THE ROLE OF TREE DIVERSITY FOR INDIVIDUAL TREE GROWTH, CROWN ARCHITECTURE AND BRANCH DEMOGRAPHY

Kumulative Dissertationsschrift zur Erlangung des akademischen Grades
Doktor der Naturwissenschaften
(Dr. rer. nat.)

Angefertigt am Institut für Ökologie, Fakultät Nachhaltigkeit
Leuphana Universität Lüneburg

vorgelegt von

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2012

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eingereicht am 29.02.2012

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1 SUMMARY

1 SUMMARY

In the light of the concurrent loss of biodiversity, biodiversity and ecosystem functioning (BEF) research attracted a great deal of attention and emerged as one of the important fields of research in ecology. Since important ecological interactions such as competition occur between individuals, the understanding of individual tree growth was considered to be fundamental for forest related BEF research. Individual tree growth is determined by the above- and belowground interactions of a tree individual with its local neighbourhood. To obtain a deeper understanding of BEF relationships, I broadened the focus from individual tree growth (usually measured as diameter or biomass increment) to the arrangement and dynamics of the above-ground modules of trees in dependence of their local neighbourhood. More precisely, the main objective of the present thesis was to analyse the impact of tree diversity on individual tree growth, crown architectural and branch demographic variables. Thereby I considered crown architectural variables as important indicators of the competition for light. In addition, crown architectural variables impacted ecosystem services such as erosion control. Furthermore, the results of the present thesis contributed to the current discussion on species coexistence theories, which may be differentiated by two opposing views: one that relies on neutral processes and one that implicates a role for meaningful differences in the ecological strategy (niche) of co-occurring species.

The studied forest ecosystems were the subtropical broad-leaved evergreen forests of south-east China, which have been under high human pressure due to a long history of intensive land-use. The area is of particular interest for BEF research due to the high species richness of woody plants, including many, yet poorly studied species, and due to the rough terrain with steep slopes, which cause severe soil erosion. The present thesis combines three observational with two experimental studies, applying the local neighbourhood approach along an age gradient from tree saplings to mature trees. In the Gutianshan National Nature Reserve (GNNR), I conducted two observational studies on permanent plots which were chosen according to a space-for-time substitution design. The aim of the first study was to reveal the effects of diversity (species richness, functional diversity) together with other biotic and abiotic variables on morphological growth parameters (crown area, crown displacement and stem inclination) of target trees of four tree species (*Castanea henryi*, *Castanopsis eyrei*, *Quercus serrata* and *Schima superba*). In the second study, the same target trees together with their neighbours were used to analyse the relation between stand related functional diversity and the horizontal and vertical structure of the canopy. The third study was conducted in a

young secondary broad-leaved evergreen forest. Using two target species (*Castanopsis fargesii* and *Quercus fabri*), the role of diversity, intra- vs. inter-specific competition and the mode of competition (symmetric vs. asymmetric) on the target individuals was tested by analysing five-year radial growth increments. The two other studies were carried out in an experimentally established plantation, using saplings of four tree species (*C. henryi, Elaeocarpus decipiens, Q. serrata* and *S. superba*), which were planted in monoculture, two- and four-species combinations and in three densities. The fourth study focused on mechanisms of coexistence and the role of species richness, species composition, species identity and density on sapling growth. The fifth study tested the effect of sapling density and identity on the througfall kinetic energy, which represents a measure for the erosive power of rain.

It was found that functional diversity does affect crown architectural and canopy related parameters of forests in the GNNR. However, no effects of species richness on radial-growth were detected in the younger forest. Since I also did not find strong effects of species richness on saplings in the experimental plantation, diversity effects may evolve at a later age stage. The importance of the diversity effect may be related reversely to that of species identity in an age gradient of forest stands.

The findings suggest that different mechanisms of coexistence operate simultaneously but that their relative importance may shift through the life stages of trees. During the sapling stage, species-specific differences in growth and architectural traits support niche theory. In older forest stands, no species-specific differences in growth parameters could be detected. However, I did find effects of functional diversity on horizontal canopy structure. I conclude that mechanisms of coexistence may not only change with forest stand age, but may also differ for distinct traits.

The present thesis, being the first to apply the local neighbourhood approach with regard to crown architecture and branch demography within the BEF field of research, stresses the importance of this individual based approach. Although the observed forest systems are very complex, crown architectural and canopy structural variables were found to be affected by diversity. The finding that the degree of erosive power of rain could be elucidated by crown architectural variables, encourages further studies to reveal possible relations between biodiversity and other ecosystem functions or services, which might be mediated by crown architectural and canopy structural variables.

ZUSAMMENFASSUNG

Angesichts des Verlustes der biologischen Vielfalt hat die Beziehung zwischen Biodiversität und Ökosystemfunktionen (BEF – Biodiversity and Ecosystem Functioning) große Aufmerksamkeit erlangt und sich zu einem wichtigen Forschungsfeld der Ökologie entwickelt. Da wichtige ökologische Interaktionen wie Konkurrenz auf der Ebene der Individuen ablaufen, bildet das Verständnis individuellen Baumwachstums die Grundlage für die Wald-BEF-Forschung. Das individuelle Baumwachstum ist hierbei von einer Vielzahl von ober- und unterirdischen Interaktionen des Einzelbaumes mit seiner lokalen Nachbarschaft geprägt. Um ein umfassenderes Verständnis der BEF Beziehungen zu erlangen, erweitere ich den Fokus in dieser Arbeit von der Analyse des individuellen Baumwachstums (häufig erfasst durch Durchmesser- oder Biomasse-zuwachs) hin auf die Ausrichtung und Dynamik der oberirdischen Module des Baumindividuums innerhalb seiner lokalen Umgebung. Die Hauptfragestellung dieser Arbeit ist die Analyse des Einflusses von Baumartenzahl und funktionaler Diversität auf das individuelle Baumwachstum sowie auf kronenarchitektonische und astdemographische Variablen. Zudem betrachte ich kronenarchitektonische Variablen als wichtige Anzeiger von Lichtkonkurrenz. Auch Ökosystemdienstleistungen wie die Verminderung von Erosion werden von kronenarchitektonischen Variablen beeinflusst. Die Ergebnisse dieser Arbeit können zudem zur aktuellen Diskussion um Theorien der Koexistenz von Arten beitragen, die sich durch zwei gegensätzliche Standpunkte und Interpretationsansätze auszeichnen: der eine beruht auf neutralen Prozessen, während sich der andere auf Unterschiede in den ökologischen Anpassungsstrategien (den Nischen) koexistierender Arten stützt.

Die untersuchten subtropischen, immergrünen Laubwälder südöstlichen China waren aufgrund Jahrhunderte langer intensiver Bewirtschaftung starken anthropogenen Einflüssen ausgesetzt. Das besondere Interesse an diesen Waldökosystemen für die BEF-Forschung wird durch die hohe Vielfalt der Gehölzarten gestärkt, über deren Ökologie bisher jedoch sehr wenig bekannt ist. Die vorliegende Arbeit kombiniert drei beobachtende und zwei experimentelle Studien, und wendet dabei den Ansatz der lokalen Nachbarschaft über einen großen Altersgradienten der Braumgruppen (von Sämlingen bis zu ausgewachsenen Bäumen) an.

Im Gutianshan National Nature Reserve (GNNR) wurden auf Untersuchungsflächen, die nach einem „space-for-time substitution“-Design ausgewählt wurden, zwei beobachtende Studien durchgeführt. Das Ziel der ersten Studie war, die Effekte von Diversität (Artenzahl und

funktionelle Diversität) und anderen biotischen und abiotischen Faktoren auf Wachstumsparameter (Kronenschirmfläche, Kronenasymmetrie und Stammneigung) von Baumindivduen vier verschiedener Zielarten (*Castanea henryi, Castanopsis eyrei, Quercus serrata* und *Schima superba*) zu ermitteln. In der zweiten Studie wurden Individuen dieser Zielarten und ihre konkurrierenden Nachbarbäume herangezogen, um den Einfluss der funktionalen Diversität auf die horizontale und vertikale Kronendachstruktur zu analysieren. Die dritte Studie wurde in einem jungen immergrünen Sekundärwald durchgeführt. Anhand zweier Arten (*Castanopsis fargesii und Quercus fabri*) wurde analysiert, welchen Anteil Diversität, inner- und zwischenartliche Konkurrenz und asymmetrische Konkurrenz an der Erklärung der Durchmesserzuwächse haben. Die beiden weiteren Studien wurden in einer experimentellen Pflanzung durchgeführt, in der Sämlinge von vier Arten (*C. henryi, Elaeocarpus decipiens, Q. serrata und S. superba*) in Monokultur, Zwei- und Vier-Artenmischung und in drei Pflanzabständen gesetzt wurden. Mechanismen der Koexistenz und die Bedeutung von Artenzahl, Artzusammensetzung, Artidentität und Pflanzabstand für das Wachstum der Sämlinge waren Untersuchungsgegenstand der vierten Studie. In der fünften Studie wurde der Effekt von Pflanzabstand und Artidentität auf die kinetische Energie der Kronentraufe, die ein Indikator für die Stärke der Erosionsfähigkeit des Regens ist, untersucht.

In den älteren Waldbeständen des GNNR waren kronenarchitektonische sowie das Kronendach beschreibende Variablen von der Bestandesdiversität beeinflusst. Ein Einfluss der Artenzahl auf das Durchmesserwachstum konnte hingegen nicht festgestellt werden. Da bei der Untersuchung der Sämlinge lediglich geringe Diversitätseffekte gefunden wurden, könnten sich diese erst mit zunehmendem Alter stärker ausprägen. Entlang eines Gradienten des Bestandesalters könnte hierbei die Bedeutung des Diversitätseffektes umgekehrt proportional zu der des Arteffektes sein.

Die Ergebnisse dieser Arbeit weisen darauf hin, dass verschiedene Mechanismen der Koexistenz von Arten nebeneinander vorkommen und sich ihre relative Bedeutung in unterschiedlichen Altersstufen ändert. Die Sämlinge der untersuchten Arten zeigten artspezifische Wachstumsmuster und Kroneneigenschaften, was die Nischentheorie stützt. In älteren Beständen wurden keine artspezifischen Unterschiede in Wachstumsparametern gefunden. Allerdings war ein Einfluss von funktionaler Diversität auf die horizontale Kronendachstruktur nachweisbar. Daraus schließe ich, dass Mechanismen der Koexistenz von Arten sich nicht nur mit dem Bestandesalter ändern, sondern sich auch zwischen den untersuchten Variablen unterscheiden.

In dieser Arbeit wird zum ersten Mal der Ansatz der lokalen Nachbarschaft im Hinblick auf Kronenarchitektur und Astdemographie im Rahmen der BEF-Forschung angewendet. Die Ergebnisse betonen die Bedeutung dieses Individuen-bezogenen Ansatzes. Ein Diversitätseffekt auf kronenarchitektonische und Kronendach bezogene Variablen konnte sogar in diesen komplexen Waldökosystemen gefunden werden. Die Erkenntnis, dass die Erosionsstärke von Regen mit Hilfe von kronenarchitektonischen Eigenschaften erklärt werden konnte, sollte folgende Studien anregen, die Beziehungen zwischen Diversität und weiteren Ökosystemfunktionen und -dienstleistungen zu untersuchen, wobei indirekte Effekte von kronenarchitektonischen oder Kronendach bezogenen Variablen eine wichtige Rolle spielen könnten.

2 GENERAL INTRODUCTION

2 GENERAL INTRODUCTION

Growing human pressure induces rapid changes of the abiotic and biotic compartments of the planet (Vitousek *et al.* 1997). Thereby, the changes of the abiotic components of ecosystems (e.g. the changes in the carbon pools, element cycling and climate) and concurrent changes in the biotic components (e.g. species introduction and extinction, fragmentation of natural communities by changes in land-use) are no separated phenomena but are interrelated (Tylianakis *et al.* 2008). Global environmental change impacts the species composition and diversity of communities and landscapes and could have substantial indirect effects on ecosystem processes (Chapin III *et al.* 2001). As a consequence, the relation between biodiversity loss and ecosystem functioning has become one of the major topics in ecology (Loreau *et al.* 2001).

The present thesis aims to reveal the relation between the diversity of trees and individual tree growth. Following the local neighbourhood approach (Pretzsch 2009), I investigated if competition between tree individuals is reduced with increasing diversity of the neighbourhood. Thereby I focused on growth and crown architectural variables, which on stand level determine ecosystem functions such as productivity, the cycling of water and nutrients indirectly via the canopy structure and litter decomposition (Prescott 2002).

In this introductory chapter, I first define and give a general overview of BEF research and its findings, with a focus on BEF forest experiments. Following, I introduce the main objective of and hypotheses addressed by the present thesis. Chapter 4 describes Material and Methods, and chapter 5 the Results of the studies, which are included in this thesis. Furthermore a general Discussion and Conclusions may be found in chapter 6.

2.1 Biodiversity and Ecosystem Functioning – a Definition

Biodiversity

Biodiversity was defined by the Convention on Biological Diversity (CBD) in 1992 as

‘*the variability among living organisms from all sources including,* inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.’*

In the dependence on this definition, biodiversity is commonly divided into genetic diversity, species diversity and the diversity of ecosystems. The term “biodiversity” is not only scientific, rather it is embedded in a social and political framework (see CBD) and widely used and connoted as being intrinsically good (Jax 2010).

Measuring biodiversity

For practical reasons, species number is the most commonly used unit describing biodiversity (Hillebrand & Matthiessen 2009). The number of species largely depends on the size of the observed area. Thus, for comparisons of species richness patterns respective values need to be standardised (e.g. Gotelli & Colwell 2001). BEF research aims to explain the effect of diversity on ecosystem functions, and the number of species is not always appropriate to detect these relations. Thus, assemblages are characterised based on functional traits, which are those components of the organisms' phenotypes which determine their effects on ecosystem processes (Petchey & Gaston 2006). There exists a range of methods how to measure this functional diversity: from straight forward grouping of species according to particular traits to more complex methods which assess differences in traits between pairs of species and relate them to their relative abundances (Rao's quadratic entropy; Botta-Dukat 2005).

Ecosystem functions and functioning

Ecosystem functions are often considered as being synonymous to ecosystem processes (Reiss *et al.* 2009; Jax 2010). Some authors use the term ecosystem functions also interchangeably with 'interactions', which refer to '*changes in energy and matter over time and space through biological activity'* (Reiss *et al.* 2009).

Ecosystem functioning, by contrast, describes a broader view, combining all ecosystem processes which sustain an ecosystem. On the one hand, this means a broadening of BEF research to the multifunctionality of ecosystems. On the other, the overall network of processes of an ecosystem is in focus, asking for its performance (e.g. regarding invasibility, resilience). The latter includes the human perspective in the definition of what the 'performance' of an ecosystem actually means. This becomes even more obvious when considering ecosystem services, which are ecosystem functions that are of value to humans.

2.2 Biodiversity and Ecosystem Functioning - the Emergence of a New Research Field

The first impulse for BEF research was the concern of the impact of ongoing biodiversity loss on ecosystem functions and functioning. The pioneers of this emerging field of science focused on bivariate analyses, plotting ecosystem functions against a gradient of biodiversity (Naeem *et al.* 2009). The measure of biodiversity was mainly species richness, and single ecosystem processes were observed (Reiss *et al.* 2009).

The first experiments that manipulated biodiversity started in the 1990s. Besides the use of mesocosms, which are small-scale ecosystems comprising different trophic levels (Naeem *et al.* 1995), a number of grassland studies were conducted (e.g. Cedar Creek - Tilman *et al.* 1996; Reich *et al.* 2001; BIODEPTH - Hector *et al.* 1999; Jena Experiment - Marquard *et al.* 2009). The focus on grasslands may be explained by the relatively straightforward manipulation of short-lived, and comparatively small herbaceous species. A positive relationship between biodiversity and productivity was found in these experiments. Two processes have been considered to determine this relationship: positive species interactions such as facilitation or complementarity and the sampling effect (Hector *et al.* 1999), i.e. the increased chance to include a highly productive species in a community at high diversity levels (Loreau *et al.* 2001).

During the following phase the range of ecosystems which were explored and experimentally manipulated was broadened to freshwater, stream, wetland, microbial, coral reefs, marine and forest ecosystems. Biodiversity was now often measured trait-based, and functional diversity rather than species diversity per se was found to influence ecosystem processes (Reiss *et al.* 2009). Jiang *et al.* (2008) pointed out that the diverse (positive, negative and neutral) BEF relationships are dependent on how the functional impacts of species relate to their competitive abilities within the community.

Important findings were (Balvanera *et al.* 2006):

- The stability of ecosystems was found to increase with biodiversity but is also influenced by community composition (Stachowicz *et al.* 2007).
- The experimental design and the type of studied system influence the BEF relationship.
- With increasing trophic links between the manipulated and the measured level, productivity-related diversity effects decrease.

As a reaction, BEF research persuited a number of advancements and formulated future directions of research. Complexity in different dimensions was added to improve the interpretability and comparability to real-world ecosystems of experimental results:

- The incorporation of trophic complexity (vertical diversity) produced a greater variety of BEF relationships than that predicted for single trophic levels (Duffy *et al.* 2007; Schmid *et al.* 2009). Both, the degree of specialisation/linkage between trophic levels and whether systems are top-down or bottom-up controled was found to have an impact on BEF (Reiss *et al.* 2009).
- Different ecosystem processes should be addressed at the same time, since overall ecosystem functioning is sustained by multiple processes. Overall functioning is more susceptible to species loss than single functions due to the multicomplementarity of species (Gamfeldt *et al.* 2008). For globally distributed drylands a significant positive relation between species richness and multifunctionality (C, P and N cycling) has been found (Maestre *et al.* 2012). Gamfeld *et al.* (2008) also found multifunctional redundancy to be lower than single-function redundancy.
- An incorporation of spatial and temporal heterogeneity in experiments may enhance the likelihood to detect complementarity between species (Stachowicz *et al.* 2007; Hillebrand & Matthiessen 2009). In addition, observed BEF relationships may change over time with varying species becoming dominant. Thus, more species are needed to allow for higher community flexibility and stability in time, which enhances the importance of diversity for ecosystem functioning (Hooper *et al.* 2005; Hillebrand & Matthiessen 2009; Allan *et al.* 2011).

Most recently, in a meta-analyses it was found that a combination of these factors (different ecosystem functions, temporal and spatial heterogeneity, different environmental change scenarios) requires a high plant diversity (84% of all observed species) to maintain ecosystem functioning (Isbell *et al.* 2011).

BEF research and theories of coexistence

Almost all postulated relationships between diversity and ecosystem functions require individuals to possess different traits (Hillebrand & Matthiessen 2009) and thus follow the idea of the ecological niche (Hutchinson 1959). The concept of overyielding was explained by niche separation: diverse mixtures can use resources more sufficiently (i.e. in a complementary way) and produce more biomass than even the best monoculture (Naeem *et al.* 1994; Hector *et al.* 1999).

However, in the debate of theories for species coexistence, Niche theory is opposed to Neutral theory. The Neutral theory as formulated by Hubbel (2001, 2005) is based on the hypothesis of functional equivalence, meaning *'that trophically similar species are, at least to a first approximation, demographically identical on a per capita basis in terms of their vital rates, of birth, death, dispersal – and even speciation'* (Hubbell 2005). Both concepts underly ongoing experimental testing, especially in the extremely species-rich tropical and subtropical forest ecosystems (Condit *et al.* 2006; Wills *et al.* 2006; Kraft *et al.* 2008; Legendre *et al.* 2009), where estonishing numbers of woody species coexist using all the same restricted pool of resources.

