rates related to a high variation in species-specific shade tolerances, resulting in greater complementarity of light use (Coomes *et al.* 2009). As such, within defined forest age classes, FD has been found to be positively related to aboveground biomass (Bu *et al.* 2014). Similarly, in the Cedar Creek experiment, functional complementarity of grassland species resulted in higher C and N accumulation in soils (Fornara and Tilman 2007). Com-

plementarity in resource use is expected to emerge in trait space and be reflected by a higher variation and dispersion of values of relevant traits (Lavorel *et al.* 2008). In principle, a trait can contribute to complementarity of a particular EF in the community, either spatially via above- or belowground resource partitioning (Bessler *et al.* 2009; von Felten *et al.* 2009), or temporally via differential resource use in different seasons (Dedeyn and Vanderputten 2005). Trait value distribution in the community can be expressed mathematically by FD measures, such as in the regularity of the distribution of trait abundances (Villéger *et al.* 2008), as designated by Rao's quadratic entropy (FDQ) (Rao 1982). It should be noted that in communities, the FD of a particular trait is not independent of the CWM of the same trait, as trait variation is constrained by the mean (Dias *et al.* 2013). In consequence, both the FD and CWM of a single trait explain some degree of variation in EF. Thus, separating FD from CWM poses a similar problem as separating environmental variables from biodiversity effects.

In summary, variation in productivity as an important ecosystem function (EF) in forests may be largely explained by variation in environmental variables, variation in community-weighted mean (CWM) trait values, and variation in functional diversity (FD). The contribution of each of these components on a certain EF can be visualized as a triangle, where environmental variables, CWM, and FD represent the three corners. The location of a particular plant community in this triangular space will depend on the relative impact of the abiotic environment, species-specific properties, and biotic interactions. For example, aboveground net primary production (ANPP) in alpine grasslands was found to be dependent on both nutrient supply (quantified by a nitrogen nutrition index) and FD in vegetative height (which reflects light acquisition complementarity), but not by the CWM of any particular trait (Díaz *et al.* 2007). Taking all predictors together, 44% of the total variation in ANPP was explained by abiotic conditions alone, and inclusion of FD did not improve the model's explanatory power. However, to our knowledge, no attempt has been made to quantify the contribution of environmental variables, CWM, or FD in forest communities. One important caveat that must be considered in the above context is that it would be unusual for all of the three explanatory corners in the aforementioned triangle to have the same range of variation in any particular study, making it unlikely for any of the factors to have the same chance to influence variation in the dependent variable. In this study, variation was particularly high in CWM and FD because the plots originated from a biodiversity experiment that ensured a large range of species richness levels and, as a consequence, resulted in a large variation in

CWM and FD. Nevertheless, the very large topographic and hydrological variation at the experimental site also ensured a high environmental variation.

It might be argued that partitioning the effect of environment, CWM, and FD is only necessary in natural communities but not in designed experiments, where biodiversity is manipulated and environmental variation should be accounted for. To control environmental variation, experimental plots are often established in homogeneous environments, such as a flat piece of land with uniform land-use history and soil properties. However, even comparatively low environmental heterogeneity can strongly affect EF, as was demonstrated in the Sardinilla forest experiment in Panama (Healy *et al.* 2008). Under environmental heterogeneity, fully randomized experiments cannot prevent certain plots from exhibiting exceptional site conditions. For example, in the Sardinilla experiment, all six-species diversity plots were located at sites with low water drainage (Healy *et al.* 2008). As homogeneity declines with increasing study size, many experiments have employed blocking techniques, for example, with respect to distance from the river in the Jena Experiment (Roscher *et al.* 2004). However, blocking is only useful when there are few and clear gradients across the experimental site (Bruehlheide *et al.* 2014), and in very heterogeneous environments, blocking may not be feasible. In many regions of the world, forests mainly occur in topographically heterogeneous environments, as the often more fertile flat lands are used for agriculture (Sandel and Svenning 2013). As such, in field-based forest biodiversity–EF experiments, such environmental effects are often confounded with biodiversity and have to be accounted for in the same way as in natural communities.

The aim of our study was to partition the effects of 11 environmental variables and CWM and FD variables calculated from 41 species traits to one key ecosystem function in the early stage of a large forest-based biodiversity experiment in subtropical China (Bruehlheide *et al.* 2014). A set of 40 broadleaved tree species native to the natural vegetation was planted in richness levels of 1, 2, 4, 8, 16, and 24 tree species. We used results from one of two sites, which had been planted in 2009 with 1-year-old saplings (Yang *et al.* 2013; Bruehlheide *et al.* 2014). To measure tree productivity, we chose mean annual crown width growth between 2011 and 2012, as it best reflected tree growth at the early growth stage of the experiment (Li *et al.* 2014). We expected forest growth at this early stage to be mainly dominated by abiotic conditions, based on the finding of Li *et al.* (2014) that growth of individual trees is related to aspect and soil nitrogen content but not to Shannon diversity of the local tree neighborhood. Crown width growth rate data referred to Li *et al.* (2014), and data were aggregated at the plot level, with plot mean

values being subjected to the analysis framework of Díaz *et al.* (2007). A stepwise approach was used to disentangle the effects of the three groups of predictor variables mentioned above, as suggested by Díaz *et al.* (2007) and by sequentially fitting the influence of different predictors of the environment, CWM, and FD. The objective of our study was to identify the single environmental, CWM, and FD predictors that best predicted plot-level tree growth. In particular, we hypothesized 1) that there are single variables from the three predictor groups (environmental variables, CWM, and FD) that significantly explain tree growth and 2) that, comparing the best predictors from the three groups, the environmental variables have the highest explanatory power for tree growth rate at the early stage of the experiment. To our knowledge, our study is the first to disentangle the effect of environmental variables, CWM, and FD in a biodiversity functioning experiment with trees. Our results are the first ones on trait–EF relationships from all forest diversity experiments worldwide.

## Materials and Methods

### Study site

We conducted our study on a field experiment (BEF-China) in southeast subtropical China (29.08–29.11 N, 117.90–117.93 E). BEF-China is a large-scale biodiversity and ecosystem functioning study on subtropical tree species (Yang *et al.* 2013; Bruelheide *et al.* 2014), which was established on the site of former *Pinus massoniana* and *Cunninghamia lanceolata* conifer plantations that were harvested at ~20-year intervals. After clear-cutting the conifer plantations, aboveground plant biomass was removed from the study site (Yang *et al.* 2013) and a pool of 40 species native to the regional broadleaved forest was established across 38 ha in 2008/2009. The diversity gradient employed comprises monocultures and plots with 2, 4, 8, 16, and 24 species. Here we present the results of one of the two experimental sites (Site A), for which we evaluated data on tree growth measurements from 231 plots (25.8 × 25.8 m) and 23 species planted at the site. We analyzed annual increment of crown diameter as the response variable, which was calculated from two monitoring sessions undertaken in 2011 and 2012 (Li *et al.* 2014). We used data on 23 species, of which 14 and 9 species were deciduous and evergreen, respectively. Accordingly, the majority of species was classified as early successional (Li *et al.* 2014), and none of the species were N<sub>2</sub>-fixing. All growth data were aggregated at the plot level by taking the arithmetic mean of the absolute crown diameter increment across all individuals measured in each plot.

### Assessment of environmental variables

A 5 m digital elevation model (DEM) was established based on differential GPS measurements carried out in 2009. The DEM was used to derive plot mean values for elevation, aspect, mean slope, solar insolation, profile curvature, and plan curvature as descriptions of the environmental conditions (Evans 1979; Zevenbergen and Thorne 1987; Dietrich and Montgomery 1998; Shary *et al.* 2002). Sine and cosine transformations of the aspect were used to express eastness and northness, respectively (Roberts 1986). All calculations were made using ArcGIS 9.0 (ESRI Corp., Redlands, CA).

Soil variables were based on nine soil samples per plot, collected in 2010 by taking soil cores at a depth of 0–5 cm. The nine soil samples per plot were thoroughly mixed, and one bulk sample per plot was analyzed for total carbon (C) and total nitrogen (N) content. Prior to the chemical analysis, soil samples were air-dried and sieved (<2 mm). For the C and N analyses, dry soil samples were ground with a ball mill and subjected to total C/N analysis based on gas chromatography (Vario EL, Elementar, Hanau, Germany). Minimum, maximum, and mean values and standard deviation of all environmental variables is shown in Table S1.

### Assessment of leaf traits

All traits were used to calculate community-weighted means (CWMs) and functional diversity (FD) as predictive variables. These included the following: (1) traits connected to the leaf economics spectrum, such as specific leaf area (SLA) and leaf nitrogen content (LNC); (2) traits related to stomatal conductance, such as maximum and mean stomatal conductance; (3) traits related to xylem properties, such as specific hydraulic conductivity of the xylem ( $K_s$ ) and the xylem pressure at which 50% loss of the maximum specific hydraulic conductivity occurred ( $\Psi_{50}$ ); and (4) leaf microscopic traits, such as stomata density and thickness of the palisade parenchyma. In assessing leaf traits, only sun-exposed, fully developed, and nondamaged leaves were sampled, with at least five individuals per species being sampled. Traits related to stomatal conductance were extracted from diurnal measurements on tree individuals from the same experiment. Traits directly related to stomatal conductance, such as stomata density and size, were assessed on the same leaves from which measurements of stomatal conductance were taken. Three individuals per species were sampled to generate the xylem dataset. The wood traits were measured on the same wood samples that were assessed for xylem hydraulic measurements. The complete trait datasets and the specific measurement pro-

protocols were provided by Kröber and Bruehlheide (2014); Kröber et al. (2014a,b).

## Statistics

To test for spatial autocorrelation between the plots, Moran's  $I$  was calculated, using the *ape* package in R (<http://cran.r-project.org/web/packages/ape/index.html>). To test for interrelationships between all traits, we calculated Gower's distance between traits, which allows for the processing of traits of different scales using the *ade4* package of R (Dray & Dufour 2007). Thereafter, a principal coordinate analysis (PCoA) was carried out, and the correlations between traits and PCoA axes were obtained by post hoc correlation using the *envfit* function in the *vegan* package (Oksanen et al. 2013).

CWM values of traits were calculated according to Garnier et al. (2004) and  $FD_Q$  (Rao's quadratic entropy) according to Botta Dukát (2005). Both CWM and  $FD_Q$  were weighted by the frequency of the tree species in each plot. According to the design of the BEF-China experiment, all tree species in each plot were represented by the same number of trees. However, due to mortality, the number of trees per species on which growth rates were measured varied somewhat, so we made sure that the same proportions of trees that were used to calculate plot means of crown diameter growth rates were also used for calculating CWM and  $FD$ . All predictor variables were scaled by mean and standard deviation, which allowed for the interpretation of the effect sizes with regard to their importance on crown width growth rate. In a first step, we analyzed the impact of each single predictor on crown diameter increment using separate linear models. We then tested the trait complexes in combination according to Díaz et al. (2007) for their explanatory power in

predicting crown growth. As many different trait combinations can equally explain plant growth (Marks and Lechowicz 2006a,b), we tested all possible combinations of the predictor variables and then selected the best model that had a maximum of five predictor variables based on Akaike's information criterion, corrected for small sample sizes (cAIC) using the *MuMIn* package in R (Barton 2014). The independent effect of each predictor variable in the final model on crown growth was assessed by plotting the residuals of crown width growth rates against this predictor variable. The residuals were obtained from a model that contained all predictors except the focus variable. Finally, to test the impact of the three predictor groups (environment, CWM and  $FD$ ), we applied variance partitioning with all the significant predictors using the *vegan* package in R (Oksanen et al. 2013). For all statistical analyses, we used the software R version 3.1.0 (R Core Team 2014).

## Results

The analysis of spatial autocorrelation of tree crown diameter increment showed a Moran's  $I$  value of 0.0059, which was not significantly different ( $P = 0.1128$ ) from the expected value ( $-0.0044$ ). Contrary to our expectations, environmental factors had no significant effects on plot means of annual crown width growth rates (Table 1). The best environmental predictor was slope inclination (SLOPE), which nonetheless only had a marginally significant effect on crown width (CW) growth rates ( $P = 0.091$ ). Testing for combinations of all environmental variables in all possible multipredictor models, the minimal model only retained altitude and eastness, both of which had a negative impact on tree growth (Table 3). This means that the plot mean of tree crown diameter

**Table 1.** Impact of environmental variables on crown growth.

Abbreviation	Predictor	Source	Estimate	$r^2$	$P$
ALT	Altitude	DEM	-0.05	0.01	0.11
SLO	Slope	DEM	-0.38	0.01	0.09
SOLAR	Solar radiation	DEM	0.00	0.00	0.31
CURV X	Profile curvature	DEM	0.02	0.00	0.50
CURV Y	Plan curvature	DEM	0.00	0.00	0.94
NORTH	Aspect northness	DEM, cosine of slope	-0.47	0.00	0.81
EAST	Aspect eastness	DEM, sine of slope	-3.62	0.01	0.11
PH	Soil pH (KCl)	Soil sampling, pH electrode	0.80	0.00	0.92
N	Soil nitrogen content	Soil sampling, total CN analyzer	13.99	0.00	0.71
C	Soil carbon content	Soil sampling, total CN analyzer	-0.28	0.00	0.88
CN	Soil carbon nitrogen ratio	Soil sampling, total CN analyzer	-0.31	0.00	0.62

The effect of environmental predictors on crown width growth rate, assessed as plot mean values between 2011 and 2010. All environmental variables are scaled by mean and standard deviation; as such, the estimates show the direction and magnitude of impact on CW growth rates. DEM: digital elevation model.

growth at the plot level was larger at low elevations (valleys and foot slopes) and on west-facing slopes than high elevations and east-facing slopes (Fig. 1). However, the minimal environmental model only explained 3.8% of the total variation in crown width growth rates (Table 3).

The results of the principal coordinate analysis (PCoA) of all 41 traits are shown in Figure 2A,B for axis one versus two and one versus three, respectively. The first axis reflected the leaf economics spectrum with leaf toughness and C/N ratio versus SLA, while the second axis was characterized by wood density and LDMC and the third axis by leaf hydraulics. Numerous traits had significant effects on plot tree growth, which was also evident by the inclusion of many CWM and FD predictors in the minimal multiple regression models (Table 3). In total, 25 and 15 of the 41 variables produced significant single predictor models for CMW and FD, respectively (Table 2). The best single CWM predictor for CW growth rates was number of palisade parenchyma layers (PALSTR,  $r^2 = 0.24$ ), while the best FD predictor was the presence of extra-floral nectaries (EXTRAFLOREAL,  $r^2 = 0.10$ ), a trait only encountered in four of the 23 species (i.e., *Diospyros japonica*, *Melia azedarach*, *Triadica cochinchinensis*, and *T. sebifera*, Table S2). Many significant CWM predictors were typical traits of the LES, such as specific leaf area (SLA), leaf nitrogen, potassium and magnesium content (LNC, K, MG), and the leaf carbon to nitrogen ratio (CN). However, except for magnesium, these variables had lower estimates compared to morphological and anatomical variables such as leaf toughness, leaf dry matter content (LDMC), leaf thickness, the presence of a subepidermis, number of palisade parenchyma layers, and the presence of a column of sclerenchyma cells through the leaf (Table 2). In the minimal multipredictor model (Table 3), some of these variables, such as water potential (WPOT), stomata size (STOMSIZE), or wood density (WOODDENS), had positive effects on crown width growth rates, while leaf toughness (LEAFT) and leaf mag-

nesium content (MG) had negative effects (Fig. 3). A principal component analysis revealed that trait interrelationships did not influence the final minimal model (see PCA scores in Table S3A, S3B, S3C).

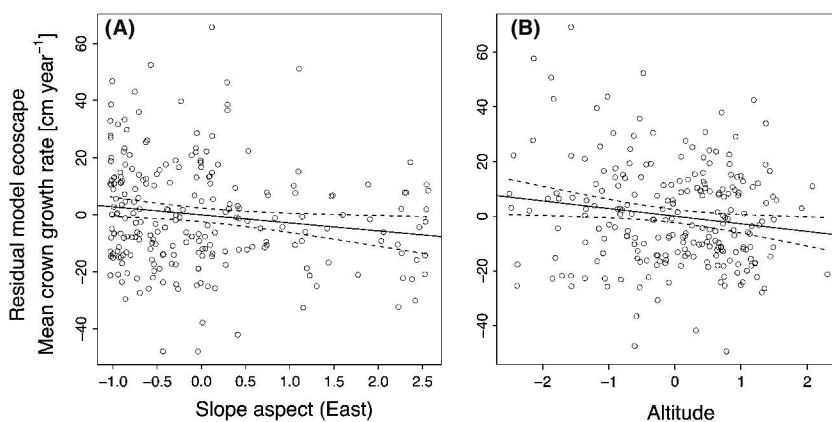
Significant FD variables were essentially a subset of the significant CWM variables, except for wood density, leaf area (LA), leaf calcium content (CA), the ratio of palisade to mesophyll layer thickness (LOG10RATIO), and the presence of extra-floral nectaries (EXTRAFLOREAL), for which only FD but not CWM had a significant effect on CW growth rate. In addition, there were two variables, hydraulic conductance ( $K_s$ ) and vein length (VEINLENGTH), for which FD had a higher explanatory power than CWM.