2.3 Biodiversity and Ecosystem Functioning - BEF Forest Experiments

Forest ecosystems attracted increased attention in BEF research since the workshop 'Functional significance of tree diversity in temperate and boreal forests', organized in Weimar in 2002 (Scherer-Lorenzen *et al.* 2005a). In particular, the importance of forest ecosystems for the worldwide carbon fixation and stocks and for the loss of biodiversity have been stressed (see Thompson *et al.* 2009 and references herein).

In addition, there is a long debate of increased stand productivity as a result of two or three tree species mixtures with different functional traits (e.g. shade-tolerant vs. shade-intolerant) (Pretzsch 2005). However, the first experiment to test explicitly for biodiversity effects along a gradient of multiple species was the Finnish Satakunta tree diversity experiment established in 1999 (Scherer-Lorenzen *et al.* 2005b). The number of BEF experiments with woody species increased rapidly and with the establishment of the BEF China in the Subtropics there now exist 12 experiments across all types of forest biomes (Tab.1).

In Fig. 2.1, I present important findings of BEF research of observational and experimental studies in forest ecosystems of the tropical and subtropical region. Tropical and subtropical forest ecosystems are of particular interest for BEF research due to their high species richness and due to the pressure from intensive land-use.

Observed differences in BEF relationships between boreal/temperate and subtropical/tropical forests have often been attributed to lower species numbers of boreal/temperate forests (Thompson *et al.* 2009). In boreal and temperate forests, niche differentiation is presumably comparatively low, due to species extinction in the course of the ice ages and slower (co-) evolutionary processes of the long-lived tree individuals (Pretzsch 2005).

Table 1 BEF Forest experiments (modified after Bruelheide 2010)

Experiment	Country	Biome	Year	Plot size (m^2)	No.of plots	No. of trees	Diversity variables	Diversity gradients
Satakunta Exp.1	FIN	boreal	1999	400	114	19,760	Species richness No. of functional groups (FG)	1, 2, 3, 5 species 1, 2 FG (decid./conif./mix)
Satakunta Exp. 2	FIN	boreal	2000	400	49	4,900	Genetic diversity of *Betula pendula*	1, 2, 4, 8 clones
BIOTREE-species	GER	temperate	2003-2004	5,760-10,368	56	185,000	Species richness	1, 2, (3) 4, 6 (10) species
BIOTREE-FD	GER	temperate	2003	1,700	25	22,000	Functional diversity (FD)	FD gradient: low to high, always 4 species
BIOTREE-Simplex	GER	temperate	2003	256	36	2,100	Dominance, density	dominant, co-dominant, even; high, low density
Kreinitz Exp.	GER	temperate	2005	25	98	2,900	Species richness Identity of functional groups	0, 1, 2, 3, 5, 6 sp. Slow/fast decomposing decid./conif.
ORPHEE	FRA	temperate	2007-2008	400	256	25,600	Species richness No. and identity of functional groups	1, 2, 3, 4, 5 species deciduous (early/late), evergreen
FORBIO	BEL	temperate	2009	1,800	84	70,400	Species richness genetic diversity of *Quercus* and *Fagus*	1, 2, 3, 4 species different provenances
Canada Exp.	CAN	temperate	2009	12.25	216	5,400	Species richness functional diversity assemblage identity	1, 2, 4, 12 species 8 levels of FD native vs. exotic sp.
BEF China	CHI	subtropical	2008 - 2010	667- 2,667	153	300,000	Species richness shrub species richness	1, 2, 4, 8, 16, 24 sp. 0, 4, 8, 16 shrub sp.
Sardinilla Exp.	PAN	tropical	2001	324- 2,025	48	6,270	Species richness identity of functional groups	1, 3, 6, + 6, 9, 18 sp. Pioneer/shade-tolerant
Sabah Exp.	Malaysia	tropical	2002	40,000	124	165,300	Species richness no. of genera tree height	1, 4, 16 species 2 vs. 4 genera 2 vs. 3 height classes

In contrast to other ecosystems, the size and longevity of trees causes heterogeneity in space and time as well as in environmental factors, which play an important role for forest observations, and analyses should therefore control for a large number of covariates (Vilà *et al.* 2005; Nadrowski *et al.* 2010). Vance-Chalcraft *et al.* (2010) pointed out that differences in diversity-productivity relationships may be related to former land-use and successional state. In a subtropical Chinese forest, Bruelheide *et al.* (2011) found richness of adult trees to increase with successional stage, which seemed to be caused by continuous random immigration over time.

In conclusion, the results of BEF research of forest ecosystems allow first insights into BEF relationships as regards some important ecosystem functions such as productivity and invasibility. However, there is little evidence for the impact of diversity (including genetic diversity) on multitrophic interactions and more specific ecosystem functions and services such as soil erosion or coarse woody debris dynamics. In addition, some of the findings are ambiguous and differences between vegetation zones seem to be prevalent.

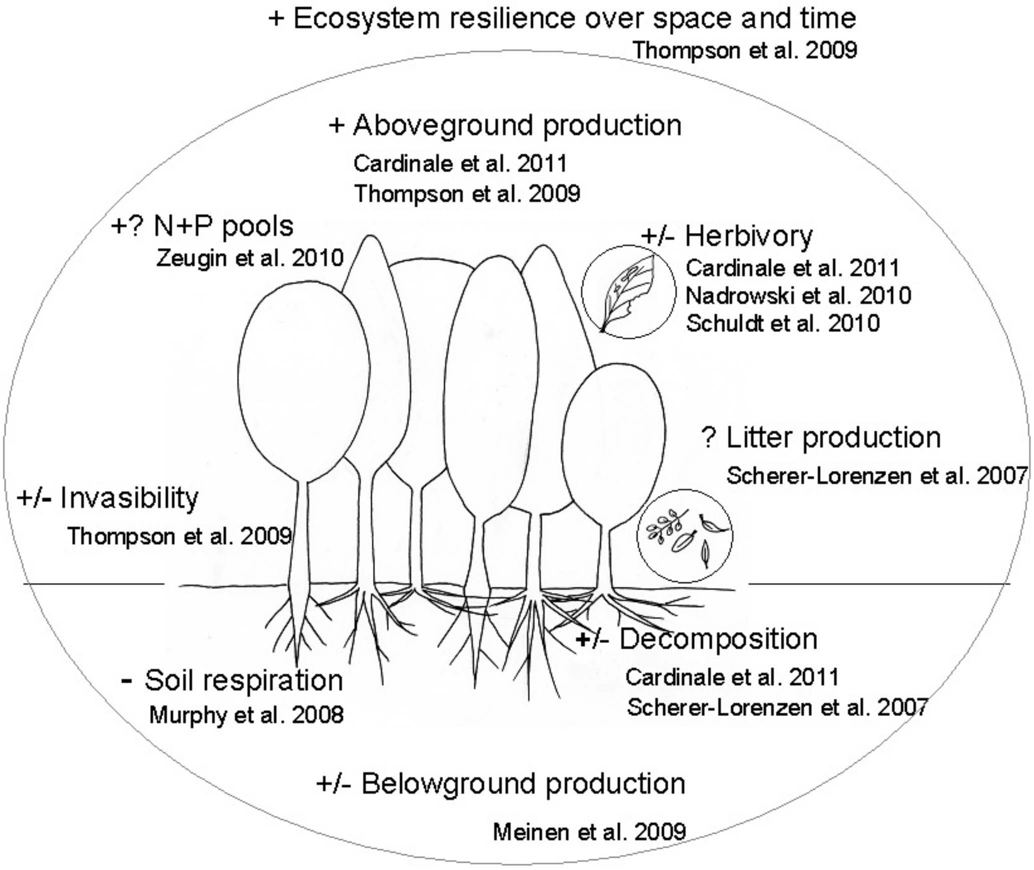

Fig. 2.1 Effects of biodiversity in tropical and subtropical forest ecosystems. The cited studies report a positive (+), negative (-) or no (+/-) relation between biodiversity and ecosystem functions. Unclear relationships are indicated by “?”.

3 OBJECTIVE AND HYPOTHESES

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The main objective of the present thesis is to study the impact of tree diversity on tree individual growth, crown architectural and branch demographic variables. Conventionally, analyses in forest research have been conducted on the spatial scales of the stand. However, since a stand could be considered as the collective of individual trees and their interactions, the individual tree may be seen as the critical unit in the maximation of fitness (Pretzsch 2009).

The "neighbourhood approach" follows the recognition of the stand as a spatial, structural-functional collective of tree individuals. It assumes that ecologically important processes, which take place between, and will be influenced by the closest neighbouring tree individuals and by the local abiotic conditions, determine the stand structure. Following, there might be close feedback loops between individual growth conditions, tree growth and stand structure which determine forest stand dynamics (Pretzsch 2009).

Since light is broadly recognized as one of the most critical factors determining tree growth, the competition for light between tree individuals may be seen as one of the most important processes in a forest stand. The above-ground competition for light was found to be size asymmetric, i.e. that larger individuals have a disproportionate higher effect on smaller individuals by shading (Schwinning & Weiner 1998). Morphological responses of the crown architecture may thereby be the most important result of size-asymmetric competition for light (Grams & Andersen 2007). Shade-avoidance responses of tree individuals to surrounding and overtopping vegetation are induced by lower photosynthetically active radiation and a decreased red to far-red ratio (Ballaré 1999). Since different species cast distinct qualities of shade, species identity of neighbouring trees was found to influence the growth of shoots and branches (Lintunen & Kaitaniemi 2010).

Tree crowns respond to anisotropic light availability with stronger lateral crown expansion towards high light conditions (phototropic growth), resulting in crown asymmetry. The higher relative competitive strength of a neighbouring tree may cause crown asymmetry (Brisson 2001). The development of asymmetric crowns may thereby be intensified by correlative inhibition, i.e. the growth of branches in favourable conditions is increased at the expense of the growth of branches in unfavourable conditions (Stoll & Schmid 1998; Takenaka 2000). Thus, crown responses to competition are the aggregated effects of the differential development of single branches and it is crucial to explore branch demography in more detail (Stoll & Schmid 1998; Sumida *et al.* 2002).

Differences between species or functional groups with regard to shade-avoidance responses and crown architecture may evidence complementary strategies of foraging for light. This complementarity may lead to reduced competition of tree individuals, which belong to different species or functional groups, promoting species coexistence at the same time. The main objective of this thesis is, thus, to reveal if competition on a local neighbourhood scale is reduced with increasing species richness of neighbouring trees. If so, diversity effects on the stand-level may be the aggregated effects of diversity effects on the local neighbourhood level. Following these assumptions, species coexistence in the observed systems would be ruled by niche differentiation as opposed to neutral mechanisms (Hubbel 2001).

More specifically, the following hypotheses have been addressed by the set of five papers (see appendix I-V), which are the basis of the present thesis:

- Growth responses of stem and crown on forest slopes are species-specific (paper I).
- Morphological responses of crown and stem are influenced by both, biotic and abiotic variables of the local neighbourhood (paper I).
- The functional diversity of the stand as well as its successional stage influence the horizontal and vertical heterogeneity of the upper canopy (paper II).
- The number of hetero- vs. conspecifics as well as the species richness of neighbouring tree individuals affects the radial growth of a tree individual (paper III).
- Species richness, species composition, species identity and stand density affect the coexistence, growth patterns and crown architecture of tree saplings (paper IV).

In an additional study the focus has been shifted from the plant-plant interactions towards an ecosystem service, soil erosion control, which is an important topic from both an ecological and economical point of view. In particular in subtropical China, where high rainfall intensity causes severe and continuous soil losses, soil degradation by erosion and its control is one of the major environmental problems. In this study, the impact of tree saplings on the kinetic energy (KE) of rainfall was tested. More specifically it was hypothesised that:

- The planting density and species identity of saplings affect the KE of throughfall (paper V).

4 MATERIALS & METHODS

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4.1 Study Area: Climate, Geomorphology, Vegetation and Land-use

The study area is located in the border region of the two provinces Zhejiang and Jiangxi, south-east China, about 400 km west of Shanghai (Fig 4.1).

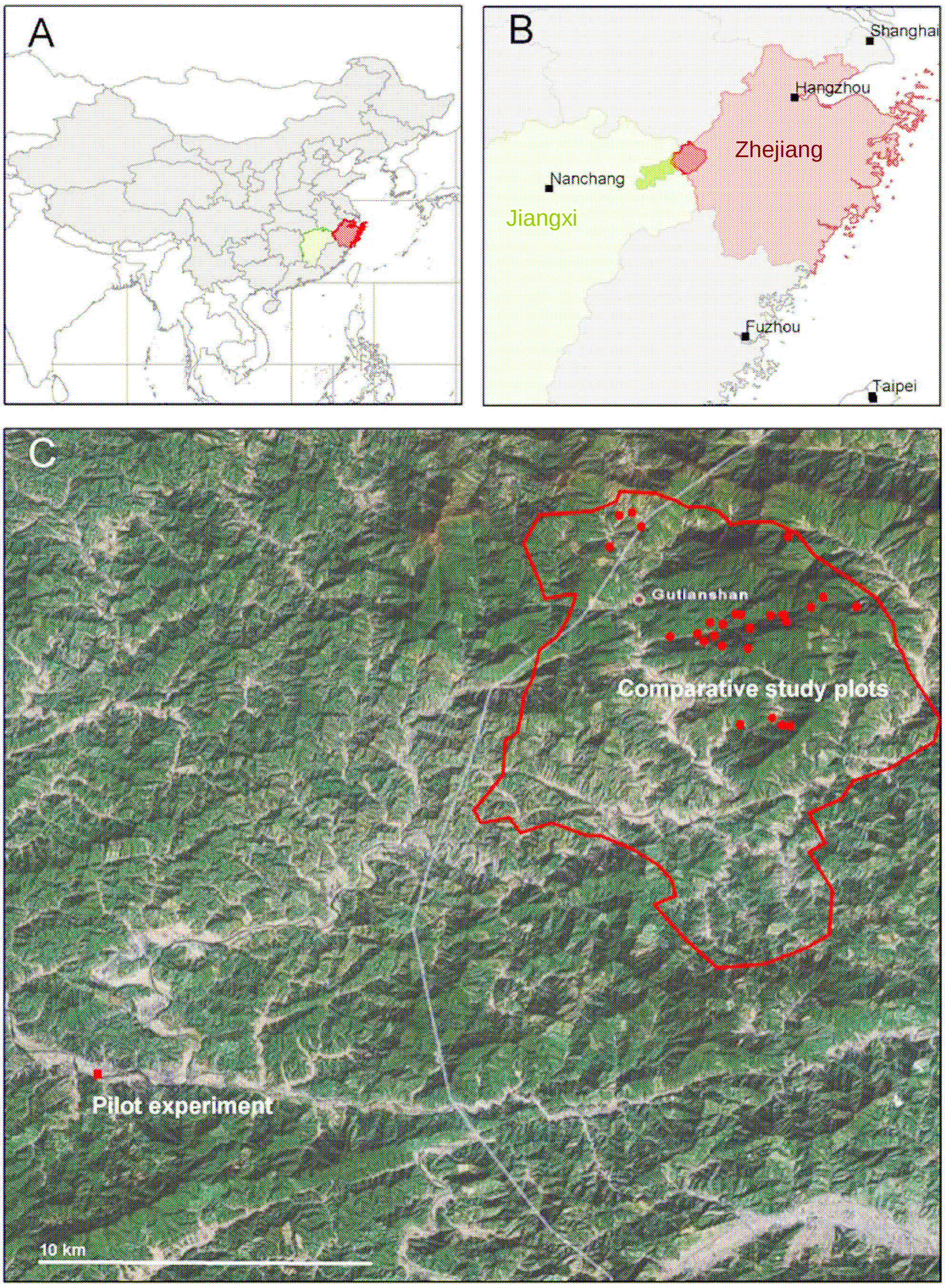

Fig. 4.1 Location of the study sites in south-east China, Zhejiang and Jiangxi province (A, B) and position of the pilot experiment (paper IV and V) in relation to the Gutianshan National Nature Reserve (paper I and II, C). The location of the study described in paper III is about 20 km southwest from the pilot experiment (maps by Erik Welk).

The region is characterised by a subtropical climate with mean annual temperature of 15.1° C and mean precipitation of 1960 mm (Fig. 4.2). Precipitation rates achieve a maximum in summer (May to June), while there is a short dry season in winter (October to December).

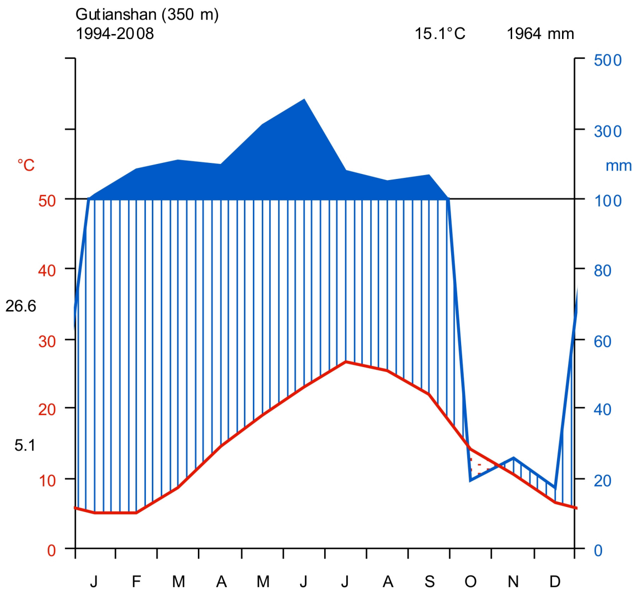

Fig. 4.2 Walter and Lieth climate diagram of Gutianshan NNR (Geißler *et al.* 2010)

The area can be described as fold-and-thrust belt stretching from SE to NW. Slopes are typically convex shaped and thus show low inclinations in the upper part and 20-35° at midslope positions. The footslopes are the steepest with a mean inclination of 30-40°. The soil cover of these footslopes and also ridges is widely eroded (Bruelheide 2010). The soils of the region are mainly Cambisols, interfered by Regosols on ridges and crests, and in the lower parts of the landscape Acrisols and Ferralsols.

The predominant forest type is evergreen subtropical forest, comprising approximately equal numbers of deciduous broad-leaved and evergreen broad-leaved species, but with the evergreen being dominant in abundance (Wu 1980; Yu *et al.* 2001). Species of plant families with temperate (e.g. FAGACEAE), subtropical (e.g. ANACARDIACEAE, LAURACEAE) or tropical distribution range (e.g. SYMPLOCACEAE, THEACEAE, MYRSINACEAE) form the species pool. The Gutianshan National Nature Reserve (GNNR), where the permanent plots have been established, hosts a number of 1426 seed plant species of 648 genera and 149 families, of which 258 species are woody (Lou & Jin 2000).

In the study region, agricultural land-use in the valleys comprises the cultivation of rice, corn, legumes and other vegetables. The construction of terraces is a widespread technique to allow for extended land-use - mainly tea plantations - at lower parts of the slopes. Predominant land-use of the midslopes and higher up are plantations of *Cunninghamia lanceolata* (Lamb.) Hook. and *Pinus massoniana* (Lamb.). These plantations are manually clear-cut every 20-25 years. Due to the long history of intensive land-use, few remnants of old-growth broad-leaved evergreen forest are left today; those of which remained have been preserved as National Parks or NNRs (Yu *et al.* 2001; Wang *et al.* 2007). The majority of broad-leaved evergreen forest stands in China now represent younger secondary forests (Wang *et al.* 2007).

As a response to the vast deforestation, the Chinese Governement established the National Forest Protection Program (NFPP) in 1998, which started in 2000 and is devoted to state-owned forests and forest land. The program comprises a logging ban (or at least logging restrictions) on 30.4 Million hectares of currently existing natural forest area in the upper reaches of the Yangtze and upper and middle reaches of the Yellow River, and the plan to afforest 30.8 Million hectares of degraded land (Jintao *et al.* 2002). The ultimate aim is to develop a sustainable forest management in China.

A second important governmental program is the Sloping Land Conversion Program. '*The main objective of the Sloping Land Conversion Program is to reduce erosion by converting private cropland on steep slopes and some degraded land to grasses and tree-cover*' (Jintao *et al.* 2002). The incentive mechanism is subsidiarity by provision of grain, cash, and saplings to farmers who are willing to convert their land.

4.2 Study Design and Measurements

This thesis combines observational studies with experimental, and tree individuals from the sapling stage up to an age of more than 80 years were examined.

In the GNNR, 27 permanent plots (each 30 x 30 m on ground) were randomly selected, stratified by successional age (< 20 yrs - > 80 yrs) and by excluding slopes steeper than 50°. A complete inventory of woody species (> 1 m height) was carried out to determine species richness. Functional diversity was calculated as Rao's Quadratic Entropy (Rao's Q) for each plot as:

(1) $$FD_Q(\mathbf{p}) = \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} d_{ij}\, p_i\, p_j$$

where N is the number of species in a plot (**p**), d_{ij} is the trait difference between the *i*th and *j*th species, and p_i and p_j are the proportions of the *i*th and *j*th species, calculated as number of individuals per species related to the total number of individuals in the community (Botta-Dukat 2005). Differences between traits d_{ij} were calculated as the Euclidian distance between traits devided by the number of traits:

$$dij = 1/n \sum_{k=1}^{n} (X_{ik}-X_{jk})^2$$

(2)

where n is the number of traits considered, X_{ik} value of trait k in species i. Functional diversity as Rao’s Q of a plot equals the sum of differences in species traits, weighted by the abundance of the respective species within the plot. In addition, a number of abiotic variables (such as e.g. inclination, aspect, soil depth, functional diversity) was measured at plot level.

Four tree species of high abundance were selected: *Schima superba* Gardn. et Champ., *Castanopsis eyrei* (Champ. Ex Benth.) Hutch., *Quercus serrata* var. *brevipetiolata* and *Castanea henryi* (Skan) Rehd. et Wills.. Seventy target trees (20 per species; except *C. henryi* (10)) were chosen randomly within the permanent plots from all target species individuals complying with pre-defined criteria (for more details I refer to papers I and II). All trees growing within a circular plot with a radius equal to half of the target tree’s height (Ammer *et al.* 2005) and fulfilling the criterion of minimum diameter at breast height (dbh, measured at 1.3 m above ground) were considered as neighbours. This resulted in a total number of 996 observed tree individuals in the 27 permanent plots. For each tree the position in relation to the target tree, the dbh, the total height and the height of the first branch were measured. Stem inclination was calculated by triangulation (see paper I). The crown radii in the eight subcardinal directions were measured and the crown projection area was calculated as a polygon. Crown projection maps were constructed using the geoinformation system ArcGIS (Version 9.0, ESRI). A set of abiotic parameters was surveyed on the level of target groups (e.g. slope inclination and aspect, species number and number of functional groups of neighbouring trees). To characterise the competitive power of the target tree the distance-independent competition index (CI) of Daniels *et al.* (1986) was chosen:

(3) $$CI_j = dbh_j^2 * n / \sum_i dbh_i^2$$

where j is the subscript for the target tree, i for the neighbour and n stands for the number of neighbours.

The study presented in paper III was conducted in a forest stand in Jiangxi province, close to Dexing city. We chose 40 target trees of the two species of the family FAGACEAE, one evergreen: *Castanopsis fargesii* (Franch.) and one deciduous: *Quercus fabri* (Hance). Target trees were at least 40 m away from each other. Neighbours were identified in the same way as described above. The relative position of neighbours to the target tree and tree morphological parameters (dbh, total height, height of the first branch, crown radii) were measured for all tree individuals. The target tree was cut and stem discs were taken at ground and at breast height. Tree age was determined from the basal stem discs, and the annual radial growth of the previous five years was measured from the stem discs at breast height. Various biotic and abiotic variables were surveyed for each target group. Different competition indices were calculated (for more details see paper III).

In addition, an experimental plantation using tree saplings was established on a former agricultural field, which was ploughed, harrowed and divided into four blocks prior to setting up the experiment in March 2009. Four highly abundant, early-successional species were chosen for the experiment: *S. superba*, *Elaeocarpus decipiens* Hemsley (evergreen), *Q. serrata* and *C. henryi* (deciduous) (Yu *et al.* 2001). We manipulated species richness and species composition of tree saplings on plots of 1 m² size. Three plot-related species richness levels were established: monocultures, two-species and four-species combinations. The four monocultures of each species, all six possible two-species combinations, and one four-species combination made a total of eleven species compositions. Finally, the species richness and species composition treatments were fully crossed with a density treatment. The low density treatment comprised only one individual per plot, whereas the experimental plots with high and intermediate density each contained 16 individuals, planted in an array of four by four. Planting distances between saplings in the high and intermediate density treatment were 15 and 25 cm, respectively. Sapling growth (height and diameter growth), biomass allocation (determination of dry weight of leaves, branches and stem in 25 cm sections) and architecture (e.g. crown length, length of longest branch, branch number) were recorded for the central individuals (for further details see paper IV).

For the study presented in paper V, we used the high density plots of all monocultures and of the four-species combination. Five splash cups were placed in the central positions of each plot and mean values per plot were used for further analyses. For a more detailed description of the method of splash cups I refer to paper V.

4.3 Statistical Analyses

Statistical analyses were performed using R 2.10. (R Development Core Team 2010; except for paper III). Mixed effects models represent the main statistical model that was used throughout the present thesis. The model represents a powerful tool to deal with data in a hierarchical structure, it avoids pseudoreplication and allows the distinction of explanatory variables into random and fixed effects. For the analyses of mixed effects models the package “nlme” was used (Pinheiro et al. 2009). Multiple comparisons were performed by means of the package “multcomp” (Hothorn et al. 2008). In paper III, simple and multiple regression models to predict the radial growth were developed using SPSS 17.0 (SPSS Inc., Chicago, IL).

5 RESULTS

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5.1 Effects of the Local Neighbourhood

The effect of neighbouring tree individuals on target tree growth, morphology and crown architecture was tested throughout all studies. The projected crown area was negatively (p = 0.003) and the relative crown displacement was positively (p = 0.009) related to the competitive strength of neighbours (paper I). In the third study, up to 78 % of diameter growth could be explained by the strength of local neighbourhood competition (paper III). In addition, competition was found to be size asymmetric. Diameter increment was significantly reduced with higher sapling density in experimentally planted saplings (paper IV). At the same time the total height of saplings was constant, whereas the crown length tended to be reduced with increasing density (Fig. 5.1).

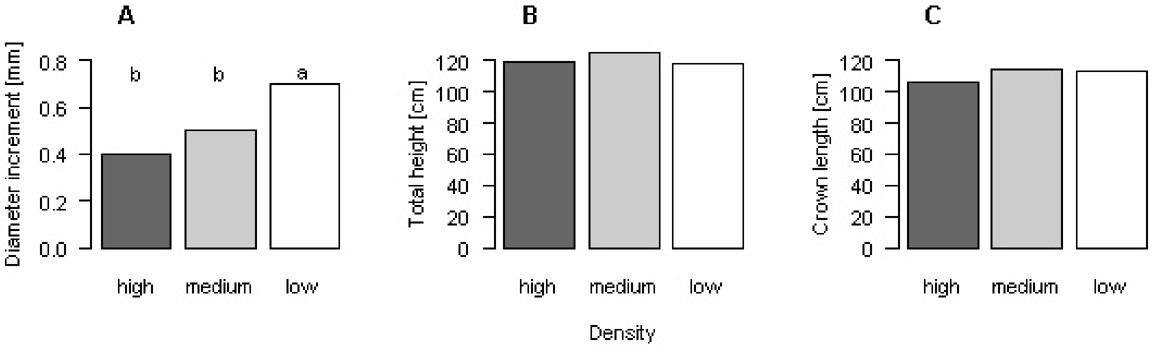

Fig. 5.1 The effect of density on sapling diameter increment (A), total height (B) and crown length (C). Significant differences between treatments are indicated by different letters (for further results see paper IV).

5.2 Diversity Effects on Tree Growth and Architecture

In stands older than 20 yrs, the projected crown area of target trees increased with higher functional diversity of neighbouring trees (p = 0.029; paper I). Moreover, the horizontal heterogeneity of the upper canopy was found to increase with higher stand functional diversity (measured as Rao's Q; p = 0.025; paper II). No significant effect of local species richness on radial growth increment could be detected (paper III). Similarly, no significant effect of species richness on growth and biomass production of saplings could be revealed (paper IV). In contrast, branch turnover (p = 0.043) and pruning (p < 0.001) of saplings was significantly enhanced with higher species richness.

5.3 Species Identity and Effects of Species Composition

Species-specific differences in tree growth and crown architecture may evidence the potential for complementary mechanisms if tree species occur together. In the permanent plots no species-specific differences in crown area, relative crown displacement and stem inclination were found (paper I). Rather the variation in the growth response of stem and crown within species was very high; i.e. individuals of all species are highly flexible in adjusting to their local environment. In contrast, species identity was a strong predictor of all growth and crown architectural variables in tree saplings (paper IV). Furthermore, complementarity with regard to biomass and crown length was found for specific species compositions of saplings (Fig. 5.2).

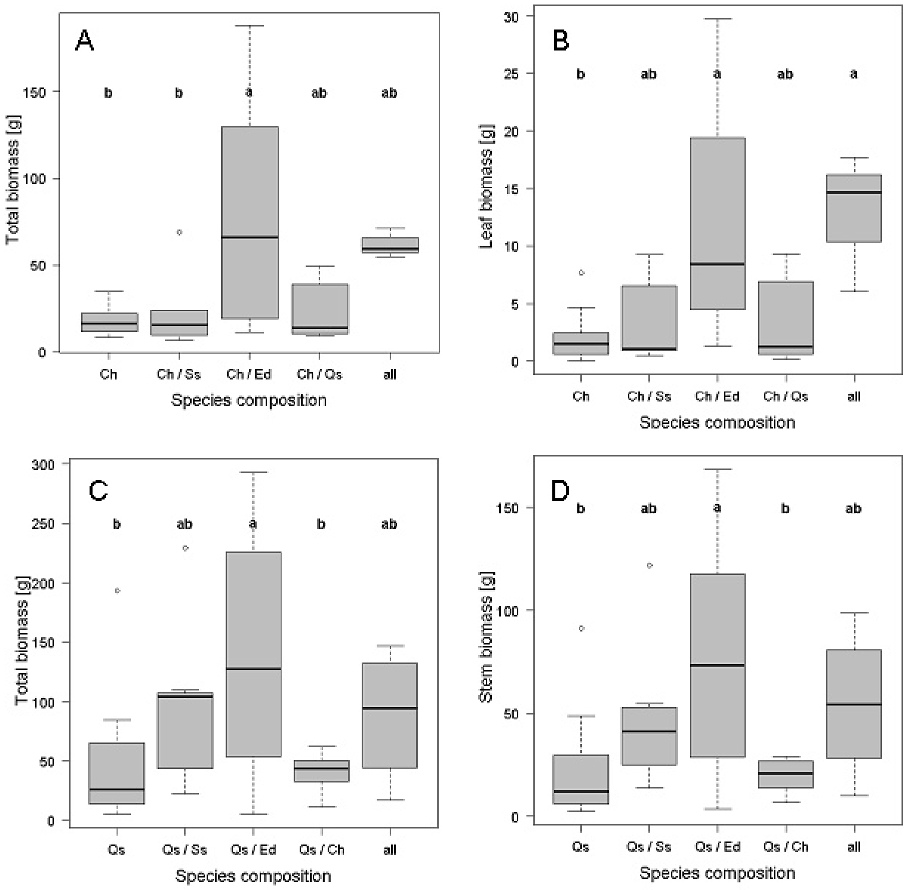

Fig. 5.2 Boxplots of the individual total biomass (A) and leaf biomass (B) of *C. henryi* and of total biomass (C) and stem biomass (D) of *Q. serrata* in the different species compositions (paper IV). Significances of post-hoc Tukey tests of the explanatory variable “species composition” tested by Models 2b are indicated by different letters. Species codes: Ch: *C. henryi*; Ed: *E. decipiens*; Qs: *Q. serrata*; Ss: *S. superba*.

5.4 Species Effects on Throughfall KE can be related to Crown Architectural Traits

The throughfall KE was significantly impacted by the rainfall KE, by the height of the saplings and by the species identity of saplings (paper V). In addition, the interactions of rainfall KE and sapling height and the interaction of rainfall KE and species identity of saplings were significant ($p < 0.05$). At the same time species were found to have a significantly different crown architecture with regard to total height, the number of branches and the angle of the first branch.

6 GENERAL DISCUSSION & FUTURE RESEARCH NEEDS

6 GENERAL DISCUSSION AND FUTURE RESEARCH NEEDS

To my knowledge this thesis is the first to study local neighbourhood effects in subtropical forest ecosystems in the framework of BEF research. The special focus on, and detailed analyses of, crown architectural and branch demographic variables presents a unique approach for competition analyses of neighbouring trees in these ecosystems.

6.1 Effects of the Local Neighbourhood

In accordance with the findings of the Panama project (Potvin & Gotelli 2008; Potvin & Dutilleul 2009), all studies of the present thesis dealing with growth characteristics of tree individuals proved the significance of the local neighbourhood. Distinct attributes of neighbouring trees were found to affect different growth parameters over a large age gradient, reaching from experimentally manipulated saplings (> 1 yr) to mature trees (> 80 yrs). Thus, it might be advisable to widely include local neighbourhood analyses into forest ecology research. The factors forming competition within the local neighbourhood are manifold:

The experimentally manipulated density of neighbours negatively impacted the diameter increment of saplings (paper IV). Increased density leads to enhanced competition for light (Cournede *et al.* 2008). This was underpinned by a reduced crown length at constant height, when comparing low density with high density plots.

In competition indices, increased density of neighbouring trees translates to a higher competition index, since the values for all neigbouring trees are commonly added (e.g. (Biging & Dobbertin 1992). Competition accounted for a high percentage of radial growth variation (paper III) and for a reduction in crown area (paper I).

However, competition is not only about the density of neighbouring trees. The size (quantified by dbh, total height or projected crown area) and the distance (in the case of distance-dependent indices) of neighbouring tree individuals is incorporated in the index as well. The importance of tree size was stressed by the finding of size asymmetric competition between neighbouring tree individuals (paper III). In addition, competition might be affected by diversity.

6.2 Diversity Effects on Tree Growth and Architecture

Different measures of diversity have been applied throughout the present thesis. Species richness as the number of species per plot was used as well as two different measures of functional diversity: the number of functional groups of the neighbouring trees (paper I) and stand functional diversity, calculated as Rao's Q of leaf traits (paper II). If we tested for both, species richness and functional diversity, in the same model (paper I and II), functional diversity proved to be a superior predictor of the parameters observed (crown area and canopy cover).

I have two hypotheses with regard to the impact of diversity on the observed variables:

(1) The commonly found relation between biodiversity and productivity of forest ecosystems may partly be explained by an indirect effect of diversity on individual tree crown area and stand level canopy structure.

A more diverse stand is characterised by a more heterogeneous canopy and by increased crown areas of tree individuals in sufficiently old stands (paper I and II). The differentiation in horizontal canopy space may be the effect of niche separation of individual tree crowns and promotes the development of increased crown areas. Larger crown areas caused by increased diversity, in turn, should be transformed to increased radial growth of the tree individuals (Fig. 6.1). Radial growth could be predicted by means of competition indices using crown area (paper III). Although, this study failed to detect any direct effect of species richness on radial-growth increments in young forests and saplings (paper III and IV), it seems reasonable that larger crown areas in diverse versus monospecific forest stands return increased yields. Besides being of economic advantage, a more heterogenous canopy offers multiple niches for organisms increasing overall biodiversity of the stand. By means of modelling it was recently found, that in the long-term competition for light alone induces a positive effect of tree species richness on productivity. This was due to complementarity of tree species in shade tolerance, maximum tree height and growth rates (Morin *et al.* 2011).

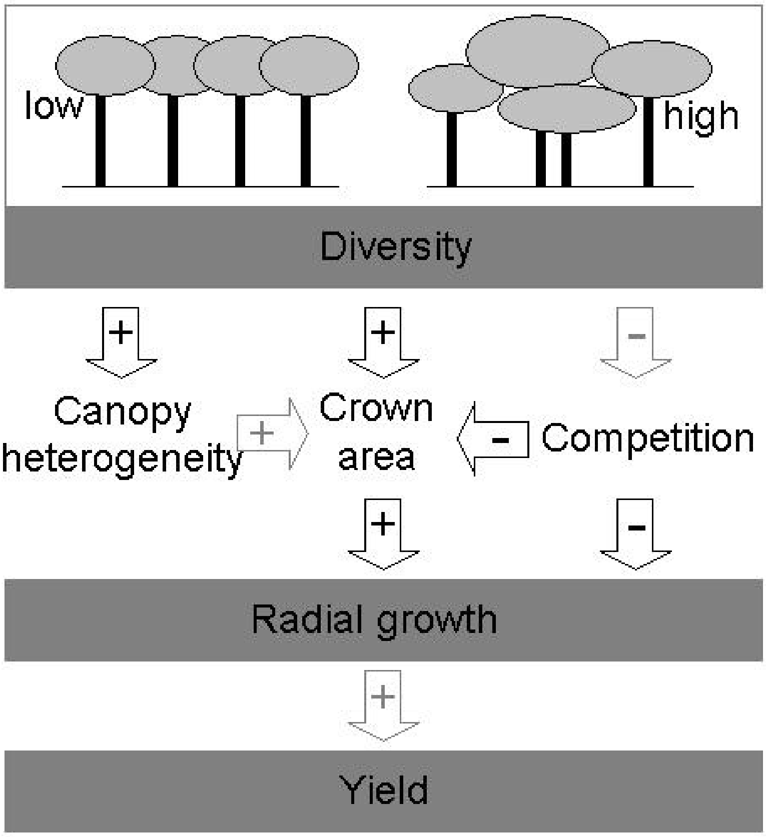

Fig. 6.1 The relation between biodiversity and productivity of forest ecosystems may partly be explained by an indirect effect of diversity on individual tree crown area and stand level canopy structure. Black arrows indicate correlations, found by this thesis; grey arrows indicate probable correlations; + means a positive, - a negative correlation.