Interestingly, the minimal multipredictor model for the FD-growth relationship included variables with both positive (WPOT, VEINLENGTH, EXTRAFLOREAL) and negative effect sizes, such as stomata index (STOIND) and number of palisade layers (PALSTR, Fig. 4).

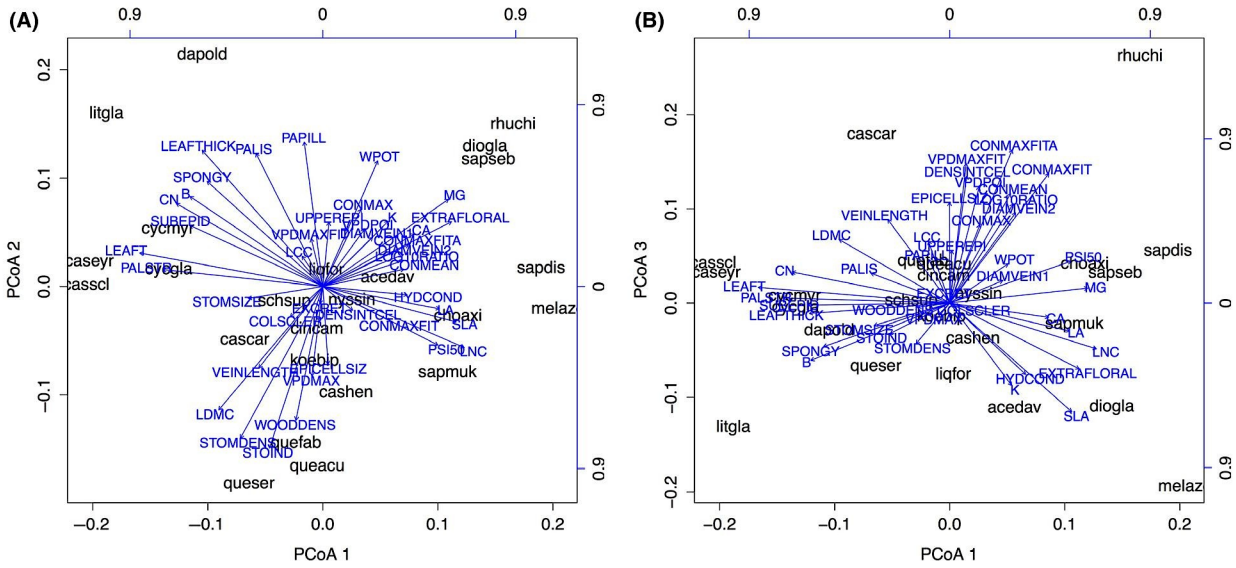
In combination, the three best multipredictor models of environment, CWM, and FD explained 51% of variation of plot-level crown width growth rates (Fig. 5). CWM explained most variation, both in terms of exclusive impact on tree growth that was not captured by environment or FD and in terms of shared variance with environment and FD. For example, of the 31% variance in crown diameter growth explained by FD, two thirds (i.e., 22%) were also shared by CWM predictors. There was almost no variation left that was exclusively explained by environment (1%).

## Discussion

Using the combined information of selected environmental variables, community-weighted means, and functional diversity, we could account for 51% variability of crown width growth rates. Contrary to expectations, no single variable explained crown diameter growth to a sufficient



**Figure 1.** Mean annual crown width growth rate as predicted by the environment multipredictor model. The residuals from all other terms in the model are plotted against (A) slope aspect (East) and (B) altitude. Each dot represents a single plot. All predictor variables are scaled by mean and standard deviation; as such, the slope of the regression shows the direction and magnitude of impact on CW growth rates. The panels have been arranged in the sequence of decreasing order of effect sizes. For statistical details, see Table 3.



**Figure 2.** Principal coordinate analysis (PCoA) biplots of the traits listed in Table 2. (A) PCoA axes 1 and 2, and (B) PCoA axes 1 and 3. See Table 2 for coding of trait names. Eigenvalues: axis 1 = 0.352, axis 2 = 0.236, axis 3 = 0.208, with cumulative proportion of explained variance 20.9, 34.9, and 47.2%, respectively. Species abbreviations refer to genus and species epithet; see supplementary material Table S2 for full species names.

degree. The largest proportion of variance explained by a single variable was 24% (number of palisade parenchyma layers). Nevertheless, our first hypothesis was confirmed as we identified some single key variables for tree growth, albeit with the most powerful ones being based on community mean trait values. In contrast, environmental variables turned out to be weak predictors for crown growth and explained less than 4%, while functional diversity explained up to 31% and community-weighted means up to 42% of crown growth. Thus, we have to reject our second hypothesis of a dominant impact of environment on tree growth at this early stage of the experiment.

The low importance of environment was unexpected, given the high topographic heterogeneity and large size of the experiment. Altitude had a negative impact on tree growth, which was opposite to the findings on initial tree survival at the same site (Yang et al. 2013). Altitude affected productivity in a similar way in the Sardinilla study from central Panama (Healy et al. 2008). In Sardinilla, the single environmental variable with the highest impact on productivity was slope inclination, followed by water drainage quality. Total variance of productivity explained by environment in Sardinilla was 35%. However, the Sardinilla plots only differed by 8 m in altitude, while our site varied by 170 m, but with a total experiment size of 26.7 vs. 8 ha in Sardinilla (Bruehlheide et al. 2014). Interestingly, many environmental variables with reported effects in the literature did not have any significant impact on plot mean crown diameter growth in the BEF-China experiment, such as pH. Soil pH is well-known to limit

nutrient availability (Lambers et al. 2008) and was found to limit tree growth in primeval forests in the Changbaishan in northeastern China (Yang et al. 2009). Increasing soil pH, in addition to increasing elevation, showed negative effects on aboveground biomass increment in tropical Andean forests (Unger et al. 2012).

The negative effect of higher elevation might be explained by a temperature gradient, with lower temperatures at higher elevations being disadvantageous in winter and spring, or lower slope locations being more sheltered from wind. However, there is no indication that elevation has indirect effects via differing soil conditions, as all these did not result in significant models. The fact that higher crown width growth rates were observed in plots on west-facing slopes may be due to the longer lasting effects of morning dew in summer, which might result in lower values of vapor pressure deficit (vpd) in the morning, which in turn would allow trees to have a prolonged period of gas exchange and, consequently, higher rates of carbon assimilation before stomata closure occurs at increasing vpd values. We have to consider that the selection of environmental variables included in this study might not have captured the key environmental drivers for tree growth. For example, direct microclimate measurements would have been desirable; however, we expect that microclimate reflects topography and would show strong differences between north- and south-facing slopes. Similarly, further nutrients would be expected to covary with total soil C concentration, which had no effect on tree growth.



**Table 2.** Impact of CWM and FD on crown growth.

Abbreviation	Predictor	Source	CWM			FD		
			Estimate	$r^2$	$P$	Estimate	$r^2$	$P$
PSI50	Loss of 50% initial flowrate	Scholander pressure bomb	0.84	0.00	0.50	-0.40	0.00	0.75
$K_s$	Maximum flowrate	Laboratory measurements	2.46	0.02	0.05	5.19	0.08	0.00
B	Parameter b (Sigmoid Regression)	Scholander pressure bomb	-6.20	0.11	0.00	-3.44	0.03	0.01
CONMEAN	Average stomatal conductance	Steady state porometer	5.27	0.08	0.00	2.66	0.02	0.03
CONMAX	Maximum stomatal conductance	Steady state porometer	3.99	0.05	0.00	1.21	0.00	0.33
VPDMAX	Vpd at CONMAX	Steady state porometer	-0.82	0.44	0.51	-0.32	0.00	0.80
CONMAXFIT	Relative fitted Max. stomatal conductance	Steady state porometer	2.32	3.57	0.06	1.62	0.01	0.19
CONMAXFITA	Absolute fitted Max. stomatal conductance	Steady state porometer	5.00	0.07	0.00	2.73	0.02	0.03
VPDMAXFIT	Vpd at CONMAXFIT	Steady state porometer	1.73	0.01	0.16	0.25	0.00	0.84
VPDPOI	Vpd at point of inflection of fitted stomatal conductance	Steady state porometer	0.50	0.00	0.69	0.29	0.00	0.81
WOODDENS	Wood density	Laboratory measurements	0.42	0.00	0.74	4.42	0.06	0.00
WPOT	Water potential	Scholander pressure bomb	7.74	0.17	0.00	4.68	0.06	0.00
LA	Leaf area	Laboratory measurements	1.10	0.00	0.38	4.55	0.06	0.00
LDMC	Leaf dry matter content	Laboratory measurements	-7.24	0.15	0.00	2.09	0.01	0.09
SLA	Specific leaf area	Laboratory measurements	4.05	0.05	0.00	0.66	0.00	0.59
LEAFT	Leaf toughness	Leaf toughness device	-7.65	0.17	0.00	-0.40	0.00	0.75
STOMDENS	Stomata density	Microscope	-3.40	0.03	0.01	1.80	0.01	0.15
STOMSIZE	Stomata size, ellipse from stomata length and width	Microscope	1.87	0.01	0.13	1.24	0.00	0.31
STOIND	Stomata index	Microscope	-2.95	0.02	0.02	1.82	0.01	0.14
LNC	Leaf nitrogen content	CN analyzer	2.88	0.02	0.02	-1.99	0.01	0.11
LCC	Leaf carbon content	CN analyzer	0.62	0.00	0.62	0.73	0.00	0.56
CN	Leaf carbon nitrogen ratio	CN analyzer	-3.48	0.03	0.00	-0.80	0.00	0.52
CA	Leaf calcium content	Atom absorption spectrometer	-1.55	0.01	0.21	3.35	0.03	0.01
K	Leaf potassium content	Atom absorption spectrometer	4.30	0.05	0.00	-0.19	0.00	0.88
MG	Leaf magnesium content	Atom absorption spectrometer	6.78	0.13	0.00	1.27	0.00	0.31
DIAMVEIN1	Diameter veins 1st order	Microscope	2.41	0.02	0.05	0.79	0.00	0.53
DIAMVEIN2	Diameter veins 2nd order	Microscope	3.88	0.04	0.00	2.75	0.02	0.03
VEINLENGTH	Length of first-order veins per cm <sup>2</sup>	Microscope	-3.09	0.03	0.01	4.49	0.06	0.00
UPPEREPI	Upper epidermis thickness	Microscope	-1.28	0.00	0.30	0.78	0.00	0.53
PALIS	Palisade parenchyma thickness	Microscope	-3.73	0.04	0.00	2.70	0.02	0.03
SPONGY	Spongy parenchyma thickness	Microscope	-3.88	0.04	0.00	1.42	0.01	0.25
LOG10RATIO	Log ratio of the palisade to spongy parenchyma thickness	Microscope	0.28	0.00	0.82	2.81	0.02	0.02
LEAFTHICK	Leaf thickness	Microscope	-5.33	0.08	0.00	1.57	0.01	0.21
SUBEPID	Presence of a subepidermis	Microscope	-5.32	0.08	0.00	-3.96	0.04	0.00
EPICELLSIZ	Ratio of the cell size of upper and lower epidermis	Microscope	4.58	0.06	0.00	-2.37	0.02	0.05
PALSTR	Number of palisade parenchyma layers	Microscope	-9.10	0.24	0.00	-1.01	0.00	0.41
EXCRET	Presence of excretory glands	Electron microscope	-0.11	0.00	0.93	0.05	0.00	0.97
DENSINCEL	Density of spongy parenchyma	Microscope	1.33	0.01	0.28	2.35	0.02	0.06
COLSCLER	Presence of a column of sclerenchyma cells through the leaf	Microscope	-5.30	0.08	0.00	-3.93	0.04	0.00
PAPILL	Presence of papillae	Electron microscope	-3.06	0.03	0.01	0.36	0.00	0.77
EXTRAFLORAL	Presence of extra-floral nectaries	Observation	1.85	0.01	0.13	5.96	0.10	0.00

The effect of community-weighted mean (CWM) values and functional diversity (FD) of single traits on crown width (CW) growth rate, assessed as plot mean values between individual differences crown width in 2011 and 2010. All variables are scaled by mean and standard deviation; as such, the estimates show the direction and magnitude of impact on CW growth rates.

**Table 3.** Multipredictor model coefficients for environmental variables, CWM, and FD.

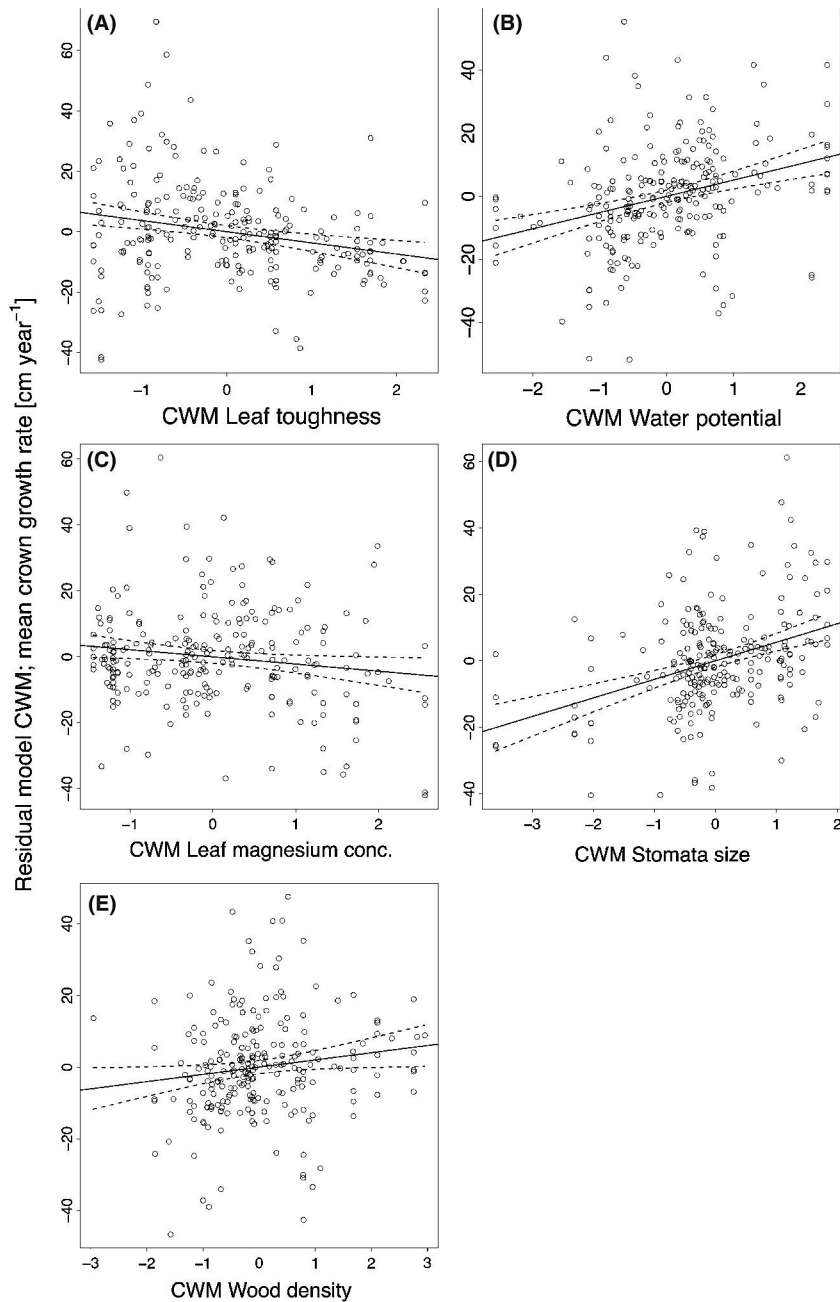
Model	$r^2$	Significant predictors	Abbreviation	Estimate	$P$
Environment	0.04	Altitude +	ALT	−0.08	0.0129
		Aspect (east)	EAST	−6.03	0.0125
CWM	0.44	Leaf toughness +	LEAFT	−14.5	<0.001
		Leaf magnesium content +	MG	−11.1	<0.001
		Stomata size +	STOMSIZE	7.2	<0.001
		Wood density +	WOODDENS	2.9	0.0103
		Water potential	WPOT	13.0	<0.001
FD	0.31	Extra-floral nectaries +	EXTRAFLOREAL	3.93	0.0011
		Number of palisade layers +	PALSTR	−8.41	<0.001
		Stomata index +	STOIND	−11.46	<0.001
		Vein length +	VEINLENGTH	9.27	<0.001
		Water potential	WPOT	12.14	<0.001
Combined	0.51	Altitude + aspect (east) + leaf toughness + leaf magnesium content + stomata size + wood density + water potential + extra-floral nectaries + number of palisade layers + stomata index + vein length + water potential			

Results of the minimum multipredictor models for environmental variables, community-weighted mean (CWM) values, and functional diversity (FD) and the overall model combining these three multipredictor models. All variables are scaled by mean and standard deviation; as such, the estimates show the direction and magnitude of impact on CW growth rates.