(2) The importance of the diversity effect may be related reversely to that of species identity in an age gradient of forest stands (Fig. 6.2). While species identity, but not species richness was a strong predictor of growth and architectural variables of tree saplings (paper IV), functional diversity was a strong predictor in older stands, and no species-specific differences in growth parameters were detected (paper I). However, the weak effects of species richness (paper IV) may as well be due to the limited number of species used in the experiment.

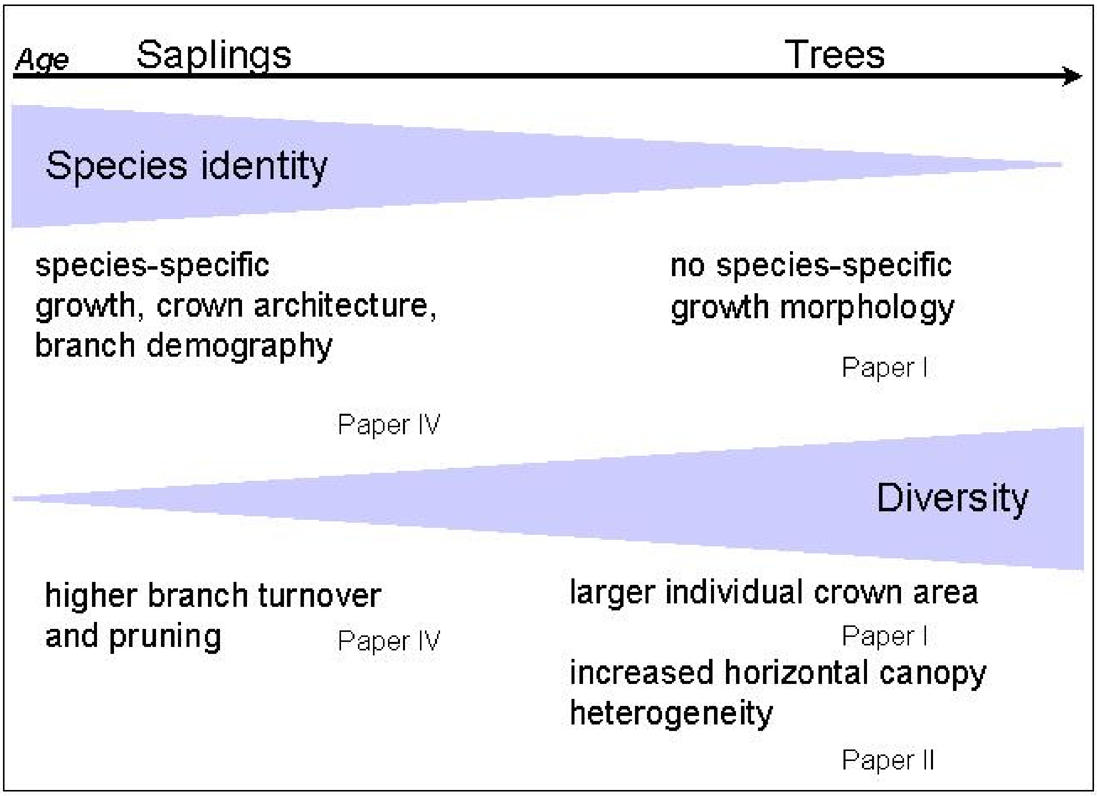

Fig. 6.2 The importance of the diversity effect may be related reversely to that of species identity in an age gradient of individual trees. Species-specific differences and diversity effects, found by this thesis are shown.

6.3 Evidence for Mechanisms of Coexistence

The findings of the present thesis suggest that mechanisms of coexistence (neutral and niche-based) operate simultaneously, but that their relative importance may change through the life stages of the subtropical tree species observed. During the sapling stage, species-specific differences in growth and architectural traits support the niche theory. In addition, I found evidence for facilitative or complementary mechanisms between specific species.

In older forest stands, no species-specific differences in growth parameters could be detected. The variability of the observed parameters within species was higher than between species (paper I). In accordance, Böhnke *et al.* (2012) stated the functional equivalence of species with respect to wood traits using the same permanent plots. This supports the neutral theory of community assembly with regard to these traits. However, I found a relation of stand functional diversity and horizontal canopy structure (paper II) and an effect of functional diversity on crown area.

I conclude that mechanisms of coexistence may not only change through life stages but may also differ for distinct traits. Since the relationship between diversity and ecosystem functions relies on differences in traits, the relationship itself may change through life stages and may depend on the observed ecosystem functions.

6.4 The Importance of Crown Architectural Traits for the Prediction of Ecosystem Functions

Crown projection areas proved to be a significant factor for the prediction of radial-growth increment by means of competition indices (paper III). Differences in crown architecture and branch demography were found to add to the competitive performance of species in the sapling experiment (paper IV). In addition, the effect of species on the kinetic energy of rainfall could be related to their species-specific architectural traits of crown and branches (paper V). Several studies show the effect of crown architectural traits on growth of individual-trees (Biging & Dobbertin 1992; Brown *et al.* 2004; Drobyshev *et al.* 2007) and relate them to the competitive abilities of species (Menalled 2001; Aiba & Nakashizuka 2009). However, to my knowledge, this is the first study relating crown architectural traits to ecosystem functions within the BEF framework and in the species rich subtropical forest ecosystems. I expect crown architecture and canopy structure to indirectly influence a number of additional BEF relations.

6.5 Future Research Needs

The present thesis provided new insights in possible mechanisms driving the positive relation between tree species richness and productivity. It improved the knowledge of subtropical tree species, and of important factors of local neighbourhood relations and finally it raised awareness for further research needs. Following, I point to the most important future research questions:

(1) Does species richness or functional diversity of the local neighbourhood reduce competition between tree individuals?
Although the present thesis revealed a positive effect of diversity on the crown area of mature trees, the direct effect of diversity on radial growth in older stands needs further investigation. In addition, it remained open if diversity effects on plot level are the aggregated effects of local neighbourhood interactions.

(2) How does the high steepness of slopes of many subtropical and tropical forest ecosystems together with the species richness of these forests determine the spatial arrangement of crowns?

To sufficiently explain the effect of slope inclination on the horizontal and vertical canopy structure, a three-dimensional analysis is necessary. Eventually, the light environment in dependence of slope aspect and inclination could be calculated and set in relation to structural parameters of the canopy.

(3) Are mechanisms of coexistence similar between tropical, subtropical and temperate systems? Does inter- and intra-specific competition between tree species follow similar mechanisms in these systems?

Individual tree growth was found to be mainly affected by the local neighbourhood in the subtropics (paper III) as well as in the tropics (Potvin & Gotelli 2008; Potvin & Dutilleul 2009). Thus, it is conceivable that differences in e.g. the proportion of co-occuring evergreen vs. deciduous species between both systems may be reflected in the local neighbourhood interactions. At the same time the positive relation between stand diversity and productivity was found in subtropical and tropical systems likewise. Thus, basic mechanisms between species or tree individuals such as complementarity may act in a similar way. Therefore it is interesting to compare the mechanisms of complementarity between subtropical and tropical systems.

7 ACKNOWLEDGEMENTS

7 ACKNOWLEDGEMENTS

First, I want to thank Goddert von Oheimb for his constant support, patience, encouragement, empathy and good humor. It was always possible to discuss urgent scientific but also science-related questions.

I am thankful for all the help, assistance and confidence of Werner Härdtle who made it possible for me to do this PhD-thesis within the BEF-China project.

I appreciate very much to share the office, lots of Chinese experiences and some spare time with Dr. Andreas Schuldt. He is always willing to help me and after some thinking he would usually hand a paper to me with some nice helpful information. Thanks!

It was just great that I had the chance to meet all the PhD collegues from the BEF China. I think that, being that bunch of different characters, we have been a great team (!), grown together in a –at the beginning sometimes hostile, foreign world. Living and working together with you, with some closer than with others, was a very nice experience. And most of you turned out to be very good friends!

Of course the BEF China is not only the PhDs and I am particularly greatful to the whole group of researchers. It was always possible to get advice and I was and am very impressed by all of your enthusiasm for science and for the BEF China especially.

In the field, I got a lot of help of Ilka Wäsche, Jonas Daldrup, Markus Püschel and Anna Saave. Thanks!

Thank you Fang Teng! Nǐ shì wǒde lǎo shī and if I am still allowed to say wǒde gēgē.

I would also like to thank Xuefei, who was able to explain a lot of Chinese culture and life to me. With her knowledge of European lifestyle she proved to be a translator between worlds.

Mr Lian and Mrs Liu and her daughters, but also Chen Lin, Yang Bo and Uncle Wang became my ”Chinese family”. Xièxie nǐmen.

Statistics was one of my personal biggest challenges of this thesis and I am very happy to know that I can always ask Henrik von Wehrden for his help, advice and opinion. It is great to have an expert just in the next building.

Although I did not spend that much time in Lüneburg, I appreciate very much the atmosphere and all the very nice people from my working group here. Thanks for all of your help!

I love to live in my house WEGEE because of you – my flatmates. Thanks for being so patient with me during the bad times, when the mountain of work seemed too high, and thanks also for sharing the happiness when life was easy!

Thanks to my family who is always there and supporting me in any situation.

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Overview of articles, included in the present thesis:

Paper	Reference	Own contribution
I	**Lang A.C.**, Härdtle W., Bruelheide H., Geißler C., Nadrowski K., Schuldt A., Yu M. & Von Oheimb G. (2010). Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *Forest Ecology and Management* 260: 1708-1715.	Main (1.0)
II	**Lang A.C.,** Härdtle W., Bruelheide H., Kröber W., Schröter M., von Wehrden H. & von Oheimb G. (2012). Horizontal, but not vertical canopy structure is related to stand functional diversity in a subtropical slope forest. *Ecological Research* 27: 181-189.	Main (1.0)
III	von Oheimb G., **Lang A.C.**, Bruelheide H., Forrester D.I., Wäsche I., Yu M. & Härdtle W. (2011). Individual-tree radial growth in a subtropical broad-leaved forest: The role of local neighbourhood competition. *Forest Ecology and Management*, 261: 499-507.	Important (0.5)
IV	**Lang, A.C.**, Härdtle, W., Baruffol, M., Böhnke, M., Bruelheide, H., Schmid, B., von Wehrden, H., von Oheimb, G. (accepted). Mechanisms promoting tree species coexistence: Experimental evidence with saplings of subtropical forest ecosystems of China. *Journal of Vegetation Science* DOI 10.1111/j.1654-1103.2012.01403.x.	Main (1.0)
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	Paper I	**Paper II**	**Paper III**	**Paper IV**	**Paper V**
Conceptual design	**ACL**, GvO, WH	**ACL**, GvO	GvO, **ACL**	**ACL**, GvO, MBa, WH	GvO, TS
Development of research methods	**ACL**, GvO, WH	**ACL**, GvO	**ACL**, GvO	**ACL**, GvO, WH	**ACL**, CG
Data collection and preparation	**ACL**, CG	**ACL**, WK, MS	**ACL**, IW	**ACL**, MBa, Mbo	**ACL**, CG
Realisation of research	**ACL**	**ACL**	**ACL, IW**	**ACL**	**ACL,** CG
Data analyses	**ACL**, KN, AS	**ACL**, HvW	DIF, GvO, IW	**ACL**, HvW	**ACL**
Data presentation	**ACL**	**ACL**	GvO	**ACL**	**ACL**
Writing of manuscript	**ACL**	**ACL**	GvO	**ACL**	**ACL**, CG
Internal revision of manuscripts	**ACL**, AS, CG, GvO, HB, KN, WH, MY	**ACL**, GvO, HB, MS, WH	**ACL**, DIF, GvO, WH, MY	**ACL**, GvO, HB, MBa, MBö, WH	**ACL**, CG, GvO, TS, WH

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

Lüneburg, Februar 2012

Erklärung

Ich versichere, dass ich die eingereichte Dissertation „The Role of Tree Diversity on Individual Tree Growth, Crown Architecture and Branch Demography” 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 die 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.

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von Oheimb G., **Lang A.C**., Bruelheide H., Forrester D.I., Wäsche I., Yu M. & Härdtle W. (2011). Individual-tree radial growth in a subtropical broad-leaved forest: The role of local neighbourhood competition. *Forest Ecology and Management*, 261, 499-507.

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PAPER I

Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China

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Keywords: Gutianshan National Nature Reserve, stem inclination, crown displacement, crown projection area, functional diversity

Forest Ecology and Management 260 (2010) 1708 – 1715

Abstract

Trees are able to respond to their local biotic and abiotic environment with morphological adjustments which improve resource acquisition and, thus, growth. In forests, light is broadly recognised as one of the major factors determining growth, and morphological responses comprise changes in crown architecture and stem stature. On sloping terrain, the interplay of phototropism and gravitropism may further affect morphological growth characteristics. However, different tree species are expected to show species-specific responses. In this study, we analysed three growth characteristics of tree individuals belonging to four species of two functional groups (evergreen: *Schima superba, Castanopsis eyrei,* deciduous: *Quercus serrata* var. *brevipetiolata, Castanea henryi*) in a species-rich Chinese subtropical forest. Crown projection area, relative crown displacement and stem inclination were related to biotic (local species richness, functional richness, competition, stand age) and abiotic (slope aspect and inclination, soil depth) variables in the local neighbourhood of the tree individuals. We hypothesised that (i) there are species-specific differences in the morphological response of crown architecture and stem stature and (ii) that crown size and asymmetry as well as stem inclination are influenced by both, biotic and abiotic factors. In contrast to our expectations we were unable to reveal any species-specific differences in any of the three growth characteristics. The results of mixed effects models showed that crown area was mainly affected by the target tree's dbh and biotic variables related to neighbours (competition, functional diversity), whereas stem inclination was mainly influenced by slope. Relative crown displacement was influenced by both, biotic and abiotic variables. We conclude that growth responses resulting in crown displacement and stem inclination seem to be an important mechanism to ameliorate foraging for light in our study area, but that these responses appear to be species-independent. The interplay of stem inclination and crown displacement allows for a plastic response of tree individuals in biotically and abiotically heterogeneous environments. Our results indicate that forest management in this region should focus on functionally diverse stands which are promoting crown area positively resulting in increased growth rates of individual trees.

1 Introduction

The stature of a tree individual at any given time is the result of growth processes that closely interact with, and respond to, the local environment. In forests, light is broadly recognised as one of the major factors determining growth. In addition, light is the most important example of a resource that generates size-asymmetric competition (Schwinning and Weiner, 1998; Nord-Larsen et al., 2006, Potvin and Dutilleul, 2009).Grams and Andersen (2007) suggest that morphological responses such as crown size and crown architecture may be the most important results of size-asymmetric competition for light. Lower photosynthetically active radiation and a decreased red to far-red ratio, as an effect of shading by surrounding and overtopping vegetation, may induce shade-avoidance responses of tree individuals (Ballare, 1999). Under strong, evenly distributed competition for light by surrounding vegetation (e.g. in even-aged and mono-specific stands of high density), tree individuals may promote height growth rates as compared to lateral growth rates by increased allocation of resources to stem elongation and decreased allocation to lateral branches (Takenaka, 2000). As a result, the crown projection area (projection of the horizontal crown extent) may be lower at higher levels of competition for light. In a heterogeneous environment, tree crowns respond to anisotropic light availability with stronger lateral crown expansion towards high light conditions (phototropic growth), resulting in crown asymmetry. The development of asymmetric crowns may be intensified by correlative inhibition, i.e. the growth of branches in favourable conditions is increased at the expense of the growth of branches in unfavourable conditions (Stoll and Schmid, 1998; Takenaka, 2000). The direction or degree of crown asymmetry can be assessed by measuring the divergence of the centroid of the projected crown area from the position of the stem base (crown displacement). Following changes in resource availability, crown foliar and branch responses are generally more rapid and more plastic than stem increment or height growth responses. Crown projection area and crown displacement are, therefore, very sensitive growth responses to competition (Getzin et al., 2008).

Light conditions are, however, not only affected by the local neighbourhood (i.e. biotic) interactions, but also by abiotic factors. In addition to latitude, topography is the major abiotic factor influencing the direction and intensity of incoming sunlight. On sloping terrain the lines of equal light intensity run parallel to the ground (Alexander, 1997; Ishii and Higashi, 1997). Therefore, the most efficient height growth of trees should occur at a right angle to the ground, resulting in stems that incline in a downhill direction on slopes. However, for biomechanical reasons there has to be an optimal angle for the stem on a slope; this is neither vertical nor perpendicular to the ground, but somewhere in between (Ishii and Higashi, 1997). Crown asymmetry was also found to be affected by slope (Umeki, 1995a; Getzin and Wiegand, 2007). For example, Sumida et al. (2002) observed more primary branches inclining in a downhill than in uphill direction for *Castanea crenata*. In a downhill direction the trees can reach the upper canopy more easily because the average canopy height is lowest on this side. Thus, on sloping ground the interplay of both abiotic and biotic factors may result in stem inclination together with crown asymmetry.

Observational studies have shown that tree crowns and stems respond to anisotropic light in a species-specific way (Umeki, 1995a; Matsuzaki et al., 2006). For example, Umeki (1995a) showed that *Betula maximowicziana* had greater crown asymmetry than *Picea abies*, and that crown asymmetry of *B. maximowicziana* was more influenced by slope inclination than by neighbouring trees, while the opposite was found for *P. abies*. In a Japanese slope forest, stem inclination was lowest for the coniferous species *Cryptomeria japonica*, intermediate for *Pinus densiflora* and the evergreen oak species *Quercus myrsinaefolia*, and largest for the deciduous oak species *Quercus serrata* (Matsuzaki et al., 2006). According to niche theory, it is conceivable that these species-specific differences may promote species coexistence (Wills and Condit, 1999; Wills, 2006; Zillio and Condit, 2007; Levine and HilleRisLambers, 2009). These relationships may, thus, become particularly interesting when analysing the mechanisms underlying the exceptional species richness of tropical and subtropical forests. On a local neighbourhood scale, species identity may influence the degree and intensity of neighbourhood competition (Yoshida and Kamitani, 2000). Tree biodiversity experiments have revealed positive complementarity effects in mixtures (Pretzsch, 2005; Potvin and Gotelli, 2008). One explanation for these findings is that aboveground space is used complementarily because tree architecture is species-specific, thus enabling more efficient light exploitation (Pretzsch and Schütze, 2009).

In tropical forests, growth of species is influenced by variable degrees of intra- and interspecific competition (Hubbell, 2001b; Stoll and Newbery, 2005; Massey et al., 2006).

Morphological responses of trees might, therefore, be influenced by the local neighbourhood diversity level. For example, in a more diverse forest the canopy layer is usually more structured, with the effect that light is distributed more patchily, creating a more heterogeneous light environment. In such an environment, stem inclination might not only be influenced by slope but stems might incline towards gaps to avoid competition. As a consequence, stem inclination might be more variable in diverse stands.