With respect to community-weighted means (CWMs), we found traits of the leaf economics spectrum (LES) to affect tree growth, with a positive effect shown for specific leaf area (SLA) and leaf magnesium content (MG). Nonetheless, morphological and anatomical traits, such as leaf toughness and thickness, number of palisade parenchyma layers, and the presence of a subepidermal layer, had a higher explanatory power than typical LES traits. The number of palisade parenchyma layers had already been identified as a good proxy for maximum stomatal conductance (CONMAX) (Kröber *et al.* 2014a), and thus, increasing tree growth would have been expected with increasing number of palisade parenchyma layers. The best 5-predictor model for CWM variables comprised two traits of leaf morphology (leaf toughness and stomata size) and one of plant hydraulics (water potential), while only Mg concentration (MG) was included as a typical LES trait and wood density as a key trait of the wood economics spectrum (Baraloto *et al.* 2010; Freschet *et al.* 2010; Martínez-Cabrera *et al.* 2011). This complex of morphological, anatomical, and physiological traits supports the idea that integrating more and novel functional traits might increase the predictability of ecosystem functioning and, consequently, the reliability of products based on these relationships, such as dynamic vegetation models (Scheiter *et al.* 2013). As the different variables in the multipredictor model explained additional variation in crown width growth rates, they were not fully collinear to each other, showing that the leaf and wood economics

spectrum did not perfectly match (Baraloto *et al.* 2010). The comparably low explanatory power of LES traits on tree growth in the single predictor models and their contrasting role in the multipredictor model challenges the assumption of a universal positive growth–LES effect on tree growth. Trees may also behave differently from herbaceous plants, particularly where strong positive growth–LES relationships have been described (Grime and Hunt 1975; Poorter and van der Werf 1998). The low predictive power for tree growth has been recently demonstrated in a meta-analysis that estimated size-standardized relative growth rates for 278 tree species from 27 sites around the world and found no significant relationship to SLA or wood density (Paine *et al.* 2015). Another variable in the best multipredictor model was stomata size, which enables species to attain maximum stomatal conductance at low vpd values (Kröber and Bruelheide 2014). Furthermore, tree crown growth was positively related to xylem water potential measured in the field, showing that species grew more vigorously when they were able to keep their water status at a more moderate level. This was also reflected in leaf toughness, which had the highest explanatory power in the multipredictor model and can be interpreted as a key defense trait against herbivores (Kursar and Coley 2003). In our model, species grew better when they invested less in physical defense.

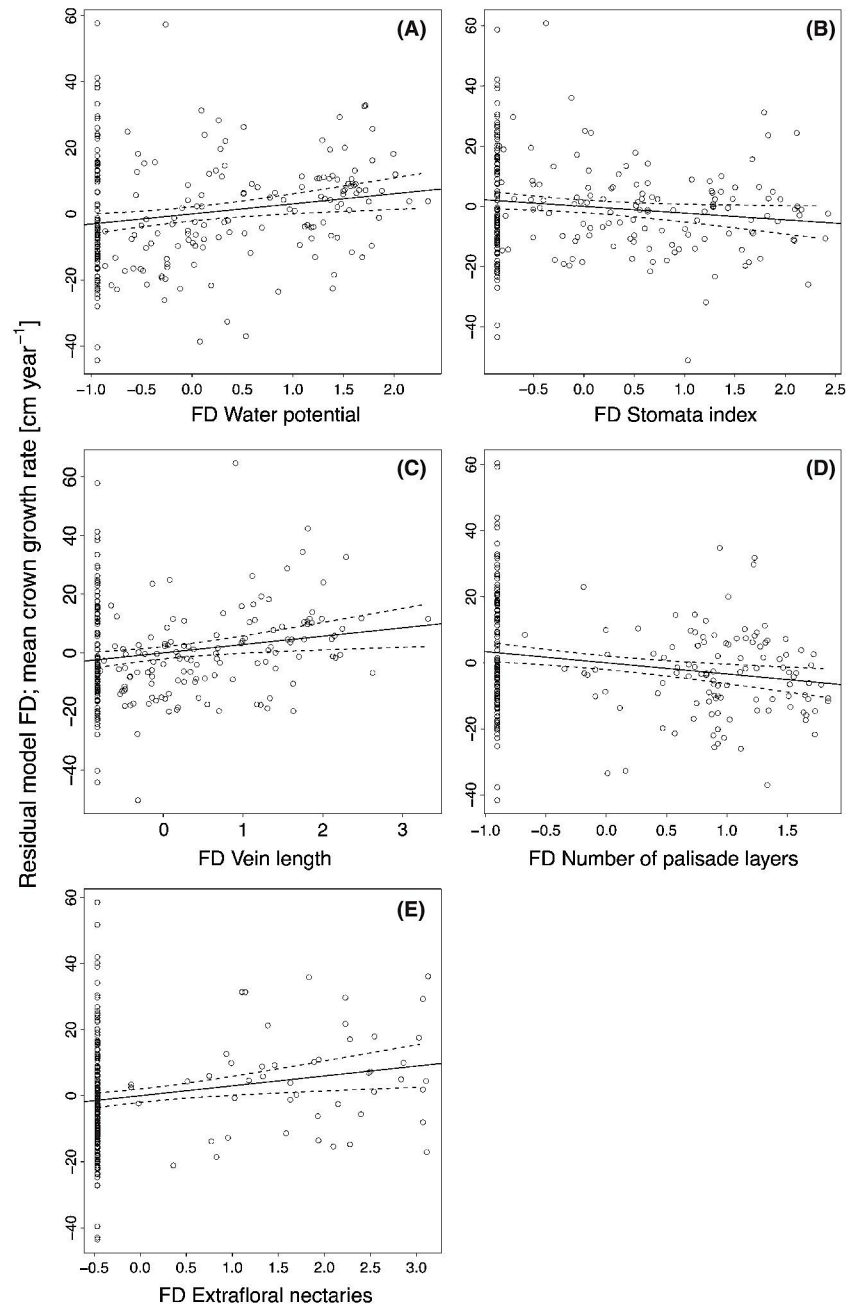
Although we encountered approximately three times the amount of significant relationships between CWM



**Figure 3.** Mean annual crown width growth rate as predicted by the CWM multipredictor model. The residuals from all other terms in the model are plotted against (A) leaf toughness, (B) water potential, (C) leaf magnesium content, (D) stomata size, and (E) wood density. Every dot represents one plot. All predictor variables are scaled by mean and standard deviation; as such, the slope of the regression shows the direction and magnitude of impact on CW growth rates. The panels have been arranged in the sequence of decreasing order of effect sizes. For statistical details, see Table 3.

than FD to single traits, there were several FD traits that showed significant effects on crown diameter increment that complimented CWM effects. The significance of FD at this early stage shows that effects of complementarity in resource use have already emerged. In principle, the traits with significant FD effects on tree growth can be thought to operate through spatial complementarity, such as wood density and leaf area. The joint occurrence of species with low and high investment in wood allows a community to quickly build up tall canopies with fast-growing species while forming a second layer of more

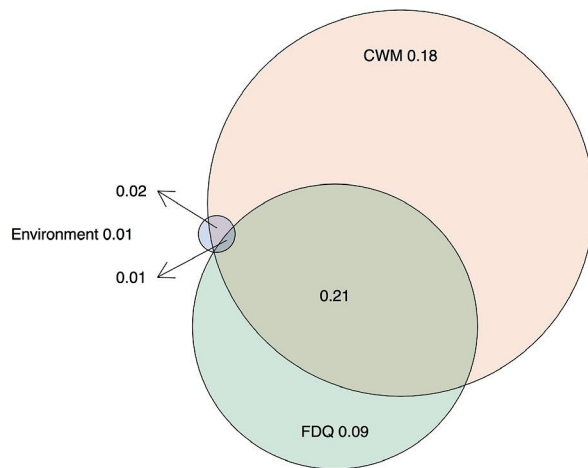
slowly growing, durable-wood species. In Iberian forests, canopy trees with denser wood had lower maximum height and wider crown widths (Poorter *et al.* 2012b). As wood density and physiological strategies of trees are closely related (Santiago *et al.* 2004), a wide range of wood density in a plot might increase the total amount of resources captured in this plot. Leaf area plays a central role in leaf trait relationships because the mass-normalized traits in the leaf economics spectrum are proportional to leaf area (Osnas *et al.* 2013). Thus, leaf area might represent a sum variable that captures variance in



**Figure 4.** Mean annual crown width growth rate as predicted by the FD multipredictor model. The residuals from all other terms in the model are plotted against (A) water potential, (B) stomata index, (C) leaf vein length, (D) number of palisade parenchyma layers, and (E) the presence of extra-floral nectaries. Every dot represents one plot. All predictor variables are scaled by mean and standard deviation; as such, the slope of the regression shows the direction and magnitude of impact on CW growth rates. The panels have been arranged in the sequence of decreasing order of effect sizes. For statistical details, see Table 3.

other variables in the LES as well as morphological traits, such as palisade parenchyma thickness (PALIS) and the palisade to mesophyll ratio (LOG10RATIO). Particularly in young plantations, large-leaved species can quickly increase a stand’s leaf area index, while species with smaller leaves follow a more invariable investment strategy. Studies on crown filling in the BEF-China experiment are still ongoing, but results from natural forests revealed that diverse plots have a higher crown overlap than species-poor plots (Lang et al. 2012). Species with small leaves

also tend to be evergreen (Kröber et al. 2014a) and may also be complementary to large-leaved deciduous species in time. In our study, traits that potentially contribute to temporal complementarity were all related to plant water relations, such as specific hydraulic conductance of the xylem ( $K_S$ ), xylem water potential, leaf vein length and diameter, and leaf stomatal conductance. FD in these water flux-related traits can increase growth rates where some species display high carbon assimilation rates under optimal humid conditions, while others continue with



**Figure 5.** Plot of the partitioned variance explained by the three different variable complexes, green = environment, purple = CWM, light blue = FD; values below 0.01 not shown. For statistical details, see Table 3.

carbon sequestration in dry spells, which frequently occur in summer at the experimental site (Zhou et al. 2011, 2013). Interestingly, FD of some traits also had negative effects on crown width growth rates, such as slope of the xylem vulnerability curve (B), the presence of a subepidermis, and the presence of columns of sclerenchyma cells in the leaf. In principle, negative estimates of FD can only be interpreted as corroborating the CWM signal of these traits, which was also negative in all these cases. While positive FD effects can only arise when growth is higher in mixtures than in monocultures, irrespective of the traits considered, negative FD effects only occur when the traits considered promote growth toward the extreme values where CWM and FD show a strong covariation (Dias et al. 2013). In addition, some traits may act through facilitation, that is, by enhancing the growth of different species' individuals. Such a trait is most likely to be the presence of extra-floral nectaries, which was the FD trait in the single predictor models with the highest impact on crown width growth. Interestingly, the presence of one of the four species with such nectaries in a plot increased overall plot mean crown growth rates. Extra-floral nectaries have previously been shown to have large effects on plant performance through ant-plant mutualism, as ants attracted by extra-floral nectaries have been found to reduce infestation levels of herbivores (Oliveira 1997). While the presence of extra-floral nectaries be beneficial for the target plant itself (Kersch-Becker et al. 2013; Pereira and Trigo 2013), they may have positive effects at the community level (Koptur 1992). The multipredictor model for the FD-growth relationship included the presence of extra-floral nectaries, which can be interpreted as facilitation. Further variables included in the

model point to temporal complementarity, while most variables related to spatial complementarity did not enter the final model.

Combining environment, CWM, and FD in the overall model confirms that environment has a very minor bearing on tree growth, which contrasts with Li et al. (2014), who carried out single-tree-level analyses at the same site and using the same crown width growth data as that for our study. This indicates that individual trees respond much more strongly to topography and soil than plot-level mean growth. However, the overall contribution of soil variables, such as C and N content, on individual tree growth was also low at the single tree level (Y. Li, unpubl. data). A further reason for the discrepancy between plot and single-tree-level data was that Li et al. (2014) treated species as a random factor and consequently assigned all trait differences between species to random variation, whereas we accounted for such differences in CWM functional traits. Similarly, FD was also only partially represented in the single-tree models of Li et al. (2014) by including Shannon diversity of the local neighborhood, which was found to not contribute to explaining crown growth. Thus, FD may capture more unexplained variation than Shannon diversity. In addition, FD effects may only play out when scales larger than the immediate neighborhood are considered, that is, on whole plots that contained 400 tree individuals.

It should also be noted that the environmental variables included in our study did not sufficiently reflect resource supply. While many variables showed only a very low amount of variation among plots, such as soil pH, other soil variables such as nitrogen content or carbon to nitrogen ratio might reflect the preplanting conditions of the conifer plantations of *Pinus massoniana* and *Cunninghamia lanceolata*, which may have levelled out differences among plots. As such, some key variables for tree growth such as phosphorus supply have been excluded in our study. However, considering that soil variables are known for their strong spatial autocorrelation (Hengl et al. 2004), we would not expect them to have such a large impact on crown diameter increment, as this response variable was randomly distributed in space.

Although our overall model explained 51% of variation in plot-level crown growth, a substantial amount of variation in the growth-trait relationship remained unexplained, which is typical of tree growth studies (ter Steege 2003; Poorter et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2010; Rüger et al. 2012). Possible causes for unexplained variation might include negative biotic interactions such as pathogens or herbivores, both of which reduce potential growth rates. As such, field studies most probably produce different conclusions to that of greenhouse trials, which assess potential growth rates under the

exclusion of biotic interactions and show strong relationships to functional leaf traits (Böhnke and Bruehlheide 2013). Moreover, juvenile trees may allocate resources to the expansion of their root system for several years without showing any substantial aboveground growth, especially in dry or nutrient-poor forests (Poorter *et al.* 2012a).

## Conclusion

It is important to note that our study was conducted at an early stage of the experiment, at which time the system is neither stable nor in equilibrium, and as trees continue to grow, tree–tree interactions will become increasingly intense. At present, forest growth is still dominated by CWM effects, but an increasing impact of FD at the expense of CWM effects may be expected in the future. The role of the environment is, however, unpredictable. A distinction can be made between environmental variables that are temporally invariable (such as slope, aspect, elevation) and those that are dynamic (such as microclimate, content of soil organic matter and nutrients, and soil reaction). While invariable abiotic site conditions are not important at present, dynamic environmental variables will become increasingly affected by tree growth. Thus, we expect that tree growth feeds back on this aspect of the environment. In particular, with respect to biodiversity, the dynamic environment can take the form of a positive feedback loop, whereby a higher variation of organisms that depend on higher tree richness modifies the abiotic environment to their own favor. Therefore, it may be the case that diversity creates conditions that are amenable to more diversity. In this respect, the process might be similar to niche construction models for single species discussed by Odling-Smee *et al.* (2003). Where biodiversity has an effect by modifying the environment, an increase in the importance of the dynamic environment components can be expected.

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## Conflict of Interest

None declared.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Plot data.

**Table S2.** Tree species data.

**Table S3.** Principal Component Scores.

## **Chapter 4**

### **Crown and leaf traits as predictors of subtropical tree sapling growth rates**

Ying Li, Wenzel Kröber, Helge Bruelheide, Werner Härdtle and  
Goddert von Oheimb

Article in press, Journal of Plant Ecology

# Crown and leaf traits as predictors of subtropical tree sapling growth rates

Ying Li<sup>1,\*</sup>, Wenzel Kröber<sup>2</sup>, Helge Bruelheide<sup>2,3</sup>, Werner Härdtle<sup>1</sup> and Goddert von Oheimb<sup>4</sup>

<sup>1</sup> Faculty of Sustainability, Leuphana University Lüneburg, Institute of Ecology, Scharnhorststraße 1, D-21335 Lüneburg, Germany

<sup>2</sup> Martin Luther University Halle Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, D-06108 Halle, Germany

<sup>3</sup> German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany

<sup>4</sup> Faculty of Environmental Sciences, Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Pienner Straße 7, D-01735 Tharandt, Germany

\*Correspondence address. Faculty Sustainability, Institute of Ecology, Leuphana University Lüneburg, Scharnhorststr.1, D-21335 Lüneburg, Germany. Tel: +49-35203-383-1329; Fax: +49-35203-383-1266; E-mail: ying.li@uni.leuphana.de

## Abstract

### Aims

Growth rates of plants are driven by factors that influence the amount of resources captured and the efficiency of resource use. In trees, the amount of light captured and the efficiency of light use strongly depends on crown characteristics and leaf traits. Although theory predicts that both crown and leaf traits affect tree growth, few studies have yet to integrate these two types of traits to explain species-specific growth rates. Using 37 broad-leaved tree species of subtropical forests in SE China, we investigated how interspecific differences in wood volume growth rates were affected by crown and leaf traits. We tested the hypotheses that (i) larger crown dimensions promote growth rates, (ii) species-specific growth rates are positively related to leaf stomatal conductance, leaf water potential and leaf chemical components, and negatively related to leaf C/N and leaf toughness and (iii) the two sets of traits better explain growth rates in combination than either alone.

### Methods

Our study was conducted in a large-scale forest Biodiversity and Ecosystem Functioning experiment in China (BEF-China), located in a mountainous region in Jiangxi Province. We related 17 functional traits (two crown dimension and three crown structure traits; six physiological and six morphological leaf traits) to the mean annual growth rate of wood volume of young trees of the studied species. Interrelationships between crown and leaf traits were analyzed using principal component analysis. Simple linear regression analysis was used to test the effect of each trait

separately. We used multiple regression analysis to establish the relationship of growth rate to each set of traits (crown traits, physiological and morphological leaf traits) and to the combination of all types of traits. The coefficients of determination ( $R^2_{adj}$ ) of the best multiple regression models were compared to determine the relative explanatory power of crown and leaf traits and a combination of both.

### Important Findings

The species-specific growth rates were not related to any of the single crown traits, but were related positively to leaf stomatal conductance and leaf water potential individually, and negatively to leaf toughness, with approximately 13% variance explained by each of the traits. Combinations of different crown traits did not significantly explain the species-specific growth rates, whereas combinations of either physiological or morphological leaf traits explained 24% and 31%, respectively. A combination of both crown and leaf traits explained 42% of variance in species-specific growth rates. We concluded that sets of traits related to carbon assimilation at the leaf-level and to overall amount of leaves exposed at the crown-level jointly explained species-specific growth rates better than either set of traits alone.

**Keywords:** BEF China, crown characteristics, physiological leaf traits, morphological leaf traits, wood volume

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## INTRODUCTION

Growth rates of plants are driven by factors that influence the resource availability (light, nutrient and water), the amount of resources captured and the efficiency of resource use (Monteith 1977; Richards *et al.* 2010). Focusing on light resources, the amount of light captured and the efficiency of resource use in trees are mainly determined by crown characteristics and leaf traits (Fichtner *et al.* 2013; Poorter and Bongers 2006; Sterck *et al.* 2001).

The tree crown is composed of structural organs (i.e. branches) and photosynthetic organs (i.e. leaves), and is a key constituent in determining the magnitude of light captured (Sterck *et al.* 2001) and the ability to shade neighboring trees (Lang *et al.* 2010; Simard and Zimonick 2005). Crown attributes (i.e. size and architecture) are, therefore, commonly used in modeling individual tree growth (Mäkelä 1997; Pretzsch 2009). The allocation of biomass to crowns is constrained by mechanistic determinants such as biomechanical stability and hydrodynamic resistance, leading to species-specific crown traits (cf. Poorter *et al.* 2012, van der Sande *et al.* 2015). Moreover, tree crowns are responsive to topographical and edaphic conditions and the size and spatial arrangement of neighboring trees (Lang *et al.* 2010; Li *et al.* 2014b; von Oheimb *et al.* 2011). In a Mexican lowland rainforest, Sterck *et al.* (2003) compared saplings of two shade-tolerant tree species in the forest understory and demonstrated that crown dimension, such as the width and depth of crown and the number of leaves, are simple and reliable predictors of interspecific variation in growth rates. Furthermore, crown structure plays a role in photosynthetic consequences (Kohyama 1987). For example, crown shape (defined as the ratio of crown length to crown diameter) is the result of the spatial organization of branches and foliage (Valladares and Niinemets 2007), which may be related to the efficiency of light utilization (Kuuluvainen and Kanninen 1992). The latter authors found that a narrow crown shape appeared to promote stemwood production per unit of foliage in young Scots pine.

Leaves are of major importance for tree productivity due to their fundamental role in carbon (C) assimilation by means of photosynthesis and transpiration (Wright *et al.* 2004). Leaf physiological and morphological traits are known to reflect the strategies of both resource uptake and resource use efficiency (Reich *et al.* 1999), and thus, these traits are expected to impact plant growth rates. However, photosynthetic rate and efficiency at the leaf-level have also been reported to fail in predicting plant growth, particularly within the same functional group, when other important factors such as dry matter partitioning or canopy structure were not considered (Lambers *et al.* 1998; Paine *et al.* 2015). Still, some single leaf physiological traits are known to be related to plant growth rates (Chaturvedi *et al.* 2011, 2014). For example, leaves of slow-growing species frequently had lower stomatal conductance, transpiration rates and nitrogen (N) concentration than

faster-growing species (cf. Chapin III *et al.* 1993). Regarding leaf morphological traits, specific leaf area (SLA), which quantifies leaf area displayed per unit dry mass invested, is often considered a key factor for plant growth (Lambers and Poorter 1992). This is mainly because SLA is positively associated with the proportion of leaf N allocated to photosynthesis and photosynthetic N use efficiency (PNUE) (Poorter and Evans 1998). A positive relation between SLA and relative growth rate was found along the canopy-understory gradient (Poorter and Bongers 2006), in low irradiance environments (Poorter and van der Werf 1998) and among woody species grown in different habitats (Cornelissen *et al.* 1996). However, Shipley (2002) reported the opposite pattern for trees grown under high irradiance. The author stressed the varying importance of SLA in determining growth rates at different levels of irradiance. Furthermore, if light conditions are equal, shade-tolerant deciduous taxa tend to have higher SLA, while shade-tolerant evergreen taxa tend to have lower SLA as compared to light-demanding species with the same leaf habit (Böhnke and Bruelheide 2013). This indicates that the SLA-growth rate relationship might be inconsistent within particular functional groups in particular growing environments.

The growth rates of trees are species-specific, and these interspecific differences have frequently been viewed as a result of niche differentiation, enabling tree species to coexist and allowing tree communities to be structurally complex (Kohyama 1993; Lang *et al.* 2012). Linking measurable crown and leaf traits to explain species-specific growth rates contributes to a better understanding of the strategies of tree growth and the structure and dynamics of forest communities (Adler *et al.* 2014). However, crown traits have often been used to predict individual growth rates of large trees and canopy trees (e.g. Fichtner *et al.* 2013, but see Takyu 1998), but have rarely been used to contribute to the explanation of interspecific variation in growth rates of young trees. The association between leaf traits and interspecific variations in plant performance has been demonstrated in trees along light gradients (Poorter and Bongers 2006, Wright *et al.* 2010), in the shaded understory of forests (Sterck *et al.* 2003), or under high-light greenhouse conditions (Tomlinson *et al.* 2014). In contrast, few studies have examined how leaf traits drive the species-specific growth of both shade-tolerant and light-demanding tree saplings under uniformly high-light field conditions (Shipley 2002). The full sun environment may substantiate the species-specific growth variations that are large enough to distinguish the growth abilities/strategies of different species (Lambers and Poorter 1992; cf. Tomlinson *et al.* 2014). Under conditions in which light is not limiting, differences in photosynthesis-related crown and leaf traits should determine light capture and light use efficiency, thus affecting growth rates. Moreover, there is little information on how growth rates are driven by functional traits in subtropical forest ecosystems (Paine *et al.* 2015). More importantly, much research effort to date has been spent on crown and, particularly, on leaf functional traits with respect to tree growth rates.

However, information is lacking on the combined effects of crown and leaf traits in explaining the species-specific growth rates (but see [Lida et al. 2014](#); [van der Sande et al. 2015](#)).

In a large biodiversity-ecosystem functioning experiment established in subtropical China (BEF-China, [Bruelheide et al. 2014](#)), growth rates of young individual trees were found to be highly species-specific and strongly affected by initial tree size and local site conditions ([Li et al. 2014b](#)). In this study our main research question was how the interspecific differences in growth rates are explained by crown and leaf traits under open field conditions, where light was not limited at this early stage. We made use of the BEF-China experiment that incorporates 37 native broad-leaved tree species grown in a high diversity of local neighborhoods. This high heterogeneity of local neighborhoods can be expected to result in a diverse range of neighborhood conditions expected under natural stands ([Li et al. 2014b](#)). To address the main research question we tested three hypotheses: (i) species-specific growth rates are related to crown traits. Specifically, larger crown sizes should result in increased growth rates. Faster-growing tree species are characterized by specific crown structures, for example a wider crown shape or a higher ratio of crown width to stem diameter. (ii) Species-specific growth rates are related to particular leaf traits. For instance, growth rates could be positively associated with stomatal conductance, leaf water potential and leaf chemical components, and negatively associated with C/N and leaf toughness. (iii) The two trait types (i.e. crown- and leaf traits) in combination better explain growth rates than either type alone.

## MATERIALS AND METHODS

### Study site

Our research was conducted in the BEF-China experimental site, located in a mountainous subtropical region close to Xingangshan Township, Jiangxi Province (N29°08′–11′, E117°90′–93′), China. At this site, the mean annual temperature is 16.7°C and the mean annual precipitation 1821 mm. The wet season lasts from April to August. The natural vegetation of this region is a subtropical broad-leaved forest with evergreen species in high abundance ([Bruelheide et al. 2011](#)). BEF-China comprises two experimental sites (sites A and B), which were established in 2009 and 2010, respectively. Prior to the experiment, the experimental sites were covered with a plantation of *Pinus massoniana* Lamb. and *Cunninghamia lanceolata* (Lamb.) Hook. After a clear-cut, a total of 566 plots (271 plots at site A and 295 plots at site B) were set up, each with an area of 25.8 × 25.8 m. The relief of both sites is highly variable, with slopes ranging from 0 to 45°. At both sites, each of 24 tree species were planted, with 8 of these species being planted at both sites. Following the broken-stick design ([Bruelheide et al. 2014](#)), six richness levels of 1, 2, 4, 8, 16 and 24 tree species were randomly assigned to 88, 68, 40, 26, 19 and 5 plots at each site. In each plot, 400 (20 × 20) trees were planted at equal horizontally projected distances of 1.29 m.

At the time of the first inventory (1 year after the establishment, see below), the median height and the median crown width were 68 and 40 cm, respectively. Further details on the design and establishment of the BEF-China experiment are given in [Bruelheide et al. \(2014\)](#) and [Yang et al. \(2013\)](#).

### Data sampling and preparation

For the growth and crown measurements, we monitored trees within the central part of every plot, specifically the central 6 × 6 planting positions (i.e. 36 tree positions per plot) in the monocultures and two-species mixtures and the central 12 × 12 planting positions (i.e. 144 tree positions per plot) in the 4-, 8-, 16- or 24-species mixtures ([Li et al. 2014a, 2014b](#)). Total tree height, stem diameter at 5 cm above ground (hereafter GD), crown base height and crown diameter along two cardinal directions (N–S and E–W) were measured annually in September and October from 2010 to 2013 for site A and from 2011 to 2013 for site B. Total tree height was determined with a measuring pole as the length from stem base to the apical meristem. GD was measured with a caliper, and the position of the diameter measurement was permanently marked on the stem with white paint. The bifurcation point of the lowest live crown branch of the tree (excluding epicormics or sprigs) was taken as the crown base. Crown diameters were determined with a measuring tape. These direct measurements were used to calculate the growth rate of wood volume and a set of crown characteristics (see below). In order to avoid confounding species-specific with size-specific effects on growth rates, in the first inventory we only included trees within a narrow range of total height of 41–95 cm (i.e., the median of 68 ± 27 cm). Within this size class, tree height and crown characteristics (the latter are calculated from the first year inventory data, see below) were weakly correlated ( $r < 0.45$ ). Three tree species were removed from the analysis due to low abundance (<5). In total, we included 37 tree species in this study ([supplementary Table S1](#)). The number of tree individuals used for quantifying the growth and crown variables per species ranged from 20 (*Acer davidii*, *Machilus leptophylla*) to 716 (*Castanopsis sclerophylla*), with a mean number of 233 tree individuals per species.

The annual growth rate of wood volume was used to represent the tree growth rate, calculated as  $dV/dt = (V_j - V_i)/(T_j - T_i)$ , where  $V_j$  is the wood volume for the last inventory year  $T_j$  and  $V_i$  is the wood volume for the first inventory year  $T_i$ . The wood volume was estimated as  $V = \text{tree height} \times \pi \times (\text{GD}/2)^2 \times f_c$ , taking account of tree growth in both a horizontal and a vertical direction. The term  $f_c$  is the cylindrical form factor, which is the ratio of total tree wood volume to the volume of a cylinder that has the same height and diameter as the tree ([Husch et al. 2003](#)). The cylindrical form factor varies with stem diameter and age, and was set equal to 0.70, which is an average value for young trees ([Hess et al. 2015](#); [Kramer 1988](#)). We calculated the growth rate of wood volume for each tree individual, and then averaged these values across all individuals of a species to obtain the mean annual growth rate per species (hereafter referred to as growth rate).

Crown length (CL) and crown projection area (CPA) are characteristics that represent crown dimension, and were used to calculate the three crown structure traits, crown ratio (CR), crown length ratio (CLR) and relative crown length (RCL, Table 1). CL was calculated as the difference between total tree height and crown base height. CPA was calculated as an area of ellipse using the crown diameters in two cardinal directions. CLR is the ratio of CL to total tree height. CR is the ratio of mean crown diameter to GD, and RCL is defined as the ratio of CL to mean crown diameter. Crown traits were calculated for each tree individual based on the data from the first inventory and then averaged for each species.

For leaf trait measurements, we randomly selected three to 13 tree individuals per species at the experimental sites. For each tree individual, at least five leaves were sampled and traits measured. All leaves sampled were sun-exposed, fully developed and non-damaged. The trait measurement protocols and the resulting datasets have been described in previous publications (Kröber and Bruelheide 2014; Kröber *et al.* 2014, 2015b). In this study, we selected 12 leaf traits, six physiological and six morphological traits, all of which are commonly used to characterize photosynthetic capacity and growth strategy of plants (Table 1). Physiological leaf traits included leaf mean stomatal conductance ( $g_{s\text{ mean}}$ ), leaf water potential ( $\Psi$ ) measured in spring, mass-based C to N ratio (C/N), leaf calcium, potassium and magnesium concentration

(Ca, K, Mg). Morphological leaf traits included leaf area (LA), leaf dry matter content (LDMC), SLA, leaf toughness (LEAFT), thickness of palisade parenchyma (PALIS) and leaf thickness (LEAFTHICK).

### Data analysis

The coefficient of variation (CV) was calculated as (standard deviation/mean)  $\times$  100% to quantify the interspecific variability of each trait. Principal component analysis (PCA) was used to present the interrelationship between all traits. Pearson correlation was used to obtain the correlation coefficients. We applied simple linear regression analysis to examine the relationships between each single trait and growth rate. All predictor variables and the response variable growth rate were scaled for comparable slopes. Multiple regression analysis was used to establish the relationship of growth rates to either the set of crown traits or physiological and morphological leaf traits or to the combination of traits from all three sets. The best multiple regression model with a maximum of five predictive variables was selected based on Akaike's Information Criterion with a correction for small sample sizes (AICc), using the MuMIn Rpackage (function: dredge). To avoid collinearity only traits that were not redundant ( $r < 0.7$ ) were included in the full model. The best models were controlled for collinearity by using the variance inflation factor (VIF  $< 2.5$ ). The AICc and adjusted  $R^2$  of the best multiple regression models were

**Table 1:** list of crown and leaf traits included in this study

Category	Trait	Explanation	Range	CV (%)	Slope
Crown traits	CL (cm)	Crown length calculated as total height minus crown base height	14.7–73.4	27.3	n.s.
	CPA (cm <sup>2</sup> )	Crown projection area calculated as an ellipse area using crown diameters in N–S and E–W directions	249.0–3647.0	56.1	n.s.
	CLR	Crown length ratio calculated as ratio of crown length to total height	0.2–1.0	24.8	n.s.
	CR	Crown ratio calculated as ratio of crown diameter to stem diameter at ground height	19.5–63.3	21.0	n.s.
	RCL	Relative crown length calculated as ratio of crown length to crown diameter	0.3–3.8	41.1	n.s.
Physiological leaf traits	$g_{s\text{ mean}}$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	Mean stomatal conductance	272.1–1324.2	31.3	3.55*
	$\Psi$ (MPa)	Water potential	(–24.9)–(–4.0)	32.7	3.41*
	C/N	Mass-based C to N ratio	16.4–40.1	18.8	n.s.
	Ca (mg g <sup>-1</sup> )	Leaf calcium concentration	27.1–59.1	16.3	n.s.
	K (mg g <sup>-1</sup> )	Leaf potassium concentration	7.5–36.0	40.8	n.s.
	Mg (mg g <sup>-1</sup> )	Leaf magnesium concentration	2.3–8.8	38.1	n.s.
Morphological leaf traits	LA (mm <sup>2</sup> )	Leaf area	520.2–51 195.7	155.2	n.s.
	LDMC (mg g <sup>-1</sup> )	Leaf dry matter content	290.0–595.6	16.9	n.s.
	SLA (m <sup>2</sup> kg <sup>-1</sup> )	Specific leaf area	7.8–19.6	21.0	n.s.
	LEAFT (N mm <sup>-1</sup> )	Leaf toughness	0.2–1.0	52.9	–3.37*
	PALIS (μm)	Thickness of palisade parenchyma	32.4–129.4	28.7	n.s.
	LEAFTHICK (μm)	Leaf thickness	105.2–366.6	29.0	n.s.