In this study, we investigated whether there are species-specific differences in the morphological response of crown and stem stature of important tree species in Chinese subtropical forests, and how crown size and asymmetry, as well as stem inclination, are influenced by biotic and abiotic factors. These forests are of particular interest for diversity research because they are almost as rich in woody species as tropical forests (Wills et al., 2006; Legendre et al., 2009). Furthermore, they represent a formerly widespread ecosystem in South and East China (Wu, 1980), which is currently under high pressure from intensive land use (Wang et al., 2007). The study was carried out in the National Nature Reserve (NNR) of Gutianshan (eastern China), where the occurrence of the majority of woody species is not significantly related to slope, aspect, elevation or convexity (Legendre et al., 2009; Bruelheide et al., in press). Although most species do not show habitat preferences, they might still show different morphological responses to abiotic site factors such as slope inclination. For the present study, four target tree species (*Schima superba*, *Castanopsis eyrei*, *Q. serrata* var. *brevipetiolata*, *Castanea henryi*) were selected because of their high abundance in this forest type (Yu et al., 2001). Crown projection area, crown displacement and stem inclination were measured for all target individuals. Furthermore, biotic (species richness, functional diversity, competition, mean upper canopy height) and abiotic parameters (slope inclination and aspect, soil depth) were recorded for each target tree together with its neighbours. To our knowledge, this is the first study to analyse crown projection area, crown displacement and stem inclination together and discuss the findings within the framework of biodiversity research.

Our specific hypotheses were: (H1) there are species-specific differences in the growth response of stem and crown on forest slopes. In particular, we expected differences between early (*Q. serrata* and *C. henryi*) and late successional (*C. eyrei*) target species, and between deciduous (*Q. serrata, C. henryi*) and evergreen (*S. superba and C. eyrei*) species. (H2) The morphological response of crown and stem is influenced by both biotic and abiotic parameters.

2 Materials and methods

2.1 Study site

This study was conducted in Gutianshan NNR which is located in Zhejiang province (eastern China, 29º8'–29º17' N, 118º2'–118º11' E) and covers an area of about 81 km². The area formerly belonged to, and was used by, a forestry company. Prior to its recent status as an NNR (since 2001), it had been protected as a National Forest Reserve since 1975. The Gutianshan NNR is situated in the subtropics with a warm temperate climate and a short dry season in winter. The mean annual temperature is 15.1 °C and the mean annual precipitation is about 2000 mm (Hu and Yu, 2008).

The predominant vegetation type is subtropical forest, with evergreen broad-leaved dominating over summergreen broad-leaved species (Wu, 1980; Hu and Yu, 2008). A total of 1426 seed plant species of 648 genera and 149 families have been recorded in this forest reserve. The area is heterogeneous with respect to the successional stages that are present in the forest, with older stands dominated by *C. eyrei* and *S. superba* and younger dominated by *P. massoniana* and *Q. serrata* var. *brevipetiolata* (for a detailed species list see Bruelheide et al., in press). Anthropogenic influences such as logging and natural disturbances such as typhoon and snow and ice breakages are evidenced e.g. by the presence of *Pinus massoniana* and *Q. serrata* var. *brevipetiolata* even in the old-growth forests. Our study sites comprise intermediate to steep slopes (ranging from 10° to more than 50°) and small-scale changes of aspect. The elevation ranges from 300 to 1250 m above sea level. Since only a few individuals showed signs of sable growth, it is assumed that ground slides do not occur regularly (other than topsoil erosion). Further details about the Gutianshan NNR are given by Lou and Jin (2000), Yu et al. (2001), Hu and Yu (2008), Legendre et al. (2009), Schuldt et al. (2010) and Bruelheide et al. (2011).

2.2 Study design

We decided on an individual-based approach to elucidate our hypotheses. We selected four tree species of high abundance (Yu et al., 2001): *S. superba* Gardn. et Champ., *C. eyrei* (Champ. ex Benth.) Hutch., *Q. serrata* var. *brevipetiolata* and *C. henryi* (Skan) Rehd. et Wills. called target species. The target species belong to different functional groups, since *S. superba* and *C. eyrei* are evergreen and *Q. serrata* and *C. henryi* are deciduous.

Data sampling was conducted during summer and autumn 2008 on 27 plots (each 30 m x 30 m on the ground) which were randomly selected within the NNR, stratified by successional age and which exclude slopes steeper than 55°. The plots were further investigated in the context of the newly established biodiversity and ecosystem functioning project China (BEF China) (Bruelheide et al., in press). It is important to cover different successional ages from young to old stands because tree growth and competitive interactions are influenced by stand age (Filipescu and Comeau, 2007). Twenty target trees per species were chosen randomly within the plots from all individuals complying with the following criteria: (i) single stemmed; (ii) diameter at breast height (dbh, 1.3 m above ground) >10 cm (intermediate and old permanent plots) or dbh >3cm (in young permanent plots); (iii) crown position in the upper canopy layer; (iv) each target species could only be selected once per plot. Thus, the 20 target trees of each species were spread over 20 of the 27 permanent plots with the exception of *C. henryi* (10 trees in 10 plots) for which only 10 individuals fulfilling all the criteria were found.

Local biotic conditions (local species richness, local functional diversity, competition) were assessed by recording the position, size and identity of the neighbours of each target tree. Neighbours were defined as all individuals whose top height (corrected for the slope position (z-axis)) cut the hull of a reversed cone with an opening angle of 70° and positioned with its tip at the foot of the target tree (following the method of Biging and Dobbertin, 1992). They also had to fulfil the minimum dbh criterion (criterion (ii) above). Each target tree, together with its local neighbours formed a group. Each target tree had a mean number of 10.9 (± 6.0 SD) neighbours, resulting in a total number of 837 surveyed individuals.

2.3 Measurements and calculated variables

Crown radii in the eight subcardinal directions were determined by means of a crown mirror. The crown projection area (hereafter crown area) was calculated using the formula for a polygon. In cases of extraordinary crown displacement – the crown projection did not include the stem base – the distances to the proximal and distal edge of the crown were measured in all possible directions (if this was only possible for one direction, four crown radii were measured as follows: the distances to the proximal and distal edge of the crown were determined and, starting at the centre of this crown diameter, on the axis perpendicular to it (Fig. 1A and B). In this case, crown area was approximated as a quadrangle). Relative crown displacement (rd) was considered to be the distance of the centre of gravity of the crown area from the stem base, divided by the mean crown radius (Longuetaud et al., 2008) (Fig. 1A). In cases where the centre of gravity perfectly matches the stem base, rd is equal to 0.

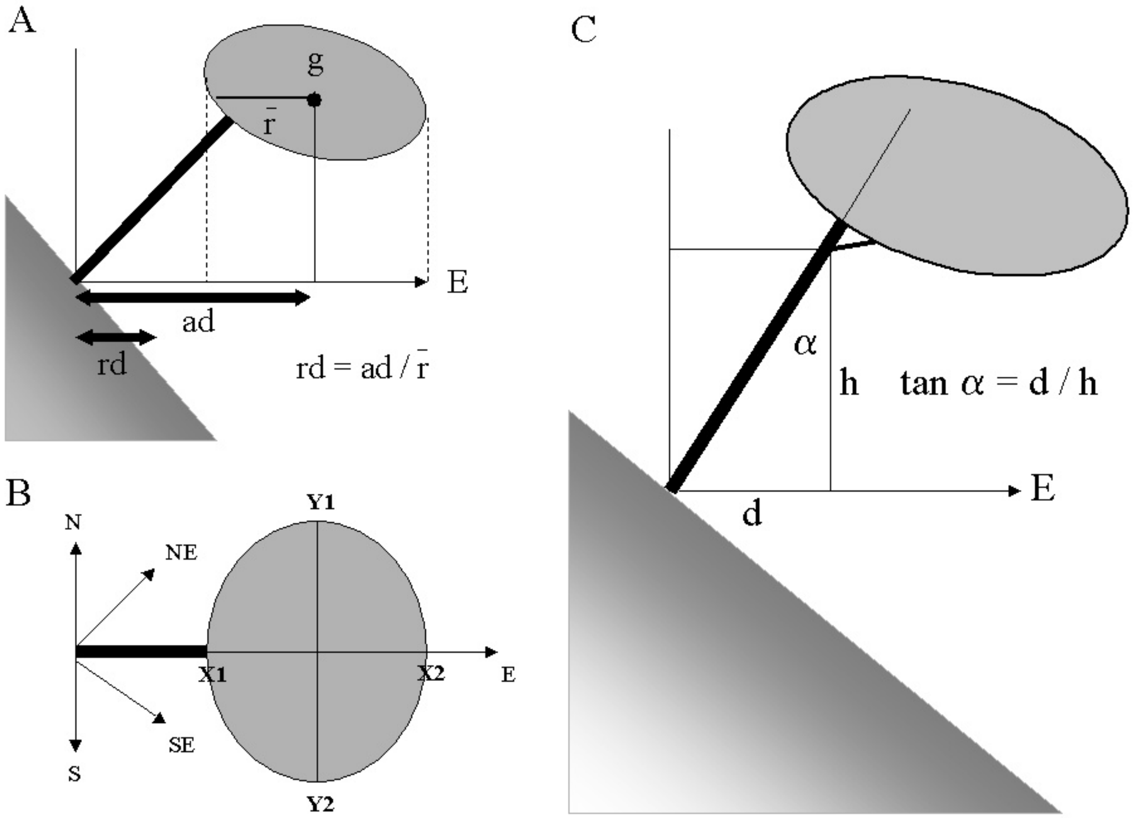

Fig. 1: Tree growth on extreme slopes. (A) Lateral view: absolute crown displacement (ad) is the distance of the stem base to the calculated centre of gravity of projected crown area (g); relative crown displacement (rd) is computed as ad divided by the mean crown radius (r); dotted line: crown projection eastwards. (B) View from above: for trees with extreme crown displacement, crown is measured twice in one, in this case eastern, direction (X1, X2) and, starting at the centre of the distance X1 to X2, on the axis perpendicular to this axis (Y1, Y2). (C) Calculation of stem inclination: angle of inclination (α) in relation to the vertical; h: height of bifurcation point d: horizontal distance of stem base to the bifurcation point of the crown.

Main tree stems may deviate from vertical stature in two different ways: stem inclination and stem bendiness, with the former involving straight but leaning stems and the latter bent or curved stems (Schamp et al., 2007). In the forest interior of Gutianshan NNR bent growth forms are confined to a relatively small number of trees. To obtain the degree of stem inclination, we first measured the height of the bifurcation point (height at which the lowest living crown branch of the tree branches off, excluding epicormics or springs), and then the horizontal distance of the bifurcation point from the stem in the direction of the slope (Fig. 1C). The angle of inclination was calculated as tan α of these two distances (Fig. 1C). If the stem was inclined towards the slope, stem inclination was considered to be negative. This method is similar to that used by Matsuzaki et al. (2006), where stem inclination was defined by referring to a straight line between the stem base and the top of the tree. However, in our study we used the bifurcation point as a reference point in order to separate the effect of crown asymmetry from that of stem inclination. Our three response variables were recorded independently. Stem inclination was measured in the direction of the slope, whereas relative crown displacement was calculated by triangulation. The correction of the crown displacement by crown radius resulted in the independent variable of relative crown displacement. Correlations between the three response variables were negligible. The dbh (measured with a diameter measurement tape) and total height were recorded for all trees. The relative position of the neighbours to the target tree was measured as the horizontal distance from stem base to stem base. All height and distance measurements were conducted using a Forester Vertex Hypsometer (Haglöf, Sweden).

All neighbours were determined to species (or the nearest possible taxonomic level; for a full species list see Table 1). Local species richness (i.e. the species richness of the group) was estimated using the rarefaction method (Hurlbert's formula, 1971) of the vegan package in R (subsample size: two trees). We applied the same method to obtain a measure for local functional diversity. For this purpose we classified the species into seven functional groups (Table 1). Since our hypotheses are based on growth characteristics of crown and stem, the trees were allocated to the functional groups according to adult tree height (canopy tree vs. sub-canopy tree) (Poorter et al., 2006), leaf longevity (evergreen vs. deciduous) (Deng et al., 2008) and leaf morphology (simple leaves, compound leaves, needles). We decided to establish an additional functional group for Fabaceae, because of their well known ability to fix nitrogen and the resulting differential preconditions for growth.

To characterise the competitive power of the target tree we chose the distance-independent competition index (CI) of Daniels et al. (1986):

$$CI_j = dbh_j^2 * n / \sum_i dbh_i^2$$

where j is the subscript for the target tree, i for the neighbour and n stands for the number of neighbours. This CI is particularly useful for the comparison of individuals of differing age, since the multiplication of the target trees' dbh with n makes it robust against heterogeneity in stand density. The higher the CI, the larger the competitive power of the target tree in the respective neighbourhood.

Upper canopy height was defined as the mean height of the highest 20% trees in the respective group. These values ranged from 7.5 to 25.2 m and were used as an indicator of the age of the stand in which the tree group was located.

For each tree group, data for slope inclination and aspect were collected and transformed after Beers (1966). Soil depth, respresenting the soil column down to the C-horizon, and therefore maximal rooting depth, was measured within one soil profile per plot.

2.4 Statistical analyses

Statistical analyses were performed using R 2.10. (R Development Core Team, 2009) together with the packages vegan (Oksanen et al., 2008) and nlme (Pinheiro et al., 2009). We tested species-specific differences of crown area, relative crown displacement and stem inclination (H1) using a mixed effects model with species as fixed effect and plot as random effect (Table 2).

We refined our models by testing for main effects of abiotic and biotic environmental variables in order to verify their effects on crown and stem parameters (H2). Biotic variables included species richness, functional diversity, competition index, the dbh of the target tree and mean upper canopy height, while the abiotic variables were slope inclination, slope aspect and soil depth. Target species identity was also included as a categorical predictor variable. Similar to the previous models (H1), plot was included as random effect. All variables were z-transformed (mean of zero and standard deviation of one) prior to analyses to meet the requirements of normal distribution and homoscedasticity. We tested for multi-linear colinearity of all predictor variables (correlations between variables did not exceed R= 0.8).

Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances).

3 Results

There were no significant differences between the four target species for any of the response variables ($p>0.05$, Table 2). However, species-specific differences in relative crown displacement were close to our significance threshold. By comparing the fixed effects structure, the crown displacement of *C. henryi* was significantly larger than that of *S. superba* (Table 2).

Crown area varied considerably between individuals and ranged from 0.36 to 58.88 m^2 (mean: 10.17 m^2 ± 10.04 m^2). The linear mixed effects model explained 64% of total variance (adjusted R^2). The significant variables in the model were related to both the biotic (dbh, competition, functional diversity) and abiotic (soil depth) environment. Crown area increased with dbh of the target tree (effect size: 0.66 ± 0.13) and soil depth (effect size: 0.23 ± 0.09). The crown area was larger if the competitive power of the target tree was higher (effect size: 0.06 ± 0.09) and with higher functional diversity (effect size: 0.13 ± 0.09).

Relative crown displacement varied from 0.00 to 6.00 (mean: 0.83 ± 1.14). Our model explained 36% of the total variance (adjusted R^2). Two predictor variables, competition index and local slope inclination, contributed significantly to the linear mixed effects model explaining relative crown displacement. Relative crown displacement decreased with competitive power of the target tree (-0.28 ± 0.14), but increased with slope inclination (0.27 ± 0.13).

Inclination of stems ranged from –3.28° (stem inclined towards the upper slope) to 41.34° (mean: 9.74° ± 7.85°) from vertical. The linear mixed effects model for stem inclination explained 23% of the total variance (adjusted R^2). The only significant predictor variable was slope inclination. Steeper slopes resulted in a higher degree of stem inclination (effect size: 0.28 ± 0.13).

4 Discussion

No species-specific differences in the growth response of crown and stem.

While studying the growth response of four tree species on forest slopes in different competitive situations, we did not find any species-specific differences in crown and stem parameters. Our findings are thus in contrast to abundant evidence that tree species differ remarkably in the extent of their morphological responses to comparable environmental challenges (Umeki, 1995a; Muth and Bazzaz, 2002; Matsuzaki et al., 2006). In particular early successional species may have higher morphological plasticity than late successional species (Pretzsch and Schütze, 2005). Early successional species show e.g. greater canopy displacement because more extensive light foraging is necessary than for late successional (Muth and Bazzaz, 2002). Matsuzaki et al. (2006) found species-specific differences in stem inclination to be determined by phototropic responsiveness of species. Of four observed tree species they found *Q. serrata* to have the largest stem inclination. We also chose *Q. serrata* as a target species and together with *C. henryi* it represents early successional species, while *C. eyrei* is a late successional. *S. superba* is a very dominant species and can be found in forests of all ages. For this reason, we expected *Q. serrata* and *C. henryi* to show more flexible growth responses. Contrary to our expectations, we could not detect any significant differences in growth characteristics between the four target species. There is a slight indication that there could be differences in the relative crown displacement between *S. superba* and *C. henryi*. However, the sample size of *C. henryi* was limited. Thus, higher numbers of replicates would be needed to confirm our results.

Our results show that the variation in the growth response of crown and stem was very high within species, i.e. individuals of all species are highly flexible in adjusting to their local environment. This would be in accordance with Hubbel's (2001a) neutral theory. All individuals, independent of species identity, have equivalent potential to correct their crown and stem growth as a response to abiotic and biotic factors. Hubbell (2001a) argued that it is precisely the ecological equivalence of species that allows their coexistence. However, we studied only four species, and additional species should be included in future studies.

Table 2. (A) Results of the fixed effect of two-factorial (species - fixed, location - random) linear mixed effects models for crown and stem parameters. (B) Fixed effects structure for the model explaining relative crown displacement. Results are considered significant at p<0.05*.

A	**Species**		
Response variables	DF	F-value	p-value
Crown area	40	1.60	0.205
Stem inclination	40	0.80	0.501
Relative crown displacement	40	2.69	0.059

B	**fixed effects for relative crown displacement**			
Species comparisons	value	t-value	p-value	
C. eyrei vs. *S. superba*	0.1270933	0.44	0.661	
Q. serrata vs *S. superba*	0.5689474	1.91	0.063	
C. henryi vs. *S. superba*	**0.8658486**	**2.40**	**0.021**	*

* Results are considered significant at p < 0.05

Table 3. Results of mixed effects models for crown and stem parameter response to biotic and abiotic environmental predictor variables. Results are considered significant at p<0.05*; p<0.01**; p<0.001***.

		crown area			**relative crown displacement**			**stem inclination**		
Fixed effects	DF	F-value	p-value		F-value	p-value		F-value	p-value	
dbh	33	**96.40**	**<.0001**	***	0.79	0.380		0.16	0.692	
Competition	33	**10.49**	**0.003**	**	**7.72**	**0.009**	**	1.76	0.194	
Species richness	33	0.51	0.478		1.91	0.176		3.71	0.063	
Functional diversity	33	**5.19**	**0.029**	*	0.65	0.427		0.00	0.989	
Canopy height	33	0.54	0.467		0.10	0.752		2.40	0.131	
Local inclination	33	0.09	0.766		**6.32**	**0.017**	*	**8.49**	**0.006**	**
Local aspect	33	0.90	0.349		0.04	0.843		3.96	0.055	
Soil depth	25	**8.82**	**0.007**	**	0.20	0.660		3.42	0.076	
Species	33	0.50	0.683		1.69	0.188		1.58	0.213	

* Results are considered significant at p < 0.05
** Results are considered significant at p < 0.001
*** Results are considered significant at p < 0.0001

Parameters influencing growth responses

Crown area was mainly influenced by biotic parameters (dbh, competition, functional diversity). Since crown area is related to the size of the tree, the influence of dbh on crown area represents an allometric function. However, local neighbourhood competition also had a highly significant positive impact on crown area. The more competitive power the target tree had, the larger its dbh in comparison to the mean dbh of its neighbours, the more extended was its crown. This is in agreement with Simard and Zimonick (2005) and Getzin et al. (2008), who found that crown area is very sensitive to competition.