Leaf traits are classified as physiological or morphological traits. Range and relative variability calculated as coefficient of variation (CV = (standard deviation/mean)  $\times$  100%) for each trait are given. Slope: standardized slope of the significant linear relationship between tree growth rate and each single trait. \*\*\* $0 \leq P < 0.001$ , \*\* $0.001 \leq P < 0.01$ , \* $0.01 \leq P < 0.05$ , † $0.05 \leq P < 0.1$ , n.s.: not significant.

compared to assess the relative importance of the different sets of traits in determining growth rates. In order to ensure that the effect of crown dimensions was not caused by size-specific differences, we included tree size (i.e. initial height) in the models and re-ran the analysis. The results were not altered by the inclusion of tree size in the initial model. All statistical analyses were conducted in R 3.0.2 (R Development Core Team, 2011).

## RESULTS

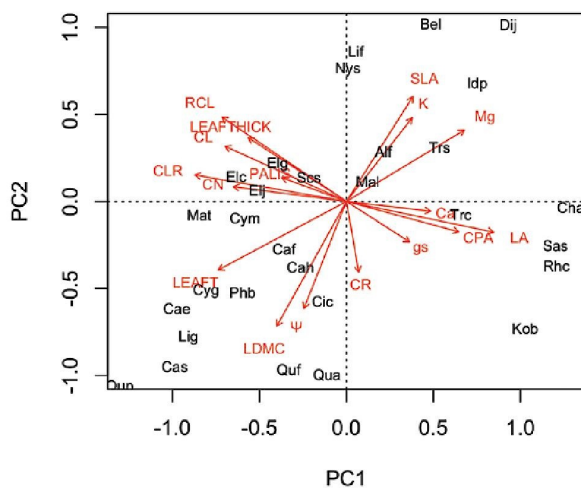
### Interspecific variation

Growth rates varied strongly among the 37 broad-leaved tree species (supplementary Fig. S1). *Meliosma flexuosa* displayed the lowest wood volume growth rates with  $77.7 \text{ cm}^3 \text{ year}^{-1}$ , whereas *Nyssa sinensis* was the fastest-growing species achieving  $1729.2 \text{ cm}^3 \text{ year}^{-1}$ . The average growth rate across all species was  $576.1 \text{ cm}^3 \text{ year}^{-1}$ .

Tree species also differed considerably in terms of crown and leaf traits (Table 1). Tree species were highly variable in CPA (CV: 56.1%) and RCL (CV: 41.1%), but much less so in CL, CLR and CR (e.g. CV of CR: 21.0%). LA showed the largest interspecific variability with a CV of 155.2%. The tree species also varied considerably in LEAFT (CV: 52.9%). Leaf traits that varied least were LDMC, Ca and C/N (CVs: 16.9, 16.3 and 18.8%, respectively).

### Interrelationships between traits

Figure 1 shows the PCA biplot with all 17 traits. The first two PCA axes explained 46.2% of the total variance. Of the crown traits, CL was not related to CPA but positively correlated to CLR ( $r = 0.87^{***}$ ). CPA was positively correlated to CR



**Figure 1:** principal component analysis (PCA) biplot showing the relationships between the species-mean values of all crown and leaf traits (arrows). See Table 1 for the abbreviations of trait names and Table S1 for the abbreviations of species names. Eigenvalues: axis 1 = 5.38, axis 2 = 2.48, with a cumulative proportion of explained inertia of 31.6 and 46.2%, respectively.

( $r = 0.66^{***}$ ) and negatively to RCL ( $r = -0.71^{***}$ ). Tree species with a higher CLR tended to have a higher RCL ( $r = 0.59^{***}$ ) (Fig. 1; supplementary Table S2). Only a few leaf traits were significantly correlated with each other (Fig. 1; supplementary Table S3). PALIS was highly correlated with LEAFTHICK ( $r = 0.81^{***}$ ). The concentration of Ca and Mg were significantly, but moderately correlated with each other ( $r = 0.56^{***}$ ). A moderate negative correlation was also found between SLA and LEAFT ( $r = -0.60^{***}$ ). Between crown and leaf traits, species with larger LA showed lower CLR ( $r = -0.75^{***}$ ), lower RCL ( $r = -0.61^{***}$ ) and shorter CL ( $r = -0.66^{***}$ ) (Fig. 1, supplementary Table S4).

### Predicting growth rates with single crown and leaf traits

Simple linear regression revealed that only three out of 17 traits were significantly related to growth rates (Fig. 2; Table 1). Of these traits, two were physiological leaf traits and one was a morphological leaf trait. None of the crown traits could significantly predict the growth rates observed. The amount of variance of growth rate explained by each single leaf traits was approximately 13% (Fig. 2). The growth rates increased with increasing  $g_{s \text{ mean}}$  (slope =  $3.55^{**}$ ,  $R^2_{\text{adj}} = 0.14$ ) and with decreasing  $\Psi$  (slope =  $3.41^*$ ,  $R^2_{\text{adj}} = 0.12$ ). Tree species with tougher leaves grew more slowly (slope =  $-3.37^*$ ,  $R^2_{\text{adj}} = 0.12$ ).

### Predicting growth rates with different sets of traits

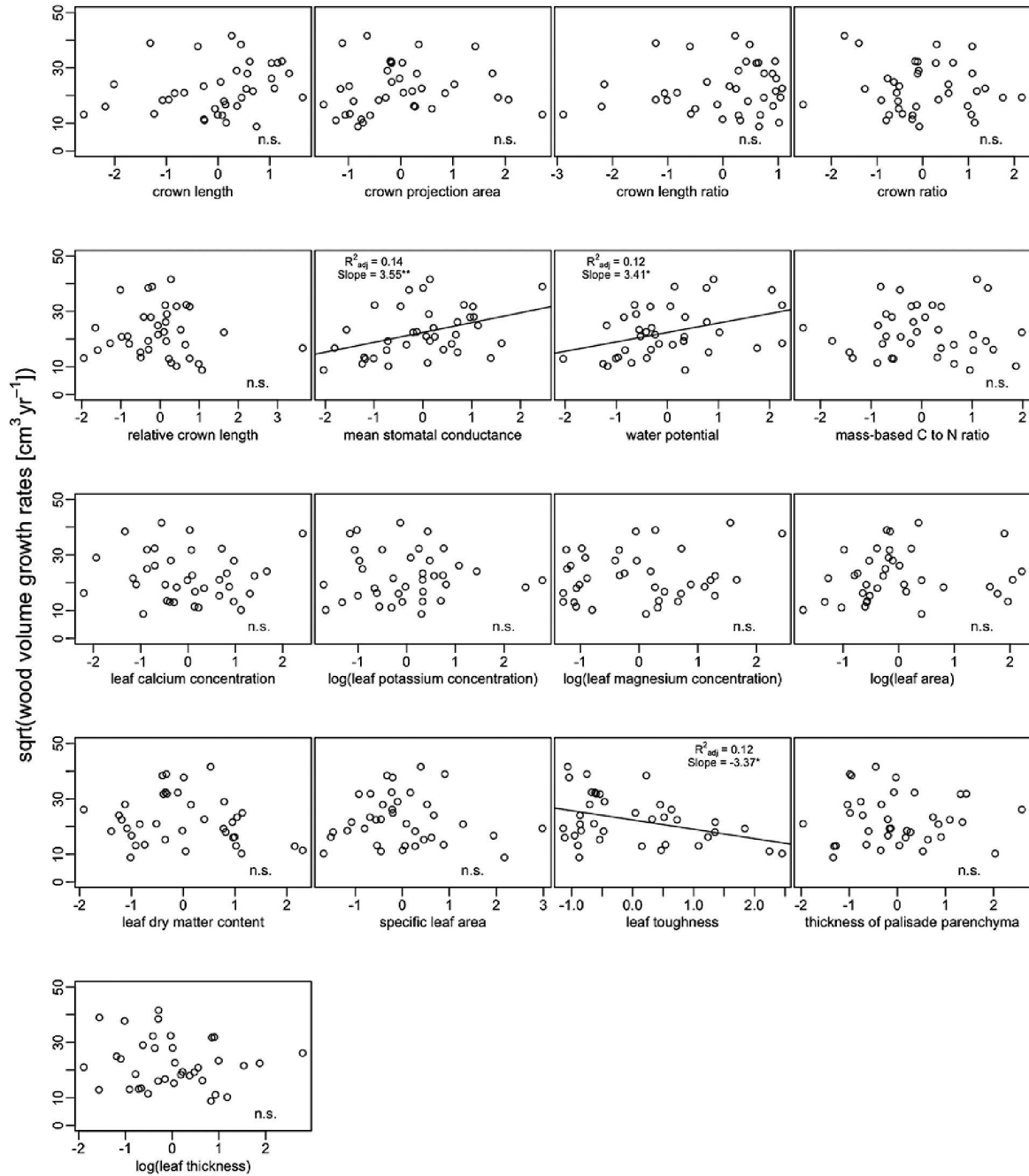
Multiple regression analyses yielded best models that contained two to five predictors for each set of traits (Table 2). The initial models for each set of traits are presented in Table 2. After model selection, none of the crown traits were included in the best crown model. The best physiological leaf traits model showed that  $g_{s \text{ mean}}$  and  $\Psi$  in combination explained 24% of the growth rate variance. Compared to this model, growth rates were better explained by a set of three morphological leaf traits including LA, SLA and LEAFT ( $R^2_{\text{adj}} = 0.31$ ). By combining crown and leaf traits as predictors, 42% of the growth rate variance was explained by the best model (including CL, CPA,  $g_{s \text{ mean}}$ , SLA and LEAFT).

## DISCUSSION

Our 37 tree species exhibited distinctly different growth rates at this early successional stage, where the canopy was not yet fully developed and stratified (Li et al. unpubl. data). The tree species showed large variability in some crown and leaf traits. This considerable variation might explain the differences in growth rates among the studied tree species.

### Species-specific growth rates explained by crown traits

The crown traits used in this study included traits characterizing both crown dimension and crown structure. Our first hypothesis was that tree growth rates are positively affected



**Figure 2:** relationships of wood volume growth rates to all crown and leaf traits included in this study. Wood volume growth rates were square root transformed and all independent variables were standardized. \*\*\* $0 \leq P < 0.001$ , \*\* $0.001 \leq P < 0.01$ , \* $0.01 \leq P < 0.05$ , † $0.05 \leq P < 0.1$ .

by crown dimension and that crown structure explains a significant amount of variance of species-specific tree growth rates. Contrary to our expectations, none of the crown dimension or crown structure traits were able to significantly predict growth rates. Our results suggest that for high-light tree saplings of the same age and size the initial crown characteristics alone seem to have no clear ecological implications

for species-specific growth rates. We explain this from the perspectives of within-crown variations, size-dependency and light conditions. Crown dimension scales positively with total LA per tree, which in turn is positively related to total light absorption (Binkley *et al.* 2013; Chmura and Tjoelker 2008). Nevertheless, the spatial distribution and arrangement of leaves within a crown can strongly modify the efficiency of



**Table 2:** results of the multiple regression analyses for predicting the growth rate of wood volume with crown traits, physiological leaf traits, morphological leaf traits and the combination of all traits

		Predictor included	AICc	$R^2_{adj}$
Crown traits	Full model	CL + CPA + CR		
	Best model	1	269.5	n.a.
Physiological leaf traits	Full model	$g_{s\ mean} + \Psi + C/N + Ca + K + Mg$		
	Best model	$(3.31^*) g_{s\ mean} + (3.15^*) \Psi$	261.7	0.24
Morphological leaf traits	Full model	LA + LDMC + SLA + LEAFT + LEAFTHICK		
	Best model	$(-3.11^*) LA + (-4.90^{**}) SLA + (-7.71^{***}) LEAFT$	260.2	0.31
All traits	Full model	CL + CPA + CR + $g_{s\ mean} + \Psi + C/N + Ca + K + Mg + LDMC + SLA + LEAFT + LEAFTHICK$		
	Best model	$(3.24^*) CL + (-2.79^{***}) CPA + (2.83^*) g_{s\ mean} + (-3.75^*) SLA + (-6.74^*) LEAFT$	257.1	0.42

Full models are the models used to start the model selection. Final models are the models with the lowest value of Akaike's Information Criterion with a correction for small sample sizes (AICc). AICc and  $R^2_{adj}$  values are only depicted for final models. See Table 1 for the abbreviations of the predictors. \*\*\* $0 \leq P < 0.001$ , \*\* $0.001 \leq P < 0.01$ , \* $0.01 \leq P < 0.05$ , † $0.05 \leq P < 0.1$ .

light harvesting per unit foliage area (Cescatti and Niinemets 2004; Jucker et al. 2015). Chen et al. (1994) argued that crowns of different shapes can intercept a similar proportion of the available light because the effects of crown shape can be partly compensated by the differences in geometry and distribution of the foliage that also alter crown light interception. Furthermore, crown architecture is the outcome of a trade-off between the optimization of light harvesting and minimization of mechanical cost (Cescatti and Niinemets 2004). For example, Sterck et al. (2003) showed that crown width of understory saplings (0.5–2.0 m tall) in a lowland rainforest positively affected vertical crown growth and negatively affected horizontal crown growth. Therefore, the potential effects of crown characteristics on growth rates might also be neutralized by other important factors such as the distribution and arrangement of modules; this, however, is beyond the scope of this study. Crown characteristics develop and change during ontogeny by the structural response of each species to different environments (Valladares and Niinemets 2007). Relative growth rates of 145 co-occurring tropical tree species increased with wider crowns, but this relationship disappeared when the stem diameter at breast height (DBH) exceeded 20 cm (Iida et al. 2014). Similarly, van der Sande et al. (2015) found no relationship of total LA to growth rates among emergent tropical canopy trees. We expected crown traits to have an important positive role for sapling performance, as found by Sterck et al. (2003) who examined this in the understory. However, under the well-lit conditions we found that none of the crown traits was important in explaining the interspecific growth variation of young trees.

### Species-specific growth rates explained by leaf traits

Our second hypothesis refers to the finding of positive relationships of  $g_s$ ,  $\Psi$  and chemical components, and negative relationships of C/N and leaf toughness to the variation in growth rates among tree species. Of the 12 leaf traits, two physiological (i.e.  $g_{s\ mean}$ ,  $\Psi$ ) traits and one morphological (i.e.

LEAFT) trait independently explained a significant amount of interspecific variance in growth rates, thus partly confirming our expectations.

With respect to the physiological leaf traits, growth rate has often been reported to be positively related to leaf N and assimilation rates (Kröber and Bruelheide 2014; Poorter and Bongers 2006), thus affecting photosynthetic capacity. In agreement with the latter studies, we found a positive relationship between  $g_{s\ mean}$  and growth rates, as also observed by Chaturvedi et al. (2011) for six tree species in a tropical dry forest and by Poorter and Bongers (2006) for 53 rainforest tree species. Under well-lit conditions, as is the case at our experimental sites, leaves are prone to suffer from dehydration, which impedes photosynthesis. The reduction in  $\Psi$  indicates water deficits in leaves (Jarvis 1976). A positive relationship between  $\Psi$  and stomatal conductance was observed in *Acer saccharum* (Yang and Tyree 1993). Similarly, Ehleringer and Cook (1984) found a linearly decreasing photosynthetic rate of *Encelia farinosa* with declining leaf water potential at high irradiance. In line with our expectation, we found a positive relationship between  $\Psi$  and growth rates. In our study,  $\Psi$  was measured in spring, i.e. during a period with low precipitation but also with low evaporational demand. This relationship might be different if  $\Psi$  was measured during summer in the wet season. Peng et al. (2010) found that relative growth rates of shrub species were negatively related to the C/N ratio under nutrient-enriched conditions. However, contrary to our hypothesis no relation was found between C/N ratio and growth rates in our study, as was also observed by Philipson et al. (2014) who investigated saplings of 15 tropical tree species. Single chemical components (i.e. Ca, K, Mg) also did not influence the species-specific tree growth rates. This finding does not conform to the positive role of K and Mg on plot-based crown growth rates of one of the sites reported by Kröber et al. (2015a).

With respect to the morphological leaf traits, slower-growing species in our study were found to have tougher leaves than faster-growing species. But no other traits (i.e. LA,

LDMC, SLA, PALIS and LEAFTHICK) were correlated with growth rates among tree species. Constructing tough leaves is a way of protecting the leaf physically from external agents (Westbrook *et al.* 2011), in particular from desiccation (Díaz *et al.* 2004), herbivores (Dominy *et al.* 2008) and pathogens (Hantsch *et al.* 2014). Across all tree species, we found a negative relationship between LEAFTHICK and growth rates, supporting our hypothesis. It implies a trade-off between physical resistance and growth. The same pattern was reported by Coley (1988) for tropical saplings in canopy gaps, while Westbrook *et al.* (2011) found that leaf toughness was unrelated to growth rates, whereas it influenced mortality in woody species in the understory of a neotropical forest. Poorter (1999) suggested the more pronounced growth rate differences among species in gaps compared to the shaded understory as an explanation of the negative relationship between leaf toughness and growth rates which was only observed in gaps.