Functional diversity in the local neighbourhood was positively related to crown area of the target trees. This result may be explained by the existence of niches that promote the coexistence of individuals of different functional groups over that of individuals of the same group. Pursuant to our classification, a more functional diverse group should form a more structured canopy in terms of height stratification as well as timing of leaf occurrence and crown density (influenced by different leaf shapes). Growing in a functionally diverse neighbourhood may allow tree individuals to invest more in lateral branch growth and, thus, increase their light foraging efficiency. As crown area is closely related to the growth rate of tree individuals (Drobyshev et al., 2007), the diversity effects at the local neighbourhood level may also add up to a positive effect of functional diversity on productivity at the stand level (Scherer-Lorenzen et al., 2005). This implies that forest management should aim for the maintenance or creation of functionally diverse stands in this region. The majority of Chinese subtropical forests now exist as secondary forests (Wang et al., 2007). To preserve functionally diverse stands single-tree harvesting is recommended which at the same time helps to avoid soil erosion. A large proportion of the present forest area in the subtropical zone of China is occupied by mono-specific stands of conifers, in particular *P. massoniana* and *Cunninghamia lanceolata*. However, converting single-species conifer stands into mixed-species stands as well as using species mixtures in reforestation is now being seriously considered for various objectives in China, such as increased stand productivity, reduced pest damage or fire risks, biodiversity conservation, carbon sequestration, and soil erosion control (Wang et al., 2007; Lei et al., 2009; Zhang et al., 2009). Our results add evidence that there might be increased stand productivity due to complementary resource use or facilitation in functionally diverse stands.

It remains open to which degree the effect of functional diversity on crown area might be coupled to the effect of former canopy gaps. By creating heterogeneity in light levels gaps are known to promote and maintain species diversity (Runkle, 1989; Schnitzer and Carson, 2001). At the same time larger crown areas may indicate past presence of gaps.

In our model, the parameter “functional diversity” was superior to the parameter “species richness”. We conclude that our classification of functional groups is more important for crown area than species identity. The only significant abiotic parameter in the model was “soil depth”. Soil depth represents the limitation of rooting space in one dimension. The significant impact of soil depth could indicate the importance of belowground competition, which is probably more severe in a more restricted space. Belowground competition was found to have an influence on aboveground plant production (see Brassard et al., (2009) and references therein). Shallow forest soil may also be a constraint for mechanical anchoring which could be of importance in a topographic situation which is characterised by steep slopes, as is the case in our study area (Chiatante et al., 2002; Di Iorio et al., 2005). Slope inclination alone has apparently no direct influence on crown area. However, soil depth could give an indirect indication of slope steepness. In our study, the two variables were not related ($R^2=0.04$).

Relative crown displacement was influenced mainly by competition and steepness of slope. Relative crown displacement was lower when the target tree had greater competitive power than its neighbours. Results confirming that neighbouring trees influence crown displacement in individual-based approaches were found by e.g. Young and Hubbell (1991), Umeki (1995a), and Brisson (2001). Explanations for crown displacement are seen in the differential growth response of crown modules to differing light environments. In forests on slopes the way in which neighbours are included in the analyses is particularly important. When considering competition for light, neighbouring trees in uphill direction of the sampled target tree impose a stronger influence than trees in downhill direction. The inverse cone method takes this into consideration by including more neighbours in uphill than in downhill direction. In our model, slope steepness had a positive effect on crown displacement. Our findings thus support the output of the model of Umeki (1995b), who modelled the relationship between crown displacement and local environment. He found the crown vector to be a function of the position and size of neighbours and slope inclination.

Anthropogenic disturbances such as selective logging, resulting in the loss of neighbours and creation of canopy gaps, might have had an influence on relative crown displacement; however it was not possible to include this in our models.

We are aware that our study is short of a historical perspective which is beyond the scope of this work. Gap dynamics as well as changing competitive interactions influence growth processes of trees throughout their whole life span. Since trees are very longlived organisms these past growth conditions are preserved in their present stature. Crowns generally react faster to changes of the environment than the stem. This might contribute to the observed pattern that biotic factors representing the current environmental status are related to crown response, but not to stem response.

To our knowledge, this is the first study to relate both biotic and abiotic variables to stem inclination. However, only the inclination of slope had a significant impact on stem inclination. This is consistent with the results of Matsuzaki et al. (2006) and the theoretical work of Ishii and Higashi (1997, 1998). In addition to the mechanism which they describe of lines of equal light intensity running parallel to the ground, we think that inclined trees in upslope position of the sampled tree should influence the sampled tree as well. Since almost all trees in our study area had inclined stems (about 80 % of all 837 measured trees inclined in a downhill direction, and as few as 17 % did not deviate strongly from a vertical stature (degree of stem inclination < + 3°)), each individual was shaded by trees growing uphill of the sampled individual. In our model, phototropism would cause an inclination towards the remaining sunlight whereas gravitropism would result in a vertical uprightening. The direction of phototropism would be influenced by the stem inclination, distance and crown extension of the upslope tree individual (Fig. 2). Stem inclination of the target tree would thus be the outcome of the interplay of phototropism and gravitropism, similar to the experiments of Matsuzaki et al. (2006). Stem bending towards the direction of incoming sunlight was also observed by Schamp et al. (2007). The tree's own weight could also add to the inclination. In studies about crown asymmetry towards gaps it was observed that the increased load on one side caused some individuals to fall into the gap (Young and Perkocha, 1994). If selfload was essential, individuals would probably invest more in stem erecting and thus less in crown expansion. This would result in an influence of slope on the crown area observed. However, this could not be demonstrated by our analyses. Stem inclination seems not to be influenced by biotic factors. In particular, we were unable to detect any diversity-related effects on stem inclination.

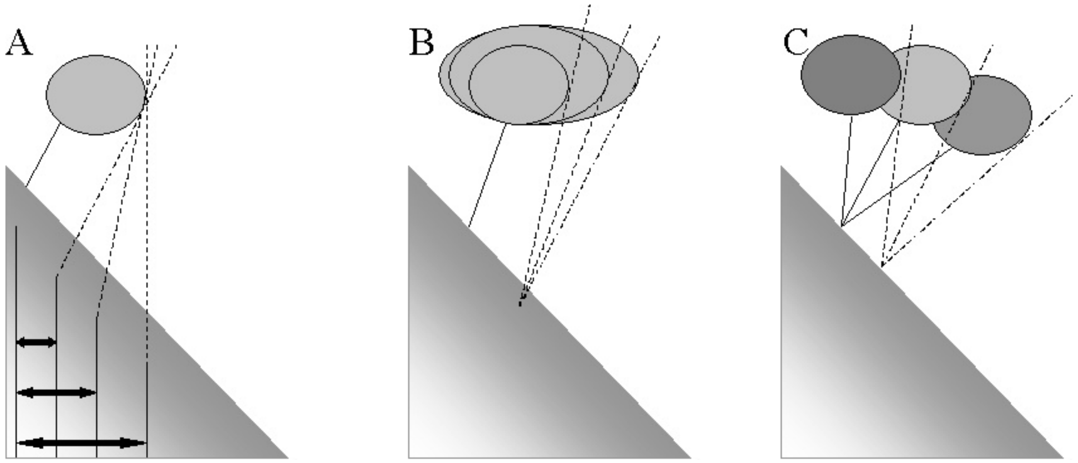

Fig. 2: **Factors influencing phototropism in a stand of uniformly inclined tree individuals**. Dotted line indicates direction of phototropism for the downslope neighbouring tree. (A) Distance of tree individual to the upslope neighbour, (B) crown extension of upslope individual, (C) stem inclination of upslope individual.

Table 1. List of all species (recorded as neighbouring trees) with family affiliation. Trees were divided into functional groups according to tree height (canopy tree: c; sub-canopy tree: s), leaf longevity (evergreen: e; deciduous: d), and leaf morphology (simple leaf: sl; compound leaf: cl; needle: nl); Fabaceae were established as separate functional group (f) (see text).

Family	Species	Functional Group
Aceraceae	*Acer cordatum* Pax	cdsl
Alangiaceae	*Alangium kurzii* Craib	cdsl
Anarcadiaceae	*Toxicodendron* spec.	cdcl
	Toxicodendron succedaneum (Linn.) Kuntze	cdcl
Aquifoliaceae	*Ilex litseifolia* Hu et Tan	sesl
	Ilex rotunda Thunb.	cesl
	Ilex spec.	cesl
Araliaceae	*Dendropanax dentiger* (Harms) Merr.	sesl
Daphniphyllaceae	*Daphniphyllum oldhamii* Hemsley	cesl
Ebenaceae	*Diospyros japonica* Sieb. et Zucc.	cdsl
	Diospyros kaki Thunb.	cdsl
Elaeocarpaceae	*Elaeocarpus chinensis* (Gard. et Champ.) Hook.	cesl
	Elaeocarpus decipiens Hemsley	cesl
	Elaeocarpus japonicus Sieb. et Zucc.	cesl
Ericaceae	*Rhododendron ovatum* (Lindl.) Planch.	sdsl
	Vaccinium bracteatum Thunb.	sesl
	Vaccinium carlesii Dunn	sesl
Fabaceae	*Albizia kalkora* (Roxb.) Prain	cdclf
	Dalbergia hupeana Hance	cdclf
Fagaceae	*Castanea henryi* (Skan) Rehd. et Wils.	cdsl
	Castanopsis carlesii (Hemsl.) Hayata	cesl
	Castanopsis eyrei (Champ. ex Benth.) Tutch.	cesl
	Castanopsis fargesii Franchet	cesl
	Castanopsis sclerophylla (Lindl. et Pax.) Schott.	cesl
	Castanopsis tibetana Hance	cesl
	Cyclobalanopsis glauca (Thunb.) Oers.	cesl
	Cyclobalanopsis myrsinaefolia Oerst.	cesl
	Lithocarpus glaber (Thunb.) Nakai	cesl
	Quercus phillyreoides Gray	cesl
	Quercus serrata Murray var. *brevipetiolata*	cdsl
Hamamelidaceae	*Liquidambar formosana* Hance	cdsl
	Loropetalum chinense (R. Br.) Oliv.	sdsl
Juglandaceae	*Platycarya strobilacea* Sieb. et Zucc.	cdcl
Lauraceae	*Lindera glauca* (Sieb. et Zucc.) Bl.	sdsl
	Litsea coreana Léveillé	cesl
	Machilus thunbergii Sieb. et Zucc.	cesl
	Neolitsea aurata (Hay.) Koid.	sesl
	Sassafras tzumu (Hemsl.) Hemsl.	cdsl
Myricaceae	*Myrica rubra* Sieb. et Zucc.	cesl
Oleaceae	*Fraxinus insularis* Hemsley	cdcl
	Osmanthus cooperi Hemsley	sesl
Staphyleaceae	*Euscaphis japonica* (Thunb.) Kanitz	cdcl
Pinaceae	*Pinus massoniana* Lamb.	cenl
	Pinus taiwanensis Hayata	cenl
Rosaceae	*Malus leiocalyca* Huang	cdsl
	Prunus schneideriana Koehne	cdsl

	Sorbus folgneri (Schneid.) Rehd.	cdsl
Sabiaceae	*Meliosma oldhamii* Miquel	cdcl
Styracaceae	*Styrax* spec.	cdsl
Symplocaceae	*Symplocos paniculata* (Thunb.) Miq.	sdsl
	Symplocos stellaris Diels	sesl
	Symplocos sumuntia Buch.-Ham.	sesl
Taxodiaceae	*Cunninghamia lanceolata* (Lamb.) Hook.	cenl
Theaceae	*Adinandra millettii (*Hook. et Arn.) Ben. et Hook.	cesl
	Schima superba Gardn. et Champ.	cesl

Acknowledgements

We are very grateful to Mr Teng Fang for all the help during the establishment of the permanent plots and for the valuable assistance in species determination. This work was funded by the German Science Foundation and carried out within the research group BEF China (DFG FOR 891/1). We are grateful for this support.

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PAPER II

Horizontal, but not vertical canopy structure is related to stand functional diversity in a subtropical slope forest

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Keywords: BEF-China, Gutianshan National Nature Reserve, niche differentiation, tree individual, coefficient of variation

Ecological Research 27 (2012): 181-189

Abstract

The aim of this study was to analyse the relation of horizontal and vertical canopy structure to tree functional diversity of a highly diverse subtropical broad-leaved slope forest, stratified for different successional stages. This is of particular interest because many key ecosystem processes and functions are related to the arrangement of forest canopies.

We assessed the effect of stand-related functional diversity (FD_Q, measured as Rao's Quadratic Entropy of leaf traits), together with other environmental variables on horizontal (measured as relative crown projection areas CPA_r) and vertical (relative crown overlap, coefficients of variation (CV) of crown positioning variables) structure of the upper canopy at the local neighbourhood level. The analyses with mixed effects models revealed a negative relation ($p = 0.025$; estimate: -0.07) between FD_Q and CPA_r. No significant effect of FD_Q on vertical canopy structure has been found ($p > 0.05$). The findings are discussed with regard to resource partitioning and niche differentiation of canopy and subcanopy species.

Successional stage positively impacted the CV of crown length ($p = 0.019$; estimate: 0.03), but did not affect other response variables. The sloping terrain strongly influenced vertical canopy structure as revealed by the significant effect of slope inclination on CV of crown length ($p = 0.004$; estimate: -0.05) and of slope aspect on CV of mean crown height ($p = 0.036$; estimate: -0.03). The high complexity of vertical crown positioning depending on the heterogeneous sloping terrain of the study area may have obscured relations of FD_Q to vertical canopy structure.

Introduction

In forests, many key ecosystem processes and functions are related to the horizontal and vertical arrangement of forest canopies (Song 2004; Pretzsch 2009). A canopy is defined by Parker (1995) as “the combination of all leaves, twigs, and small branches in a stand of vegetation; it is the aggregate of all the crowns”. The arrangement of the crown with its photosynthetically active foliage is decisive for the carbon balance of an individual tree (Ishii and Asano 2010). The local heterogeneity in abiotic and biotic conditions among modules (here: branches sensu Franco 1986) within each individual crown causes differential growth reactions of each module (Kawamura 2010). Scaling up to the higher level, the whole crowns tend to optimise the use of light, leading to strong lateral crown expansion in the direction of better light conditions under anisotropic light availability (light-related asymmetric growth of the crown; Umeki 1995; Brisson 2001). In addition, wind-induced crown collisions with neighboring trees, leading to bud abrasion and growth inhibition, shape tree crowns (Takenaka 2000). Accordingly, the crown projection area (i.e. projected area of the horizontal crown extent) is a very sensitive growth response variable of trees (Longetaud et al. 2008) and represents the horizontal canopy space use with regard to growing space and light harvesting (Pretzsch 2010).

In forest stands that are homogeneous in terms of age structure and species composition, crown asymmetry is a crucial feature that allows for a maximum crown projection area and an optimal space occupation of the horizontal canopy (Longuetaud et al. 2008; Schröter et al. 2011). In structurally complex temperate and subtropical slope forests Umeki (1995) and Lang et al. (2010), respectively, observed that crown asymmetry was influenced by both, local neighbourhood interactions and slope inclination. The use of a local neighbourhood approach in both studies reflects the growing interest in analyzing stand dynamics through individual tree-crown patterns (Seidel et al. 2011). However, the spatial response of crowns to the environmental conditions not only occurs in the horizontal, but also in the vertical dimension (Ishii and Asano 2010). In particular in mixed stands of tree species differing in shade-tolerance, leaf morphology or crown structure, stratified canopies with a high degree of crown overlap have been found (Kelty 1989, Menalled et al. 1998). Further attributes of tree architecture that enable variability in vertical crown positioning are total tree height, crown-base height, crown length and mean crown height.

The horizontal structure of the upper canopy layer can be defined as a mosaic of closed canopy and gap patches. By this mosaic a variety of light conditions is created in the lower stand layers. In addition, crown overlap in the upper canopy reduces the overall available light in the sub-canopy, but at the same time increases the heterogeneity of light distribution. Furthermore, a more heterogeneous upper canopy with regard to vertical crown positioning is assumed to promote the heterogeneity of sub-canopy light environment. Due to these interrelations, the structure of the upper canopy layer potentially shapes a mosaic of niches with regard to light (e.g. McKenzie et al. 2000; Van Pelt and Franklin 2000; Lhotka and Loewenstein 2008), nutrient and water supply (Prescott 2002) in the whole forest stand which may promote the coexistence of species by resource partitioning and niche differentiation. In turn, a more diverse sub-canopy community influences belowground competition for water and nutrients and thus impacts the growth of canopy trees. However, it is not clear whether increased tree diversity promotes belowground biomass production of fine roots which are important for the uptake of nutrients and water (Meinen et al. 2009).

Previous studies of diversity effects on canopy space use mainly focused on canopy trees. However, sub-canopy tree and shrub species often strongly contribute to overall stand diversity, and the interactions between canopy trees, sub-canopy trees and shrubs were found to be important drivers of tree growth during forest succession (Li et al. 1999; Duncan 2003). It is therefore important to include sub-canopy tree and shrub species in the definition of stand diversity and to test the relation of overall stand diversity of tree and shrub species on canopy structure.

The objective of this study was to analyse the relation of stand diversity on horizontal and vertical canopy structure of canopy trees in a complex subtropical forest ecosystem comprising different successional stages. On the one hand, it might be expected that each successional stage is composed of similar size classes of trees and shrubs with an optimal horizontal packing and low vertical stratification of the canopy (evidenced by high crown projection area and low crown overlap). On the other hand, it is conceivable that in species-rich forests, the highly heterogeneous mixture of woody species brings about a heterogeneous stand structure even within certain successional stages (von Oheimb et al. 2011), resulting in a lower crown projection area of canopy trees and higher vertical crown stratification. Thus, the overall relationship of stand diversity and canopy structure is not clear. To our knowledge, this is the first study to investigate the relation of stand diversity and the horizontal and vertical canopy structure in a highly diverse subtropical forest ecosystem.

We hypothesised that increased stand diversity results in a more heterogenous horizontal and vertical structure of the upper canopy. To validate this hypothesis we analysed the horizontal canopy structure as the sum of crown projection areas and the vertical canopy structure as crown ovelap and coefficients of variation of crown positioning parameters (total tree height, crown-base height, crown length and mean crown height) at the local neighbourhood level. To account for the complex environmental conditions we included successional stage, slope inclination and aspect, disturbance severity and anthropogenic impact in our analyses.

Materials and methods

Study site

We conducted our study in the Gutianshan National Nature Reserve (NNR) which is located in Zhejiang province (Eastern China, 29º8'18"–29°17'29" N, 118º2'14"–118°11'12" E) and covers an area of about 81 km². Prior to its recent designation as an NNR (in 2001), it had been protected as a National Forest Reserve since 1975. The Gutianshan NNR is located in the subtropics and has a warm temperate climate and a short dry season in winter (Nov, Dec). The mean annual temperature is 15.1 °C and the mean annual precipitation is about 1963 mm (Hu and Yu 2008). The study site comprises intermediate to steep slopes (ranging from 10° to more than 50°) and small-scale changes of aspect. The altitude ranges from 300 to 1250 m above sea level.