SLA as a measure of the allocation strategy reflects the potential light capture per unit LA, and thus, per unit of organic matter invested into leaves (Wright and Westoby 1999). A positive relation between SLA and plant growth rate has often been reported (Lambers and Poorter 1992; Poorter and van der Werf 1998). For our 37 tree species grown in the high-light environment, SLA alone failed to explain the species-specific growth rates. This might be attributed to the observation that the importance of SLA in explaining growth rates decreases with increasing irradiance (Poorter 1999; Shipley 2002). In line with our finding, Philipson *et al.* (2014) reported no significant association between SLA and seedling growth rates of 15 tropical tree species along different light gradients. Paine *et al.* (2015) found that over a global scale SLA alone may be unsuitable for predicting sapling growth rates. These contradictory results suggest that the SLA–growth relationship might be site-specific. LDMC is a measure of the density of the leaf tissues and thought to be a robust trait for locating plant species on a resource use axis (Wilson *et al.* 1999). LDMC was also reported to be positively related to leaf life span and negatively to relative growth rates (Pérez-Harguindeguy *et al.* 2013). The species-specific growth rates of our tree species were not affected by LDMC, as also found by Chaturvedi *et al.* (2014). It might be due to the low variation in LDMC. Negative relationships between leaf thickness and growth rates have been observed by Nielsen *et al.* (1996) and Poorter (1989). However, neither thickness of the palisade parenchyma nor leaf thickness significantly explained the species-specific growth rates. This result suggests that thin leaves are not necessarily characteristic of fast-growing tree saplings.

### Species-specific growth rates explained by combinations of different trait categories

Combining traits from different categories, we found that leaf and crown traits together increased the explained variance in species-specific sapling growth rates. Among tropical canopy trees, van der Sande *et al.* (2015) found that neither crown- nor leaf-related traits (i.e. total LA, SLA, leaf N) explained

difference in growth rates. They argued that full access to light and better-developed crowns compensated for the possible effects of leaf traits. However, crown width was found by Iida *et al.* (2014) to be a strong positive driver for the relative growth rates of tropical trees with small stem diameters in the dark understory of a lowland rainforest. Given the constant availability of light, growth rates of trees are the product of the interplay between the proportion of light captured and the efficiency of light use, which could be reflected by crown and leaf traits, respectively. Our study tree species during this early stage were probably able to obtain their maximum amounts of light because light was not limited (Poorter 1999; van der Sande *et al.* 2015). Notably, the effects of crown dimensions became significant when combined with leaf traits. We proposed that crown dimensions might further explain the interspecific difference in growth rates of trees that have similar photosynthetic efficiency. In this case, long but narrow crowns further increased the volume growth rates of tree species that had higher leaf stomatal conductance, lower SLA or less tough leaves. This finding corresponds to the strategy of crown construction in open high-light environments that minimizes biomechanical cost and potential damage from photoinhibition by means of narrow and longer crowns (cf. Pearcy *et al.* 2004). In contrast, wider and shorter crowns are preferable in light limited environments as they result in less self-shading (Sterck *et al.* 2003). Confirming our third hypothesis, the combination of crown and leaf traits was the best model to predict the growth rates as it explained more interspecific growth rate variance than traits from either category alone. This result provides empirical evidence for the production ecology equation, i.e. that the growth rates are the integrated outcome of resource captured and resource use efficiency provided by the constant resource availability. The inclusion of functional traits at different organizational levels into one model has rarely been examined. However, plants encounter diverse trade-offs, which are governed by different traits (Iida *et al.* 2014; Sterck *et al.* 2006). Therefore, the species-specific growth rates were better explained by traits that mirror both components of growth rates (i.e. light interception and light use efficiency) than by traits related to just one of the components.

To summarize, at the early stage of this subtropical forest, differences in growth rates among a large number of native tree species were to some extent driven by morphological leaf traits, followed by physiological leaf traits, but not by initial crown characteristics alone. We assume that when light is not limited, the light use efficiency at leaf level is more important in differentiating the species-specific growth rates of young trees than light capture at crown-level. The fact that using a combination of both crown and leaf traits greatly improved growth models reinforces the argument that functional traits at different hierarchical levels, reflecting both light interception and light use efficiency, should be considered when seeking to explain species-specific growth rates, which is in agreement with Poorter (1999). The contrasting relationship

between functional traits and plant growth rates from different studies indicates that there might be no universal combination of traits to adequately explain the species-specific growth rates of different plants or plants under different environmental conditions (e.g. light availability).

## SUPPLEMENTARY MATERIAL

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

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## **Chapter 5    Assessing tree dendrometrics in young regenerating plantations using terrestrial laser scanning**

Ying Li, Carsten Hess, Henrik von Wehrden, Werner Härdtle and  
Goddert von Oheimb

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# Assessing tree dendrometrics in young regenerating plantations using terrestrial laser scanning

Ying Li · Carsten Hess · Henrik von Wehrden ·  
Werner Härdtle · Goddert von Oheimb

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## Abstract

• **Context** Terrestrial laser scanning (TLS) provides a valuable tool for the retrieval of detailed individual-tree structural parameters, but has never previously been applied to young stands under field conditions.

• **Aims** The aim was to explore the performance of TLS in a young tree plantation located in a heterogeneous environment in subtropical China.

• **Methods** We investigated 438 young trees for congruence between direct field and TLS measurements of total tree height, stem diameter at ground height, and length and height of the longest branch using correlation tests. We applied generalized linear models to examine whether congruence was affected by the observed structural parameter or extrinsic factors (e.g., potential occlusion, point cloud quality).

• **Results** TLS made it possible to detect trees higher than 40 cm. The TLS-retrieved data were highly congruent with the

data obtained from direct measurements. The poor descriptions of stems and branches of some individuals of small-sized and leaf-on tree species were due to occlusion by ground vegetation and leaf-on branches. Observed structural parameter and extrinsic factors did not explain the variance between the two approaches.

• **Conclusion** TLS proved to be a promising tool for high-resolution, non-destructive analyses of tree dendrometrics in young regenerating plantations.

**Keywords** BEF-China · Regeneration phase · Subtropical China · Point cloud · TLS

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**Contribution of the co-authors** Ying Li: designed the study, performed the research, analyzed data and wrote the manuscript  
Carsten Hess: performed the research, analyzed data and contributed new methods

Henrik von Wehrden: analyzed data and revised the manuscript

Werner Härdtle: revised the manuscript

Goddert von Oheimb: designed the study, supervised the work and coordinated the research project

Y. Li (✉) · C. Hess · H. von Wehrden · W. Härdtle · G. von Oheimb  
Faculty Sustainability, Institute of Ecology, Leuphana University  
Lüneburg, Scharnhorststr.1, 21335 Lüneburg, Germany  
e-mail: li@leuphana.de

H. von Wehrden  
Center for Methods, Leuphana University Lüneburg,  
Scharnhorststr.1, 21335 Lüneburg, Germany

H. von Wehrden  
Research Institute of Wildlife Ecology, Savoyen Strasse 1,  
Vienna 1160, Austria

## 1 Introduction

Competition for light is broadly recognized as a key factor determining plant growth. In trees, these interactions lead primarily to morphological responses of the crown (Grams and Anderson 2007), because crown dimensions and crown architecture strongly determine the individual's ability to intercept light and to shade neighboring trees (Brisson 2001). Although the expression of crown traits in individual trees is constrained by genetic and mechanical properties, individuals may show plastic responses within certain thresholds as a reaction to local neighborhood interactions or, more generally, to local environmental conditions. Crown responses to these conditions are the aggregate effect of the differential spatial development of single branches (Stoll and Schmid 1998; Sumida et al. 2002). Therefore, detailed information on branching patterns and the growth and mortality of single branches of individual trees as well as on local site conditions are needed to explain and model the spatiotemporal development of crowns (Pretzsch et al. 2011). To obtain this information by direct field measurement is, however, challenging and time-consuming, and thus costly (Fleck et al. 2011). In recent

years, technically intensive high-resolution inventory tools have been used to acquire individual-tree data.

Airborne laser scanning (ALS) techniques have been successfully applied in determining canopy structure (Vehmas et al. 2011) and measuring essential parameters of individual-tree crown characteristics, such as crown base height, crown area and crown volume (Jung et al. 2011). Compared to field measurements, ALS slightly underestimates tree parameters (Zimble et al. 2003). More importantly, ALS is largely restricted to the top canopy layer, whereas the elements in the lower canopy are recorded in less detail due to signal occlusion by upper canopy elements (Hilker et al. 2010; Jung et al. 2011). Furthermore, ALS has some constraints in terms of the fine-scale spatial resolution (in the order of millimeters or a few centimeters) of structural elements (van Leeuwen and Nieuwenhuis 2010).

Terrestrial laser scanning (TLS) has now been established as an alternative approach for measurement of three-dimensional (3D) structural elements of trees (Fleck et al. 2011; Jung et al. 2011; Schilling et al. 2012). TLS is a light detection and ranging (LiDAR) system capable of acquiring 3D structural high-resolution information with a level of detail that is considerably higher than ALS (Lichti et al. 2002). Up to now, TLS has mainly been applied in forest science to analyze standard tree and stand dendrometrics such as stem diameter, tree height, stem position, tree density, basal area and trunk volume (Hopkinson et al. 2004; Dassot et al. 2011). Recently, the use of TLS has been intensified to analyze 3D tree topology, canopy and individual-tree crown structure as well as the wood volume of branches (Bucksch et al. 2010; Dassot et al. 2011, 2012; Schilling et al. 2012). However, as the main interest when conducting forest inventories is in the wood volume of adult trees, TLS applications have focused almost exclusively on adult trees or mature stands. A central task of forest science and forest ecology, however, is the analysis of growth dynamics in the regeneration phase. This phase is often characterized by a high tree density, but also by a mixture of various tree species, and, thus, intensive and complex tree-tree interactions. The processes operating in this early phase of stand development are essential for the future forest structure and composition (Kobe 2006), and hence, it is vital to understand the underlying mechanisms of tree-tree interactions. TLS offers the opportunity to conduct rapid, non-destructive, accurate and extensive measurements of a large number of individual trees over time in order to analyze tree growth dynamics in general, but in particular to investigate the spatial development of crowns in detail (Dassot et al. 2011). To our knowledge, however, the feasibility of TLS to determine growth parameters of young trees under field conditions has never been explored before. We are aware of only one study which applied TLS to investigate juvenile trees, albeit under controlled conditions; this study analyzed 6-year-old beech (*Fagus sylvatica*) trees planted individually in buckets and kept under a roof in an experimental botanical garden (Seidel et al. 2011a). Several

specific challenges are associated with the application of TLS for smaller trees or younger stands: (1) the dimension of the main wood components (i.e., trunk and the first- and second-order branches) may be too small to be resolved at high quality by the laser scanner; (2) the structural density is higher than in adult trees or mature stands, potentially resulting in a relatively high level of occlusion (Dassot et al. 2011); (3) the ground layer vegetation may occlude a substantial part of the individual trees; (4) adverse impact of mild to moderate wind on scan quality is largely restricted to the smallest tree constituents (Côté et al. 2011), which make up a relatively high proportion of young trees' structure.

The aim of our study is to explore the performance of TLS in a young experimental tree plantation in a heterogeneous environment by comparing TLS-derived tree structural data with those obtained by direct field measurements. We conducted the study in the framework of the BEF-China project (BEF: Biodiversity and Ecosystem Functioning). BEF-China is a new forest BEF experiment that was established in subtropical China from 2009 to 2010 (Yang et al. 2013; Bruelheide et al. 2014). A pool of 40 native tree species was planted on 566 plots and a net area of 38.4 ha. Species richness and composition were experimentally manipulated to study their effects on a range of ecosystem functions, including primary productivity, carbon and nutrient cycling, and soil processes. Conventional inventories are conducted annually to study the effect of local environmental conditions such as size and species identity of neighboring trees or slope inclination on individual-tree growth and crown dynamics. Here, we compare the performance of the two approaches, direct field measurements by inventory teams and TLS measurements, to determine the four individual-tree structural parameters total tree height, stem diameter at ground height, length of the longest branch and height of the longest branch.

Specifically, we tested three hypotheses in this study:

- (H1) TLS-derived data are highly congruent with field measurement data.
- (H2) Congruence of data varies with the observed structural parameter, decreasing in the order: total height > stem diameter > length the longest branch > height of the longest branch.
- (H3) Variance of direct field and TLS measurement data can mainly be explained by extrinsic factors (e.g. potential occlusion, point cloud quality).

## 2 Material and methods

### 2.1 Study site

The study site is located in a hilly subtropical region near Xingangshan Township, Jiangxi Province (29.08–29.11 N,

117.90–117.93 E), China. The mean annual temperature is 16.7 °C and the mean annual precipitation 1,821 mm. The potential natural vegetation of this region is subtropical broad-leaved forest with evergreen species dominating in abundance (Bruelheide et al. 2011). Each of the 556 plots in the BEF-China experiment has a projected area of 666.7 m<sup>2</sup> (25.8 × 25.8 m) and was planted with 400 tree saplings (20 × 20) in 2009 and 2010, resulting in a total of 219,200 trees (detailed descriptions of the experimental design are given by Yang et al. 2013; Bruelheide et al. 2014). The horizontal planting space is 1.29 m, resulting in a stem density of 6,000 trees ha<sup>-1</sup>. The plot tree species richness levels are 1, 2, 4, 8, 16, and 24. To maintain the designed plot compositions, herbaceous and non-planted woody species are mechanically removed from all plots in weeding campaigns conducted twice a year.

Due to the large number of trees planted in the experiment, the direct annual measurements are focused on trees within the central part of every plot. In monocultures and 2-species mixtures the central 6 × 6 planting positions (i.e., 36 trees per plot), and in the 4-, 8-, 16- and 24-species mixtures the central 12 × 12 planting positions (i.e., 144 trees per plot) are sampled. For TLS, 14 plots were selected according to the following criteria: (1) monoculture or 2-species mixture; (2) high proportion of trees larger than 1 m high; (3) high proportion of living trees in the planting positions; (4) only deciduous broad-leaved tree species or at least one out of two tree species deciduous. A total of nine tree species were recorded from the 14 plots: *Choerospondias axillaris* (Roxburgh) Burt et Hill, *Diospyros japonica* Siebold et Zuccarini, *Liquidambar formosana* Hance, *Nyssa sinensis* Oliver, *Sapindus saponaria* Linnaeus, *Triadica cochinchinensis* Loureiro, *Triadica sebifera* (L.) Small, *Schima superba* Gardner and Champion, *Rhus chinensis* Miller. All the recorded tree species are deciduous broad-leaved, with the exception of *S. superba*, which is an evergreen broad-leaved species.

## 2.2 Data collection

### 2.2.1 Direct field measurement

The direct annual field measurements were conducted at the end of the growing season from the middle of September until the end of October. Trees were surveyed under leaf-on conditions for the deciduous trees in order to measure the crown dimensions. The whole inventory was conducted by ten trained teams consisting of two persons each (hereafter inventory teams). In this study, we use the inventory data of the selected 14 plots that were recorded by seven inventory teams in September/October 2011. Each tree in the experiment is tagged with a unique numeric code. For every living tree in the total of 504 planting positions, the total tree height and the stem diameter at 5 cm above ground (hereafter ground diameter (GD)) were determined. GD was measured instead of

diameter at breast height (DBH) because of the young age of the trees. Total height was measured as the length from the stem base to the apical meristem with a measuring pole. GD was measured with a caliper to the nearest millimeter without prescribed measuring direction, and the position of the diameter measurement was permanently marked on the stem with white paint. We also measured the length and the height of the longest branch with a measuring tape and counted the number of living first-order branches (>1 cm in length) of every tree. The length of the longest branch was measured as the straight distance between the branch collar and the branch apical meristem. A summary of tree structural parameters is presented in Table 1.