The predominant vegetation type is subtropical forest, with evergreen broad-leaved tree species dominating in abundance over summergreen broad-leaved tree species (Wu 1980; Hu and Yu 2008). The NNR is characterized by a high plant species richness and hosts a total of 1426 seed plant species belonging to 648 genera and 149 families. However, traces of its former economic use can still be found with respect to forest composition and structure. The area is heterogeneous with respect to the successional stages that are present in the forest. Older stands are dominated by *Castanopsis eyrei* (Champ. ex Benth.) Hutch. and *Schima superba* Gardn. et Champ., whereas younger stands are dominated by *Pinus massoniana* Lamb. and *Quercus serrata* Murray var. *brevipetiolata.* Former anthropogenic influences such as logging and current natural disturbances such as typhoon damage or snow breaks are evident in almost all parts of the NNR. Further details about the Gutianshan NNR are given in Lou and Jin (2000), Yu et al. (2001), Legendre et al. (2009), Schuldt et al. (2010) and Bruelheide et al. (2011).

Study design and measurements

Environmental plot-related variables

Data sampling was conducted during summer and autumn 2008 on 27 study plots (each comprising 30 x 30 m on the ground) established as part of the ‘BEF (Biodiversity and Ecosystem Functioning) China’ project. The plots were randomly chosen within the whole NNR (limited by inaccessibility and excluding slopes steeper than 55°), and stratified by successional stage. Five successional stages were distinguished: 1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: ≥ 80 yrs, and confirmed by tree coring (for details see: Bruelheide et al. 2011). We assessed the following explanatory variables at the plot level: A complete inventory of woody species (> 1 m height) was carried out to determine species richness. When defining functional diversity (FD), it is important to take the range of traits present and the abundance of the species with those characters into account. We chose Rao’s Quadratic Entropy (Rao’s Q) and calculated it for each plot as:

$$FD_Q(\mathbf{p}) = \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} d_{ij}\, p_i\, p_j \tag{1}$$

where N is the number of species in a plot (**p**), d_{ij} is the trait difference between the *i*th and *j*th species, and p_i and p_j are the proportions of the *i*th and *j*th species, calculated as number of individuals per species related to the total number of individuals in the community (Rao 1982; Botta-Dukat 2005). Differences between traits d_{ij} were calculated as the Euclidian distance between traits devided by the number of traits:

$$dij = 1/\mathrm{n} \sum_{k=1}^{n} (X_{ik}-X_{jk})^2 \tag{2}$$

where n is the number of traits considered, X_{ik} value of trait *k* in species *i*. Functional diversity as Rao’s Q of a plot equals the sum of differences in species traits, weighted by the abundance of the respective species within the plot. To remove redundant information and obtain traits as uncorrelated as possible (cf. Leps et al. 2006), the 8 traits with the highest loadings on the first and second principal component analysis (PCA) axis were chosen from a PCA including 38 leaf traits (divergence to PCA axes) (these were: specific leaf area, leaf dry matter content, content of nitrogen, aluminium, calcium and phosphorus, C/N ratio, stomata density). In addition, predictors were selected, which had higher loading on either one of the axes, and not on both. FD_Q has been defined as the differences in leaf traits between all the censused species of the study plots, since these differences and their plasticity are important determinants of light interception (Niinemets 2010).

Furthermore, slope inclination and aspect of each plot were recorded. To quantify the severity of disturbance by an unusual snow break event in February 2008, we used mean values of crown loss of all measured individuals per plot. Crown loss of all observed tree individuals was estimated as the percentage loss of the formerly undisturbed crown volume. Categories were defined as: undamaged: 0% loss ≅ 0, 1-25% loss ≅ 1 etc., crown completely broken 100% ≅ 5. Altitude above sea level was interpreted as an indicator of human impact, assuming that human impact such as selective logging would be restricted by decreased accessibility with increasing altitude.

Selection of target tree groups and individual-related measurements

Our response variables were based on measurements of horizontal and vertical crown parameters of canopy tree individuals. For these measurements we focused on 70 groups of upper canopy trees (formed by a target tree and its local neighbours; in the following referred to as target groups) that were spread over all study plots. All trees growing within a circular plot with a radius equal to half of the target tree’s height (Ammer et al. 2005) and fulfilling the criterion of minimum diameter at breast height (dbh, measured at 1.3 m above ground; see criterion (ii) below) were considered as neighbours. The number of neighbours ranged from three to 38, resulting in a total number of 996 surveyed individuals. Our method of observing groups of trees follows the notion of the importance of tree individuals and their local neighbourhood for forest stands, especially in BEF research (Potvin and Dutilleul 2009; von Oheimb et al. 2011). To allow for greater generalisability of tree individual-based measurements, we selected four highly abundant tree species (Yu et al. 2001) as target species: *S. superba*, *C. eyrei*, *Q. serrata* var. *brevipetiolata* and *Castanea henryi* (Skan) Rehd. et Wills.. Target trees were chosen randomly within the plots from all target species individuals complying with the following criteria: (i) single stemmed; (ii) dbh > 10 cm for intermediate and old successional stages 3-5 or dbh > 3 cm for young successional stages 1 and 2; (iii) crown position in the upper canopy layer; (iv) no serious damage due to recent snow break (less than 30% crown loss, no newly formed gap in close vicinity of the target tree). For every individual tree belonging to the studied target groups, the dbh (measured with a diameter measurement tape) and total height as well as the crown-base height (defined as the height at which the lowest living crown branch of the tree branches off, excluding epicormics or sprigs) were recorded. The relative position of the neighbours to the target tree was measured as the horizontal distance from stem base to stem base. All height and distance measurements were conducted using a Forester Vertex Hypsometer (Haglöf, Sweden). Crown length was computed as total height minus crown-base height and mean crown height as crown-base height added to half of the crown length. To characterise the sampling trees (of our target groups) within the different successional stages more thoroughly, we analysed relative frequency distributions of height classes (Fig. 1).

Crown radii in the eight subcardinal directions (N, NE, …., NW) were determined by means of a densiometer (a gimbal mirror positioned in an angle of 45°, allowing the precise observation of objects in orthogonality to the earths magnetic field; this is especially important in sloping terrain; Röhle and Huber 1985). In cases of extreme crown displacement – the crown projection did not include the stem base – the distances to the proximal and distal edge of the crown were measured in all possible directions. Whenever this was only possible for one direction, four crown radii were measured as follows: the distances to the proximal and distal edge of the crown were determined and, starting at the centre of this crown diameter, on the axis perpendicular to this diameter.

Calculation of response variables

To convey the individual-based crown projections to the target group-level response variables for horizontal and vertical canopy structure, the crown radii were used to construct crown projection maps for each target group in the geoinformation system ArcGIS (Version 9.0, ESRI). Crown projection maps were created by connecting the crown edge points to a polygon (Fig. 2). The sum of crown projection area per target group (*CPA*) was calculated as the sum of the area of the polygons. In addition, the area of crown overlap (*O*) was calculated for each target group from the crown projection maps (dark grey in Fig. 2). In order to account for the different successional stages that are reflected in systematically higher *CPA*s of older target groups, relative *CPA* (CPA_r) was defined as the ratio of *CPA* and the circular plot area for the selection of neighbours (*C*). For the same reason, the relative crown overlap O_r was calculated as the ratio of *O* and *C*. Increasing CPA_r describes a higher horizontal canopy space use of canopy trees leading to a more closed canopy, while an increase in O_r reflects a higher vertical overlap of canopy trees. Both response variables are considered to be important factors determining canopy structure.

To further test for vertical heterogeneity of the canopy, we used individual-tree measurements of crown positioning parameters: total height, crown-base height, crown length and mean crown height. We aggregated them for each target group by coefficients of variation (CV, standard deviation / mean, Valladares et al. 2006). The CV describes the variability of a specific attribute between a number of entities and is commonly used to express plasticity. We interpret higher CV of crown positioning parameters as an increase in the heterogeneity of vertical canopy structure.

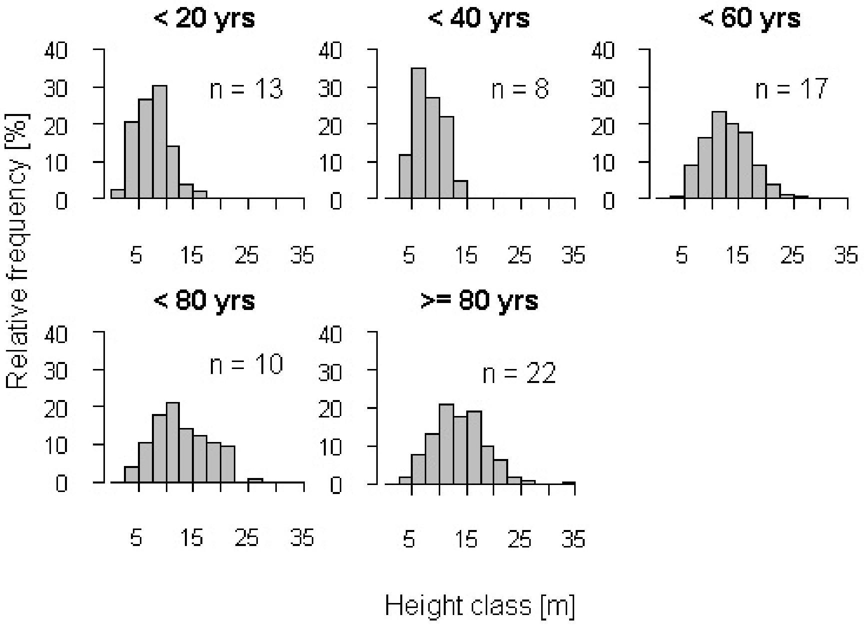

Fig. 1 Relative height frequency distributions of observed canopy trees for 5 successional stages. Height classes comprise 2.5 m each, n is the number of target groups per successional stage. Already young successional stands were highly structured.

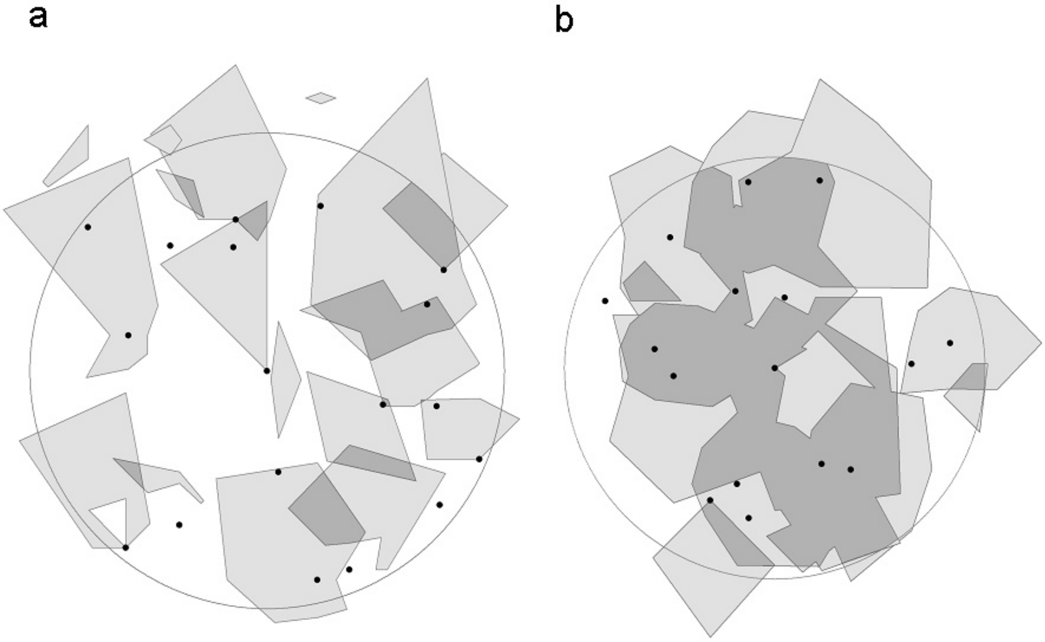

Fig. 2 Exemplary crown projection maps for two target groups (target tree and its neighbours within a circular plot with a radius equal to half of the target tree's height). (**a**) A high functional diversity stand (FD_Q) with relatively small sum of crown projection areas (*CPA*) resulting in a heterogenous horizontal canopy structure of gap and canopy patches and (**b**) a low diverse stand with a more homogenous horizontal canopy structure and fewer gaps. Symbols: dots: stem bases, light grey: crown projections with no crown overlap; dark grey: overlap of crown projections used to analyse crown overlap; dark and light grey: whole crown projection areas.

Statistical analyses

Statistical analyses were performed using R 2.10. (R Development Core Team 2010). For the analyses of mixed effects models the package "nlme" was used (Pinheiro et al. 2009).

Multiple comparisons were performed by means of the package "multcomp" (Hothorn et al. 2008). The influence of a set of explanatory variables on the response variables CPA_r, O_r and the CV of crown positioning parameters (total height, crown-base height, crown length and mean crown height) was tested by means of mixed effects models. The explanatory variables entered the model as fixed effects in the order: diversity (FD_Q and plot species richness), successional stage, slope inclination and aspect (sine of aspect (E-W orientation) and cosine of aspect (N-S orientation)), disturbance severity, altitude. Plot entered the model as a random effect. Model simplification was done by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictory variables were left ($p < 0.05$). We tested for spatial autocorrelation between the model residuals by means of correlograms with the R-package "ncf" (Bjornstad 2009). No significant spatial autocorrelation was revealed. The severity of disturbance of different successional stages was tested by a one-way ANOVA. Spearman rank correlations were calculated for FD_Q, successional stage and disturbance severity.

All variables were z-transformed (mean of zero and standard deviation of one) prior to analyses to ensure comparability of results. We tested for collinearity of all predictor variables (correlations between variables did not exceed $\rho = \pm 0.6$). Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances).

Results

CPA_r ranged from 0.25 to 1.42, with a mean of 0.78 (SD ± 0.26). Our analyses showed that CPA_r was significantly negatively affected by FD_Q ($p = 0.025$, estimate: -0.07; Table 2), but not by plot species richness. Disturbance severity also had a significant negative impact ($p = 0.001$, estimate: -0.11) on CPA_r. Since younger trees have smaller crown sizes and are still more elastic, they should suffer less from crown loss by snow and wind break. In our data young plots of early successional stages suffered less from disturbance than older successional as evidenced by one-way ANOVA ($F = 9.18$, $p < 0.001$; Fig. 3; Spearman rank correlation coefficient $r = 0.76$). FD_Q was neither correlated with disturbance ($r = 0.10$) nor with successional stage ($r = 0.16$).

The crowns of one group (*Q. serrata* of successional stage 3, on a plot with a mean of 17.5% crown loss) did not overlap at all, while the highest O_r was 0.52 (i.e. more than half of the overall canopy area was overlapping). The mean O_r was 0.24 ± 0.13. No explanatory variables could be retained in the most parsimonous model.

Stand FD_Q was not found to influence any CV of crown positioning parameters. The CV of crown length was significantly enhanced by successional stage ($p = 0.019$; estimate = 0.03). It was significantly reduced with increasing slope steepness ($p = 0.004$; estimate = -0.05). The CV of mean crown height was significantly higher in south facing than in north facing slopes ($p = 0.036$; estimate = -0.03). No predictor variables could be retained in the most parsimonous models for CV of total height and crown-base height.

Table 2: Fixed effects of reduced mixed effects model for horizontal (*CPA*$_r$ - measured as relative sum of *CPA*s of circular area *C*) and vertical canopy structure (measured as coefficient of variation (CV) of crown length and mean crown height) with plot as random intercept.

CPA				
Fixed effects	**Estimate**	**F-value**	**p-value**	
Functional diversity (Raos Q)	-0.07	5.74	0.025	*
Disturbance severity	-0.11	13.47	0.001	**
CV crown length				
Fixed effects	**Estimate**	**F-value**	**p-value**	
Successional stage	0.03	6.31	0.019	*
Slope inclination	-0.05	10.32	0.004	**
CV mean crown height				
Fixed effects	**Estimate**	**F-value**	**p-value**	
Slope aspect (N-S)	-0.03	4.94	0.036	*

*Results are considered significant at $p < 0.05$

** Results are considered significant at $p < 0.01$

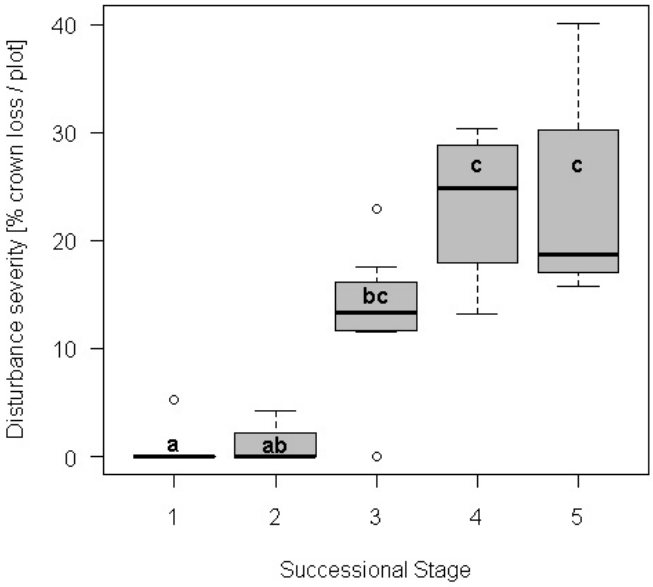

Fig. 3 Boxplots representing the disturbance severity of successional stages as mean percentage crown loss of the 27 plots in the Gutianshan NNR, China. Crown loss resulted from an outstanding snow-break event in February 2008 and was estimated for canopy trees of the target groups as percentage crown loss of the former crown. Letters show significant differences ($p < 0.05$) for post-hoc Tukey test.

Discussion

Canopy structure and stand FD_Q

We found a negative relation of stand FD_Q and *CPA*$_r$, but no relation between FD_Q and vertical canopy structure. However, because this study was based on correlative analysis it is difficult to identify cause and consequence. Does heterogeneity in canopy structure enhance FD_Q or vice versa? In our study, the reduction in horizontal canopy space use (expressed as *CPA*$_r$) with higher functional diversity of the stand may result in more or larger canopy gaps, increasing the heterogeneity of the light environment. According to the intermediate disturbance hypothesis, the heterogeneity in temporal and spatial light conditions promotes the coexistence of species that are characterised by different resource use strategies, dispersal power and competitive abilities (Connell 1978; Bongers et al. 2009). One important characteristic that adds to the spatial and temporal heterogeneity of light availability within a forest stand are canopy gaps. In a recent modelling approach, the coexistence of species was explained by spatial heterogeneity in light conditions that results from canopy gaps (Gravel et al. 2010). This was explained by complementarity in spatial and temporal light acquisition between different species (Ishii and Asano 2010). Although these studies deal with larger scale gaps resulting from treefall, the mechanism may be similar for our local neighbourhood approach. A reduction in horizontal canopy space use promotes the heterogeneity in spatial and temporal light conditions, which allows the coexistence of a larger number of functionally distinct individuals. Different functional groups may coexist due to resource partitioning and niche differentiation.