### 2.2.2 TLS data acquisition

In the selected 14 plots, TLS was conducted in March 2012 under leaf-off conditions of the deciduous trees. The scans were performed with a phase-shift FARO Laser Scanner Photon 120 (FARO Technologies, Inc., FL, USA). The vertical field-of-view of each panorama scan is 310° and the horizontal is 360°. The scanner resolution was set at ¼, corresponding to an angular resolution of 0.036° and a spatial resolution of 6.283 mm at a distance of 10 m from the device. The data acquisition rate was 244,000 points per second. Further details on technical specifications and the experimental settings are presented in Table 2. One scan with the aforementioned configuration took about 3:24 min. The laser scanner was positioned on a tripod at a height of about 1.3 m. Due to the intrinsic characteristics of the laser device and the geometric measurement pattern, the 3D point density varied along the distance from scanner to object, and spatial information on the surface of vegetative elements located behind another object is not available due to occlusion (for more details see van der Zande et al. 2006). In order to obtain a complete 3D picture of all focal trees in each plot, several scans from different angles are required (Watt and Donoghue 2005). Due to the schematic planting pattern of the trees, we were able to make use of a standardized set-up of scan positions comprising nine scans evenly positioned on the plot (Fig. 1). To co-register the point clouds from the nine scans (see below), artificial and highly reflective reference targets

**Table 1** Summary of tree structural parameters obtained from direct field measurements on 14 plots (number of trees=438)

	Range (min.–max.)	Mean ± SD
Total tree height (cm)	23–540	238.4 ± 112.6
Ground diameter (cm)	0.4–9.5	3.5 ± 1.6
Length of the longest branch (cm)	3–484	131.2 ± 88.6
Height of the longest branch (cm)	0–340	75.2 ± 59.8
Number of branches	0–59	13 ± 11



**Table 2** Technical specifications and experimental settings of the FARO LS Photon 120

FARO LS Photon 120	Hardware specifications	Experimental settings
Laser power	20 mW (Laser class 3R)	–
Wavelength	785 nm	–
Range finder/method	Phase-shift	–
Measurement range	0.6–120 m	–
Ranging error	±2 mm (at 25 m)	–
Field-of-view (V×H)	Up to 310°×360°	310°×360°
Angular step size (V, H)	Up to 0.009°	0.036°
Spatial resolution	Up to 2 mm (at 15 m)	6.283 mm (at 10 m)
Data acquisition rate	Up to 976,000 points/s	244,000 points/s

(ten polystyrene spheres, each with a radius of 7 cm and three sheet metal checkerboards each with 42×46 cm edge lengths) were placed within and around the sampling area (Fig. 1).

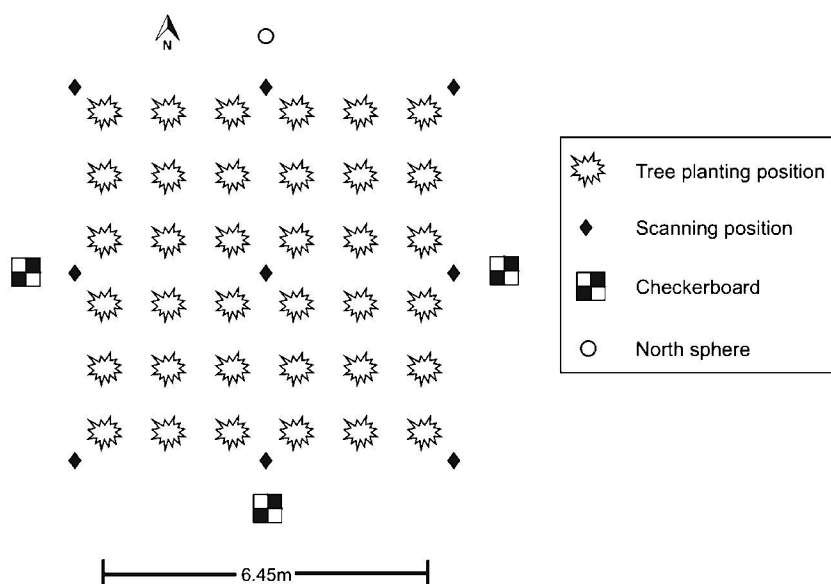
The TLS was conducted in March in order to minimize adverse impacts from high air humidity and wind as well as to avoid the occlusion from deciduous tree foliage and from high understory vegetation. During that time, air humidity is relatively low, and the scans were performed under windless conditions or at very low wind velocity. The time lag between the direct field measurements and TLS could introduce a systematic bias. Because the deciduous trees were in winter dormancy and the evergreen trees only show a very small increment between October and April (unpublished data), we assume that deviations caused by the time lag are largely restricted to a few trees where branch or stem breakage might have occurred during winter.

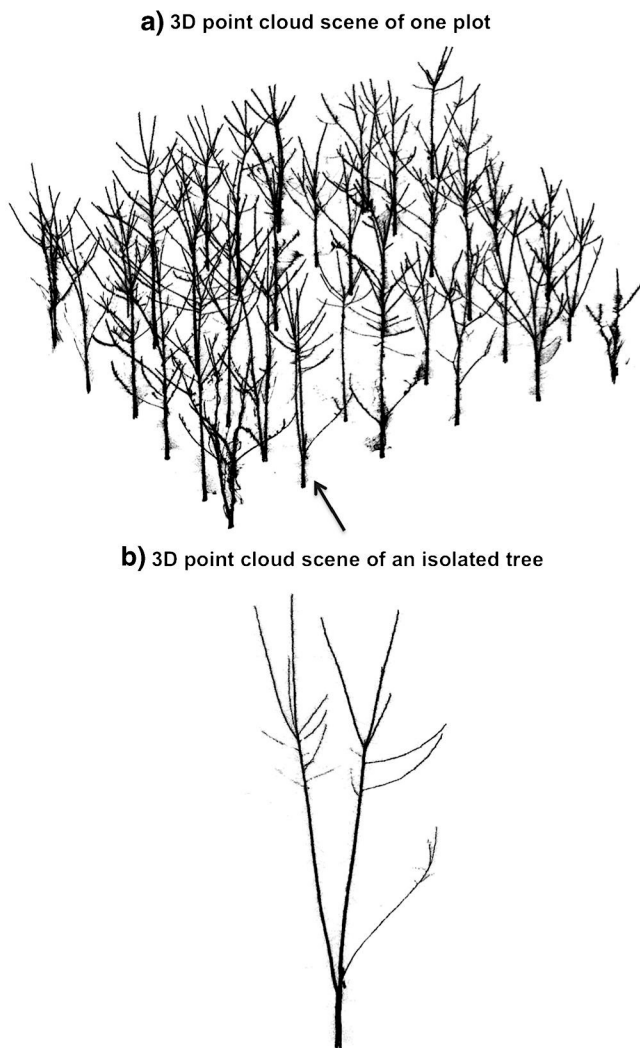
### 2.2.3 TLS data processing and extraction

The co-registration of the point clouds from nine scans within each plot was carried out with FARO Scene (V. 5.0.1) in order

to yield a complete 3D representation for each plot (Fig. 2a). The artificial reference targets were automatically identified by FARO Scene to enable positioning of each individual scan. Each point of the 3D picture is characterized by an XYZ coordinate. To enhance the point cloud quality of focal trees, outliers and points with low reflection intensity were removed by a set of predefined standard filters. As a process of segmentation, we used the software Pointools Edit (V. 1.5) to isolate the focal trees manually from all laser pulse returns that were extraneous to the focal trees (i.e. surrounding vegetation and soil) (Fig. 2b). Independently of data measured directly in the field, TLS measurements of total tree height, GD as well as length and height of the longest branch were made manually with Pointools Edit. The built-in navigation allowed an easy and quick visual identification of the focal trees and relatively quick measurements of the tree parameters. Total height was determined by averaging two measurements of the lengths from the point representing stem base to the endpoint of the highest crown. For GD measurement (Fig. 3), the stem cross-section was taken manually at the position marked with white paint, or 5 cm above ground if the mark was absent or not

**Fig. 1** Plot layout and standardized set-up of nine scan positions to acquire terrestrial laser scanning (TLS) data. The north sphere allowed for orientation to the cardinal directions. The set-up scheme of the spheres within the plot had no fixed pattern, but was adjusted depending on vegetation density and topography. The horizontal distance between two planting positions is 1.29 m, resulting in a horizontal plot size of 41.6 m<sup>2</sup>

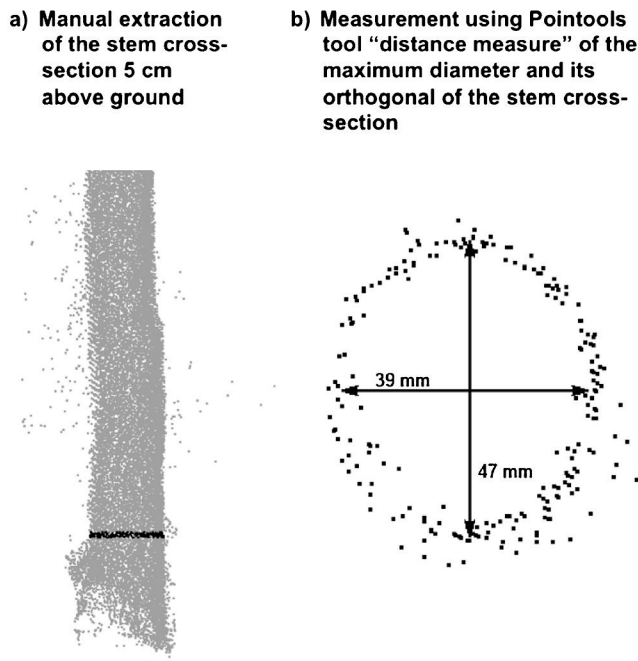




**Fig. 2** Three-dimensional (3D) point cloud scene of one plot and an isolated tree

detected due to occlusion. The maximum diameter and its orthogonal were visually determined and manually measured with the tool “distance measure”. GD was calculated as the average of these two measurements. Additionally, to examine whether the congruence of GD measurements varies according to the point cloud quality of the cross-sections, we introduced three quality classes, namely class 0, class 1, and class 2. Cross-sections with incomplete contours were classified as class 0; those with a complete contour but without white paint mark were categorized as class 1; those with both complete contour and white paint mark were grouped into class 2. The longest branch was first identified from different view angles. The length of the detected longest branch was measured as the length between the branch collar and the endpoint of the branch. The length between the stem base and the branch collar was measured as the height of the longest branch.

An overview of the numbers of measured individual trees per tree structural parameter for direct field and point cloud measurement is presented in Table 3.



**Fig. 3** Manual extraction of the stem cross-section 5 cm above ground, and visual determination and manual measurement using the Pointools tool “distance measure” of the maximum diameter and its orthogonal of the stem cross-section

### 2.3 Data analysis

We used correlation analyses to compare TLS-retrieved data with the field-measured data. Pearson correlations were applied for normally distributed data (total tree height and GD), whereas Spearman rank correlations were used for non-normally distributed data (length and height of the longest branch). Root-mean-square error (RMSE) was calculated to obtain the standard deviation of TLS-retrieved data from field measured data. We implemented generalized linear models (GLM) with binomial family to test whether the proportional deviation of the TLS data from inventory data was dependent on extrinsic factors, including potential occlusion (sum of GDs of the focal tree’s nearest neighbors, sum of all GDs on plot level), inventory team, point cloud quality of GDs, the structural parameters of the focal trees (total height and

**Table 3** Number of measured tree individuals per tree structural parameter for the direct field measurements and terrestrial laser scanning (TLS) measurements

	Number of measured tree individuals	
	Direct field measurement	TLS measurement
Total tree height	438	431
Ground diameter	438	391
Length of the longest branch	431	408
Height of the longest branch	431	408

number of branches), as well as species identity. All factors were scaled in order to make the model estimates comparable. GD data was transformed by multiplying it by 10. Data for length and height of the longest branch were square-root-transformed. Each tree structural parameter was tested against each selected factor except GD point cloud quality. Only GD was tested against the point cloud quality. For GLM with a categorical predictor, an ANOVA (using type “III” to cope for the unbalanced level proportions) was applied to test whether the variance was significantly different among the levels of one factor. Statistical analyses were conducted in R 3.0.1 (R Development Core Team). Package hydroGOF was used for calculating RMSE. The deviance percentage obtained from the chi-square test was calculated using package BiodiversityR for the proportion of the explained variance by one specific factor. Package car was used for analyzing the type “III” ANOVA.

### 3 Results

According to the direct field measurements, 438 living trees were present in the total of 504 surveyed planting positions. Of these, seven trees were branchless (Table 3). TLS data successfully detected 431 trees. For all of these trees, the total height was measured in the point clouds, GD measurements were conducted for 391 trees, and the length and the height of the longest branch was determined for 408 trees (Table 3).

The correlation coefficients between direct field and TLS measurements for total tree height, GD and length of the longest branch were very high ( $r \geq 0.95^{***}$ ), whereas that for the height of the longest branch was fairly high ( $r = 0.81^{***}$ ; Fig. 4). In height measurements, a higher proportion of comparisons showed larger values in the direct field measurements than in the TLS measurements (points below the equality line in Fig. 4a), but the absolute divergence was almost always small. Most of the outliers, however, occurred above the equality line and concerned larger tree heights ( $>250$  cm). In GD measurements, points were equally distributed above and below the equality line (Fig. 4b). A somewhat larger divergence between the measurement results was seen mostly for smaller values in the direct field than in TLS measurements (points above the equality line in Fig. 4b). The comparison of the measurements of the length of the longest branch revealed a larger number of points below the equality line, but outliers were exclusively observed above the line (i.e., value direct field measurement  $<$  TLS measurement; Fig. 4c). The distribution of the points for the height of the longest branch was relatively scattered, with several extreme outliers below the line (Fig. 4d).

As Table 4 shows, the variance of direct field and TLS measurements for total tree height was influenced slightly by the sum of the GD on both the local neighborhood level

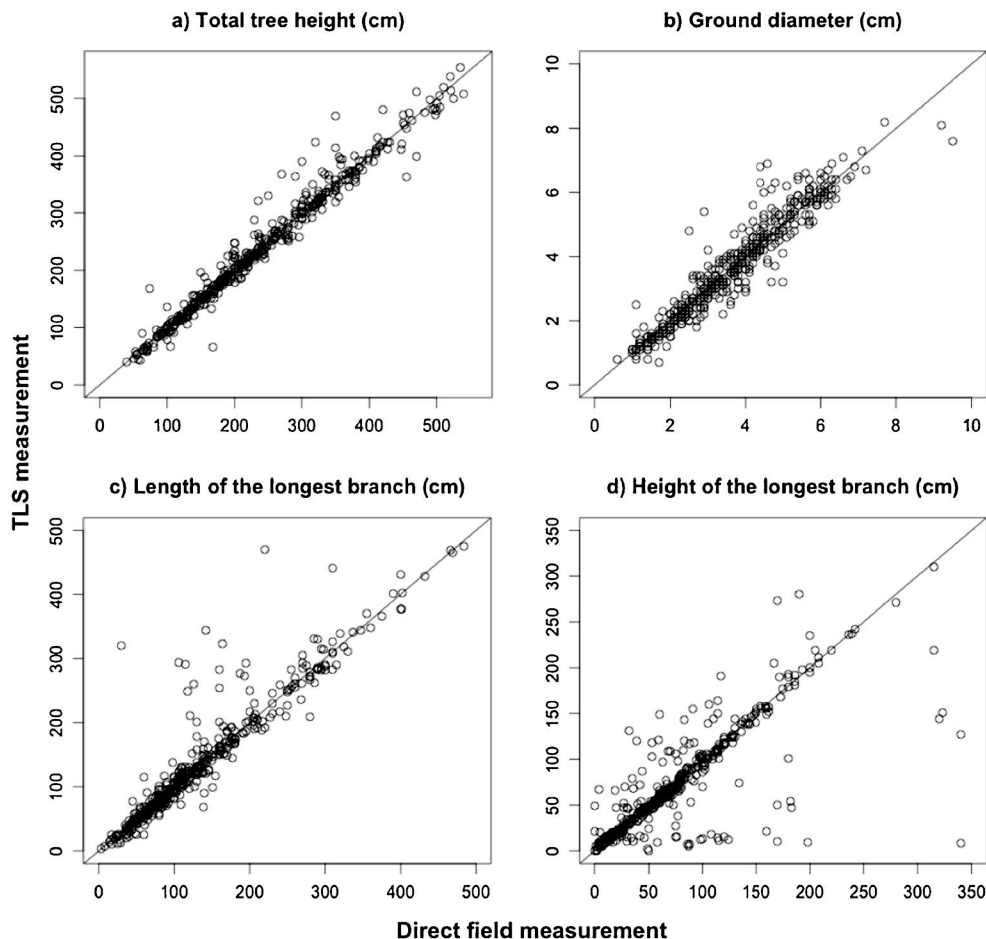
(estimate=0.01) and the plot level (estimate=0.02). Furthermore, the variance differed significantly between inventory teams and tree species. The variance of GD measurements was only significantly related to the focal tree's height (estimate=0.03), however, with an overall low explained variance ( $r = 3.13$  %). None of the factors included in the GLM contributed to the explanation of the two measurement approaches regarding the two tree structural parameters length and height of the longest branch.

### 4 Discussion

In the selected 14 plots, the survival rate of planted trees was 87 %, which corresponds exactly to the overall survival rate of planted trees in the entire BEF-China experiment during the census interval April 2009 to June 2010 (Yang et al. 2013). The TLS data successfully detected more than 98 % of the living trees. All seven trees that were not found in the point clouds were small, with a total height below 40 cm and a GD below 0.8 cm. Although the experimental plots were regularly weeded, and although most of the herbaceous vegetation retreats during the winter months, a tree height of 40 cm seems to be the minimum size that is required for tree detection and height measurements with the TLS set-up used in this study. For about 10 % of the TLS-detected trees, the GD could not be determined from TLS data. This was mainly due to occlusion of the stems caused by ground layer vegetation as well as other planted trees that were positioned between the laser scanner and the focal tree. Furthermore, in the only evergreen tree species, *S. superba*, leaved branches often reached down to low heights and occluded the stem at ground height. As a result, fragments with less than half of the cross-section contour appeared at ground height, and these trees were excluded from GD measurements. In a few cases, numerous fuzzy points occurred in the cross-section preventing a clear delineation of the stem surface. However, this was restricted to the smallest trees that were surrounded by herbaceous vegetation. Finally, in 19 trees, it was not possible to identify the longest branch. Most of these trees were *S. superba*, reinforcing the advantages of leaf-off compared to leaf-on conditions for enhancing the level of accuracy in detailed TLS measurements (Henning and Radtke 2006; Maas et al. 2008).

As expected (H1), TLS-derived data were highly congruent with data from direct field measurements. Generally, conventional measurements of height are more prone to measuring inaccuracies than those of the stem diameter (Pretzsch 2009). In our study, however, tree height data obtained by TLS approximated field-collected data even more closely than GD data. We suppose that the main reason is that the total height of the trees measured in this study still allowed for accurate direct height measurements with a measuring pole, whereas heights of larger trees ( $>6$  m) have to be obtained by

**Fig. 4** Comparison between direct field measurement and terrestrial laser scanning (TLS) measurements for **a** total tree height, **b** stem diameter at ground height (ground diameter), **c** length of the longest branch, and **d** height of the longest branch. The correlation coefficient ( $r$ ) and the root-mean-square-root error (RMSE) of the two measurements are 0.98 and 20.56 cm for total tree height, 0.95 and 0.52 cm for GD, 0.95 and 34.25 cm for length of the longest branch, and 0.81 and 38.12 cm for height of the longest branch, respectively. All correlations are truly correlated and significantly not equal to 0 ( $Pr < 0.001$ )



optical or laser tools such as a hypsometer. For time reasons, only one stem diameter measurement with a caliper was done in the field, which may cause inaccuracies in the case of non-circular stem cross-sections (see below).

On average, TLS tended to slightly underestimate total tree height and length of the longest branch. One reason for this might be that the direct field measurements were carried out under leaf-on conditions, whereas TLS was done under leaf-

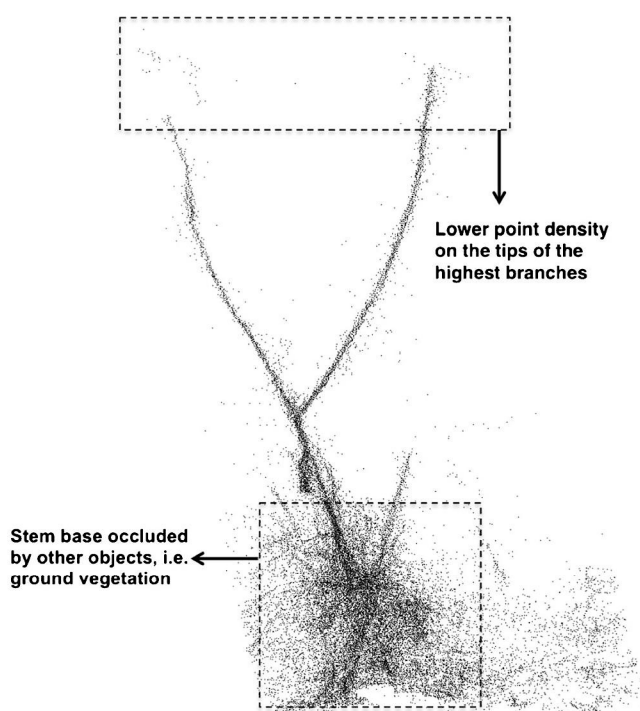
**Table 4** Results of generalized linear models (GLM) for the comparison of data on four tree structural parameters derived from direct field measurements and terrestrial laser scanning (TLS) measurements (given as estimates, i.e., the percentage of the variance explained)

		Tree structural parameter			
		H	GD	Llong	Hlong
Estimate (the explained variance)	GDN	0.01**(1.9 %)	n.s.	n.s.	n.s.
	GDP	0.02*** (4.3 %)	n.s.	n.s.	n.s.
	IT	n.d.*** (16.8 %)	n.s.	n.s.	n.s.
	PCQ	n.d.	n.s.	n.d.	n.d.
	H	n.s.	0.03* (3.13 %)	n.s.	n.s.
	NB	n.s.	n.s.	n.s.	n.s.
	Species	n.d.*** (7.2 %)	n.s.	n.s.	n.s.

Tree structural parameters: *H* total tree height, *GD* stem diameter at ground height, *Llong* length of the longest branch, *Hlong* height of the longest branch, the continuous predictors include *GDN* sum of the focal tree’s neighboring GDs, *GDP* sum of all GDs within a plot, *H* total tree height of the focal tree, *NB* the number of branches of the focal tree, the categorical predictors include *IT* inventory team, *PCQ* GD point cloud quality, *Species* species identity, *n.s.* statistically not significant, *n.d.* not determined

\*\*\* $Pr < 0.001$ ; \*\* $0.001 \leq Pr < 0.01$ ; \* $0.01 \leq Pr < 0.05$

off conditions for the deciduous trees. Some of the tree species have long leaves (15 to 40 cm), and some of the direct height or length measurements in autumn might have been erroneously carried out up to the highest leaf tip instead of to the highest apical meristem (cf. Wezyk et al. 2007). Furthermore, the spatial position of the tips of the highest branch in the tree crown and of the longest branch may differ under leaf-on and leaf-off conditions. In addition, these tips belong to the smallest tree constituents. They may be most sensitive to movements due to wind. They likely have a relatively low number of data points or could be occluded by other branches (Fig. 5; Côté et al. 2012; Schilling et al. 2012). Finally, the lowest point of each isolated focal tree was assumed to represent the stem base. However, the stem base could have been occluded by other objects (Fig. 5), resulting in a starting point for the TLS height measurements that was positioned above the stem base. Most of the outliers, however, indicated that TLS overestimated the height of trees which were larger than 250 cm. We suppose that this is mainly due to errors in the direct height measurements in the field: In some situations, the identification of the highest point of a tree could have been difficult due to a very dense canopy, meaning that a lower point was measured. In the length measurements, all outliers also showed a TLS-overestimated pattern. In these (few) cases, we assume that the tree individuals were treated differently in the two measurements: the object that was identified as the longest branch in TLS measurement was considered to be a second stem in the direct field measurement. Despite



**Fig. 5** Lower point density on the tips of the highest branches and tree stem base severely occluded by ground vegetation

these potential sources of under- or overestimation in TLS-derived total height and length of the longest branch, the agreement between the two approaches was generally very good, and the differences observed were mostly in the order of 25 cm or less.

The TLS stem diameter measurements have often been found to be underestimations compared to the direct measurements (Watt et al. 2003; Thies and Spieker 2004; Weiß 2009), but this was not confirmed in our study. The underestimation is due to the curvature of the stem surface, producing inaccurate distance and intensity measurements at the outer parts of the stem. However, this is much less relevant in multiple scan data than in single scan data. According to Pueschel et al. (2013), the full coverage of a tree stem's circumference is crucial for the reliable determination of stem diameters. With the exceptions mentioned above, this was successfully achieved in our TLS data set. Another source of variation between the two approaches results from the non-circularity of the stem cross-section (Pueschel et al. 2013). The deviation of the stem girth from a circle may generally be higher at ground height than at breast height. We, therefore, assume that much of the variation observed for the GD measurements is due to measurement procedure: in the field, only one diameter was determined with a caliper, whereas the maximum and minimum diameter was averaged in the TLS data set. In non-circular stem cross-sections this may result in over- or underestimations. As soon as possible, the DBH was, or will be, measured in the field inventory and accordingly in the TLS data. For two reasons in particular, we expect that the congruence between the two approaches will be even higher in the DBH than in the GD measurements: no occlusion from the ground layer vegetation and less deviation of the stem girth from a circle at breast height than at ground height.

The most notable differences were observed for the height determination of the longest branch. Here, we suggest that the 3D environment of the point clouds and the convenient navigation in Pointools allows for a more accurate identification of the longest branch than is possible in the field. Since this measurement is most sensitive to the identification procedure, it is conceivable that the level of congruence between the two approaches is lowest for this tree structural parameter (see H2).

Contrary to our third hypothesis, our results showed that the potential obstruction by other trees, employment of different inventory teams, as well as size and species identity of the focal tree contributed only slightly or not at all to the explanation of the variance between direct field and TLS measurements. Only tree height measurements varied due to the inventory team: in the field inventory, both team members were involved in the measurement procedure for trees >2.5 m height, enhancing the likelihood of measuring inaccuracies. A higher sum of GD of the neighboring trees can be due to a higher density and/or larger stem size. Stand density is

generally considered to have a key influence on the quality of the information from TLS (Watt and Donoghue 2005; Van der Zande et al. 2006). The density of more than 5,000 trees ha<sup>-1</sup> in our plots can be regarded as relatively high for application of TLS (Watt and Donoghue 2005). However, the low effect size (tree height) and non-significant influence (other three tree structural parameters), respectively, of the GD sum of neighboring trees implies that the scanning set-up scheme applied in our study was adequate to minimize the occlusion of focal trees. Furthermore, species identity was a significant predictor explaining the variance in height measurements, though with a small effect size. The saplings of the tree species of these subtropical broad-leaved forests differ considerably in growth rates and tree architecture (Geißler et al. 2012; Lang et al. 2012). To determine the highest point of the tree crown in the field inventory might be easier in trees with a light and simple structure crown, such as *S. saponaria*. Finally, a small proportion of the variance in the GD measurements could be explained by focal tree height. In our study, trees of greater height were predominantly *C. axillaris*. Tree individuals of this species were often multi-stemmed, leading to non-circularity of the stem cross-section at ground height, which may explain the higher deviation of the two measurement approaches with increasing tree height. However, most of the variance between direct field and TLS measurements could not be explained by the factors considered in the GLM analyses, but might be due to the factors mentioned above (i.e., small dimension of some important tree constituents, occlusion by ground layer vegetation, wind-induced movements, identification procedure).

Due to the current lack of reliable automated approaches in tree segmentation and measurements, the data retrieval of the four tree parameters from TLS is more time-consuming than by direct field measurement in small trees (per tree about 12 min from TLS and about 5 min in the field). However, as soon as the trees grow larger, the non-destructive quantification of crown parameters becomes more time-consuming or even impossible with a high degree of accuracy. However, the TLS alternative not only saves time when conducting certain measurements in larger trees, but also provides several other benefits: it is a documentation tool with the full option for future analyses, including precise time series analyses; it allows the estimation of individual-tree wood volume, both for the whole tree and various constituents (stem and branches; Dassot et al. 2012); it enables the analysis of the 3D structural topology of trees as well as the 3D distribution of plant material (Seidel et al. 2011b); and it provides the basis for tree crown modeling which can be used to investigate light harvesting and tree-tree-interactions (Seidel et al. 2011c; Metz et al. 2013). In recent years, several methods for reconstructing trees or parts of trees in 3D have been developed (Eysn et al. 2013). Automatic methods for tree modeling include voxel-based and geometric models. These approaches

are, however, sensitive to point cloud quality and varying point density, and therefore manual or semi-automatic processing is still an option to enhance the quality of results (Dassot et al. 2012; Eysn et al. 2013).

We conclude that TLS enables a reliable determination of tree structural parameters in young trees under field conditions. The scanning set-up scheme used in this study produced point clouds of high quality, enabling us to detect all trees higher than 40 cm and to reduce occlusions (Fig. 2). Furthermore, TLS data analyses proved to be more accurate in the identification of certain structural features than the direct field inventory and can help to reduce the measuring inaccuracies caused by the employment of several different inventory teams in the field. However, two factors may restrict the application of TLS to young regenerating stands: the structural complexity of these stands and the current lack of automated tools for data extraction. The regular weeding of the experimental plots was strongly beneficial to the accuracy of TLS measurements, and stands with an even higher tree density and/or herbaceous vegetation will require adjusted scan settings. In extreme cases, however, TLS will only be possible after canopy closure and self-thinning. In relatively small evergreen trees with dense crowns, the woody structures are largely occluded by leaves; however, tree growth with natural pruning of the lower branches will increase the visibility of structural elements of the crown when using ground-based TLS. Further research is needed to achieve more rapid point cloud data processing by the development of automated methods.

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## Curriculum Vitae

Ying Li

Email: [yingli8441@gmail.com](mailto:yingli8441@gmail.com)

<https://de.linkedin.com/in/ying-li-450191121>

[https://www.researchgate.net/profile/Ying\\_Li87](https://www.researchgate.net/profile/Ying_Li87)

Born: 01.04.1984 in Beijing, China



## Working experiences

04.2011–03.2016 **Research Associate**

Institute for Ecology, Leuphana Universität Lüneburg

- Planning and conducting scientific research in Deutsche Forschungsgemeinschaft (DFG) funded project BEF-China
- Developing and managing data collection
- Processing and analyzing data with R and Excel
- Data interpretation and reporting
- Conceptual design and writing of scientific papers
- Presenting and communicating scientific results in seminars and international communities
- Project management, cross-team and international collaboration
- Supervising and training

11.2009–12.2010 **Visiting researcher**

Institute for World Forestry, Johann Heinrich von Thünen-Institut

- Literature research about poverty alleviation through commercialization of natural resources
- Writing research proposal

02.2008

**Interviewing traders at Biofach Trade Fair in Nürnberg**

08.2007–10.2007 **Internship**

World Agroforestry Center (ICRAF), Kunming, China

- Literature survey in the field of value chains
- Conducting questionnaires with small holders.
- Preparing team conference

## Education

02.2012–08.2015 **Dr. rer. nat. Ecology**

Leuphana Universität Lüneburg

Dissertation: Effects of biodiversity and abiotic environment on the growth rates of native tree species in subtropical plantations

- 10.2006–11.2008 ***M.Sc. Forest Ecology and Management***  
Albert-Ludwigs Universität Freiburg  
Thesis: Earning money with Chinese non-timber forest products: the value chains of mu err, bamboo shoots and medicinal herbs in Germany
- 09.2002–07.2006 ***B.Sc. Rural and Urban Planning and Resources Management***  
Beijing Forestry University, China  
Thesis: Research on implementation of land use change prediction prototype system based GIS-ABM integrated technology

## Scholarship

- 08.2006–02.2009 Deutscher Akademischer Austauschdienst (DAAD)

## Languages

English (full professional proficiency)  
Chinese (native)  
German (fluent)

## Software Skills

R (professional)  
SPSS (basic)  
MS Office (professional)

## Publications

1. Bu W-S, Liu X-J, Schmid B, Li Y, Härdtle W, von Oheimb G, Liang Y, Sun Z-K, Huang Y-Y, Bruelheide H, Ma K-P (in press) Inter- and intraspecific variation in specific root length drives aboveground biodiversity effects in young experimental forest stands. *Journal of Plant Ecology*.
2. Yang B, Li Y, Bing D-Y, Both S, Erfmeier A, Härdtle W, Ma K-P, Schmid B, Scholten T, Seidler G, von Oheimb G, Yang X-F, Bruelheide X-F (in press) Impact of tree diversity and environmental conditions on the survival of shrub species in a forest biodiversity experiment in subtropical China. *Journal of Plant Ecology*.
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9. **Li Y, Härdtle W, Bruelheide H, Niklaus PA, von Oheimb (2014) Impacts of neighborhood species richness on individual-tree sizes evolve through time under heterogeneous environment in BEF-China main experiment. 99th Ecological Society of America (ESA) Annual Convention. Talk.**
10. **Li Y, Härdtle W, Bruelheide H, Nadrowski K, Scholten T, von Wehrden H, von Oheimb G (2014) Site and neighborhood effects on growth of tree saplings in subtropical plantations (China). *Forest Ecology and Management* 327: 118–127.**
11. **Li Y, Hess C, von Wehrden H, Härdtle W, von Oheimb G (2014) Assessing tree dendrometrics of young regenerating plantations using terrestrial laser scanning. *Annals of Forest Science* 71: 453–462.**
12. Schmitt J, Pokorny B, **Li Y** (2008) Certification of non-timber forest products in China: Effects on food quality, forest conservation and rural development. *Forests, Trees and Livelihoods* 18: 81–89.

## **Eigenständigkeitserklärung**

Ich versichere, dass ich die eingereichte Dissertation “Effects of biodiversity and abiotic environment on the growth rates of native tree species in subtropical plantations” selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß den Schriften anderer Autorinnen oder Autoren entnommenen Stellen habe ich kenntlich gemacht.

Hiermit erkläre ich, dass diese Abhandlung in der gegenwärtigen oder einer anderen Fassung noch keinem anderen Fachbereich vorgelegen hat. Den Inhalt der Dissertation habe ich noch nicht im Rahmen einer Diplom- oder anderen Prüfungsarbeit verwendet.

Lüneburg, August 2015