It is remarkable that already early successional stands in our study area were highly structured (Fig. 1). We may deduce that the high structural complexity results from a high FD_Q of fast- and slow-growing tree species already in young successional stands. No successional trend of FD_Q was found for the 27 plots (Böhnke et al. unpublished data). The negative effect of FD_Q on horizontal canopy space use could point to a type of dilution effect: We focused on target trees and neighbours that were larger than a certain threshold. This size class should represent a quantile below 50% of all woody species of our plots. We also assume that size classes different from the canopy trees contribute more to FD_Q, since FD_Q has not been corrected for stem density and, thus, the chance of finding a new trait among sub-canopy trees and shrubs is higher than among canopy trees. Hence, the reduced CPA_r of canopy trees will result in more canopy gaps that may allow the recruitment of more individuals. In other words, the observed groups of canopy trees are diluted by more individuals of smaller size classes, contributing to high FD_Q, when CPA_r is reduced.

Surprisingly, we did not find any effects of stand FD_Q on vertical canopy structure (measured as crown overlap and CVs of crown positioning). Canopy depth was found to be closely related to the attenuation of photosynthetically active radiation in the understory (Brantley and Young 2010). And canopy depth should increase with increasing crown overlap. We also predicted that higher CVs of crown positioning increase the niche gradient with regard to light intensity and growing space. Hence, both measures should promote the coexistence of species and may thus be related to stand $FD_{Q.}$ The high variability in slope inclination and aspect may have obscured these assumptions. Slope inclination was found to affect crown asymmetry (Umeki 1995; Getzin and Wiegand 2007; Lang et al. 2010) and thereby impacts crown overlap. In addition, our measurements may have been too simple to capture the high complexity of vertical canopy structure, resulting from the interplay of crown positioning and slope. Further studies are needed to provide insight into the three dimensional structure of the canopy (Seidel et al. 2011).

Canopy structure and local environment

In contrast to our expectations successional stage did not influence crown overlap. We would have expected increasing crown overlap with ongoing succession but found that this was not the case because young stands were already considerably structured (Fig. 1). One reason was probably that the functional diversity of the stand did not differ between the successional stages (Böhnke et al. unpublished data). The increase in height classes with ongoing succession was reflected in increasing CV of crown length.

The steep slopes of the study area forced tree individuals to incline their stems in down-hill direction and together with competing neighbours, slope inclination influenced crown asymmetry (Lang et al. 2010). Both mechanisms, slope inclination and competition, could potentially influence horizontal and vertical canopy structure. In particular, crown asymmetry enhances horizontal canopy space use (Olesen 2001; Longuetaud et al. 2008; Schröter et al. 2011). However, although crown asymmetry of individual trees was affected by slope inclination in the Gutianshan NNR (Lang et al. 2010), no influence of inclination on CPA_r and crown overlap was observed in this study. However, the CV of crown length was negatively influenced by slope inclination.

The CV of mean crown height was increased the in south compared to north facing slopes. The increased light availability on south facing slopes may have promoted higher vertical stratification of crowns resulting in an increased CV of mean crown height. Crown asymmetry towards southwest direction and leading to increased surface area receiving direct solar radiation was found by Rouvinen and Kuuluvainen (1997) in boreal forests.

The strong effect of disturbance severity on CPA_r resulted from a recent and outstanding snow break event in February 2008, and the formation of upper canopy gaps by falling branches may have had a strong impact on the development of canopy space use. Muth and Bazzaz (2002) observed that trees along gap edges foraged for light by occupying both horizontal and vertical canopy gap space. Besides natural disturbances, anthropogenic disturbances such as selective logging lead to the formation of gaps. We interpreted altitude of the plots as an indicator of past human impact. However, no influence of altitude on canopy structure was found.

In conclusion, we were able to relate stand based FD_Q to horizontal canopy space use of the observed target tree groups but not to vertical. The results for the analyses of vertical canopy and crown positioning variables reveal our limited understanding of the observed highly complex forest stands. Slope characteristics, as inclination and aspect are important predictors of crown positioning. Hence, variables describing the three dimensional canopy structure may help to elucidate diversity effects. For a deeper understanding of mechanisms promoting stand diversity it is important to incorporate complexity into forests diversity research such as a heterogeneous topography, different successional stages and a high species number.

Acknowledgements

This research was done as part of the BEF China Project financed by the German Research Foundation (DFG FOR 891/1). We are grateful to all members of BEF China for their support. We thank Mr Teng Fang for his enduring patience in teaching the identification of the numerous species and for his support throughout the whole project. We are also indebted to the entire staff of the Gutianshan NNR. We especially thank two anonymous reviewers and the handling editor who provided valuable advice for the preparation of the manuscript.

Table 1 List of all target group species with family affiliation.

Family	Species
Aceraceae	*Acer cordatum* Pax
Alangiaceae	*Alangium kurzii* Craib
Anarcadiaceae	*Toxicodendron* spec.
	Toxicodendron succedaneum (Linn.) Kuntze
Aquifoliaceae	*Ilex litseifolia* Hu et Tan
	Ilex rotunda Thunb.
	Ilex spec.
Araliaceae	*Dendropanax dentiger* (Harms) Merr.
Daphniphyllaceae	*Daphniphyllum oldhamii* Hemsley
Ebenaceae	*Diospyros japonica* Sieb. et Zucc.

	Diospyros kaki Thunb.
Elaeocarpaceae	*Elaeocarpus chinensis* (Gard. et Champ.) Hook.
	Elaeocarpus decipiens Hemsley
	Elaeocarpus japonicus Sieb. et Zucc.
Ericaceae	*Rhododendron ovatum* (Lindl.) Planch.
	Vaccinium bracteatum Thunb.
	Vaccinium carlesii Dunn
Fabaceae	*Albizia kalkora* (Roxb.) Prain
	Dalbergia hupeana Hance
Fagaceae	*Castanea henryi* (Skan) Rehd. et Wils.
	Castanopsis carlesii (Hemsl.) Hayata
	Castanopsis eyrei (Champ. ex Benth.) Tutch.
	Castanopsis fargesii Franchet
	Castanopsis sclerophylla (Lindl. et Pax.) Schott.
	Castanopsis tibetana Hance
	Cyclobalanopsis glauca (Thunb.) Oers.
	Cyclobalanopsis myrsinaefolia Oerst.
	Lithocarpus glaber (Thunb.) Nakai
	Quercus phillyreoides Gray
	Quercus serrata Murray var. *brevipetiolata*
Hamamelidaceae	*Liquidambar formosana* Hance
	Loropetalum chinense (R. Br.) Oliv.
Juglandaceae	*Platycarya strobilacea* Sieb. et Zucc.
Lauraceae	*Lindera glauca* (Sieb. et Zucc.) Bl.
	Litsea coreana Léveillé
	Machilus thunbergii Sieb. et Zucc.
	Neolitsea aurata (Hay.) Koid.
	Sassafras tzumu (Hemsl.) Hemsl.
Myricaceae	*Myrica rubra* Sieb. et Zucc.
Oleaceae	*Fraxinus insularis* Hemsley
	Osmanthus cooperi Hemsley
Staphyleaceae	*Euscaphis japonica* (Thunb.) Kanitz
Pinaceae	*Pinus massoniana* Lamb.
	Pinus taiwanensis Hayata
Rosaceae	*Malus leiocalyca* Huang
	Prunus schneideriana Koehne
	Sorbus folgneri (Schneid.) Rehd.
Sabiaceae	*Meliosma oldhamii* Miquel
Styracaceae	*Styrax* spec.
Symplocaceae	*Symplocos paniculata* (Thunb.) Miq.
	Symplocos stellaris Diels
	Symplocos sumuntia Buch.-Ham.
Taxodiaceae	*Cunninghamia lanceolata* (Lamb.) Hook.
Theaceae	*Adinandra millettii* (Hook. et Arn.) Ben. et Hook.
	Schima superba Gardn. et Champ.

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PAPER III

Individual-tree radial growth in a subtropical broad-leaved forest: the role of local neighbourhood competition

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Keywords: BEF-China; Competitive equivalence; Competition index; Crown area; Jiangxi Province; Mixed forest; Size-asymmetric competition

Forest Ecology and Management 261 (2011) 499 - 507

Abstract

Establishing the competitive relationships at the local neighbourhood level is essential for improving our understanding of tree growth dynamics in structurally heterogeneous and species-rich forests. We studied the competitive interactions influencing individual-tree five-year radial growth of the two species *Castanopsis fargesii* (Franch.) and *Quercus fabri* (Hance) in a diverse young secondary evergreen broad-leaved forest (EBLF) in eastern China. Different spatially explicit individual-based competition indices were examined for their effectiveness at predicting radial growth. These indices were based on one of the three tree size variables ─ diameter at breast height (dbh), total height, and crown projection area ─ and were combined with different approaches to identify potential competitors. Furthermore, we tested for competitive equivalence of conspecific and heterospecific neighbours and analysed the effects of local diversity, initial dbh (measured at the beginning of the five-year growth period) and abiotic environmental variables on individual-tree radial growth. Competition accounted for up to 78 % and 75 % of radial growth variation in *C. fargesii* and *Q. fabri*, respectively. The best results were provided by competition indices using crown projection area as the variable describing tree size and the angular height method as the approach to identify potential competitors (i.e. neighbours greater than the minimum angular height, measured from the base of the target trees, are selected as competitors). Competitive equivalence of conspecific and heterospecific neighbours was found in *C. fargesii*, whereas heterospecifics were stronger competitors than conspecifics in *Q. fabri*. We could not detect diversity effects on radial growth. The addition of initial dbh or abiotic environmental variables as further explanatory variables failed to improve the predictive ability of growth models. Our results indicate that diameter growth in this EBLF is largely a function of local neighbourhood competition and suggest that the mode of competition is primarily size-asymmetric. It appears that there may be high competitive equivalence among different species, but this remains to be experimentally tested.

1. Introduction

In the past, many studies investigating tree competition have been restricted to single-species plantations or even-aged forest stands, i.e. to stands characterised by a relatively homogeneous structure (Martin and Ek, 1984; Biging and Dobbertin, 1992, 1995; Pretzsch, 2009). This was of particular interest because monospecific stands with regularly distributed trees of similar age and size were the norm in many silvicultural regimes. However, an increasing focus on sustainable forest management practices and “close to nature forestry” in Europe has led to the promotion of more structurally complex and diverse forests managed with smaller scale interventions and more long-term regeneration regimes (e.g. Bauhus et al., 2009). As a result, interactions among trees in forests with a higher spatial variability have come into focus (Dimov et al., 2008). As a further consequence, the area covered by mixed-species forests is growing considerably, at the expense of single-species forests. In plantation forestry, species mixtures are now also being seriously considered for various objectives, such as increased stand productivity due to complementary resource use or facilitation, reduced pest damage or market risks (Kelty, 2006). In stands that are complex in structure and represent a highly heterogeneous mixture of species, there is increasing evidence that tree competition is a spatially explicit process (D’Amato and Puettmann, 2004) and that species identity may be important (Stoll and Newbery, 2005; Zhao et al., 2006). Thus, when describing the mode of competition among individual trees and the association among species as well as predicting the development in these stands, a spatially explicit individual-based approach is preferable (Zhao et al., 2006).

Individual-tree growth is a function of local neighbourhood interactions, but tree size, genotype, tree damage, and local abiotic site characteristics are also important (Pretzsch, 2009). This view reflects the transition from stand-based approaches to individual-tree approaches to explain and model tree growth (Pretzsch, 2009). One approach to an analysis of individual-tree growth is to fit the relationship between measured growth variables and a selected set of predictor variables, including a competition variable. In spatially explicit individual-based competition measures (also known as distance-dependent competition indices (CI)) the competition effects are accounted for by the distance between a target tree and its neighbours, and their relative sizes. A vast variety of distance-dependent competition indices has been introduced in studies on tree competition (Biging and Dobbertin, 1992, 1995; Pretzsch, 2009). The mathematical specifications of the relative size relationship differ between competition indices, as does the primary variable that quantifies the size of the trees (e.g. height, stem diameter, crown area). No single competition index has been shown to be generally superior and the use of multiple indices is recommended (Biging and Dobbertin, 1992; Weigelt and Jolliffe, 2003). Another important question associated with spatially explicit individual-based competition measures concerns the identification of potential competitors and, thus, the relevant scales at which neighbourhood interactions influence tree growth (“zone of influence”). Different approaches have been used to identify potential competitors (Biging and Dobbertin, 1992; Corral-Rivas et al., 2005; Pretzsch, 2009). In heterogeneous stands in particular, the outcome of a given competition index may vary considerably with different neighbour inclusion approaches (Corral-Rivas et al., 2005).

Competitive interactions among trees are either size-asymmetric (non-equivalent) or size-symmetric (equivalent) (Weiner, 1990). It is assumed that aboveground competition for light is mostly size-asymmetric (larger individuals have a disproportionate effect on smaller individuals by shading), whereas competition for belowground resources such as water and nutrients is size-symmetric (Schwinning and Weiner, 1998). In an experimental tree plantation in Panama, Potvin and Dutilleul (2009) found that size-asymmetric competition by local neighbours is the overwhelming source of variation in individual-tree growth. In mixed-species stands non-equivalent neighbour effects on individual-tree diameter growth may not only be generated by size ratios, but also tree species may differ in their competitive effects. It has often been found that conspecific neighbours are stronger competitors than heterospecific neighbours (Stoll and Newbery, 2005; Richards et al., 2008; Pretzsch and Schütze, 2009). This may be due to a high competitive equivalence within species, but not between different species. In contrast, Hubbell's (2001) neutral model assumes that all individuals, irrespective of species identity, are functionally equivalent competitors. It has been shown, however, that the neutral model performs better in some forest communities than others (e.g., Uriate et al., 2004a, 2004b; Stoll and Newbery, 2005; Canham et al., 2006; Zhao et al., 2006). Papaik and Canham (2006) suggest that the existence of competitive equivalence is related to the diversity level of the forest community, as it may only occur at very high levels of diversity. Furthermore, in species-rich forests it is conceivable that neighbour effects may vary not only between con- and heterospecifics but also among particular species or species groups (Zhao et al., 2006; Li et al., 2010).

In the subtropical zone of China, monospecific stands of conifers, in particular Masson pine (*Pinus massoniana*) and Chinese fir (*Cunninghamia lanceolata*), which have been afforested after clear-cutting, occupy a large proportion of the present forest area. However, the zonal vegetation type "Chinese evergreen broad-leaved forests" (EBLF) is extremely rich in woody species (Wang et al., 2007), which makes these forests particularly interesting for diversity research (Hu and Yu, 2008; Legendre et al., 2009; Bruelheide et al., in press). Due to a long history of intensive land-use in this region, few remnants of old-growth EBLF are left today; those which remain are preserved as National Parks or National Nature Reserves (Yu et al., 2001; Wang et al., 2007). The majority of EBLF in China now exist as younger secondary forests (Wang et al., 2007). In addition to the highly heterogeneous mixture of woody species, even younger secondary forests often exhibit a relatively heterogeneous stand structure due to non-uniform cutting for fire wood and timber. Finally, the high topographic variation with a small-scale heterogeneity of slope and aspect further adds to the overall high complexity in these forests (Legendre et al., 2009; Zhu et al., 2010).

In this study we analyse the competitive interactions influencing individual-tree five-year radial growth of the two species *Castanopsis fargesii* (Franch.) and *Quercus fabri* (Hance) in a heterogeneous species-rich EBLF in eastern China. For the first time the effects of local neighbourhood competition on radial growth are examined by means of spatially explicit individual-based competition indices in this important forest type. And for the first time we specifically test for diversity effects in competition relationships. The specific objectives are to (i) test the performance of different spatially explicit individual-based competition indices and neighbour inclusion approaches to quantify the effects of competition on five-year radial growth, (ii) test for competitive equivalence of conspecific and heterospecific neighbours, (iii) test for diversity effects on individual-tree radial growth, and (iv) analyse the relationship between five-year radial growth and a selected set of predictor variables, including neighbourhood competition, initial dbh and abiotic site variables.

2. Methods

2.1 Study site

The study was conducted in a forest stand located in Dexing County, Jiangxi Province, eastern China (28° 58´ N, 117° 32´ E). The study site covers an area of about 90 ha and is privately owned. It is situated in the subtropics with a monsoon climate. The mean annual temperature is 15.3 °C and the mean annual precipitation is about 2000 mm. The rainy season is from March to June and also in September. There is a mean annual period of 250 frost-free days (Hu and Yu, 2008). Elevation ranges from 80 to 260 m above sea level. The average slope inclination is 32°, ranging from 10 to 45°. The general slope aspect is towards the south with small-scale variation caused by several near parallel north-south ridges.

The study site is representative of a young secondary EBLF (Wang et al., 2007). This forest type is extremely diverse, particularly in terms of tree and shrub species richness (Wang et al., 2007; Hu and Yu, 2008). For example, Wang et al. (2007) found 31 and 46 species per 400 m^2 in the tree and shrub layer of a young secondary and a mature EBLF, respectively. In EBLF, evergreen species dominate throughout the succession, but in early successional stages also deciduous species are present with high abundances and species numbers (Wang et al., 2007). In the study site the canopy was closed. Canopy tree species include the evergreen broad-leaved tree species *C. fargesii*, *C. sclerophylla*, *Lithocarpus glaber*, *Schima superba*, the deciduous tree species *Q. fabri*, *Liquidambar formosana*, *Sassafras tzumu*, *Styrax dasyanthus*, *Sapium sebiferum*, *Diospyros kaki*, and the coniferous species *P. massoniana*. In order to obtain details of tree age and periods of rapid growth release, stem cores of 12 dominant overstorey trees (diameter at breast height (dbh) > 25 cm) of different tree species were taken at breast height with an increment borer (Suunto 400, Vantaa, Finland) in September 2009. Trees were distributed over the whole area and were randomly selected. Tree-ring analyses revealed that the age range of these trees was 30 to 85 years (median 41 years), and that there were no single periods of rapid growth release, which could be indicative of large-scale disturbance events. Consultation with land owners and inhabitants of the region confirmed repeated non-uniform cutting for fire wood and timber up until the year 2000. However, over the last 10 years no trees have been cut in the study site.

2.2 Study design and measurements

Both study species, the evergreen *C. fargesii* and the deciduous *Q. fabri*, belong to the Fagaceae family, and are among the most important tree species in EBLF, with *C. fargesii* being a co-dominant species in late-successional and *Q. fabri* a co-dominant species in early-successional forests (Wang et al., 2007). However, *C. fargesii* may also be abundant in early successional stages because it effectively regenerates from seeds and resprouts from stumps after cutting (Du et al., 2007; Wang et al., 2007).

Data sampling was conducted during October and November 2008. Twenty target trees per species were selected closest to 40 systematically located gridpoints. Along random bearings the nearest single-stemmed tree with the crown position in the upper canopy layer and a dbh between 6 and 14 cm was chosen as the target tree. Selected trees were located at least 40 m apart from each other. As growth rates of trees vary with the exposure of the crown to light and with ontogeny, it is important to analyse trees with a similar crown position and over a similar size range (Filipescu and Comeau, 2007). We confined the analyses to overstorey trees with this dbh range for two reasons. First, the majority of overstorey trees in the study site had this dbh. Second, a large forest biodiversity and ecosystem functioning experiment (BEF experiment), using a large set of subtropical tree and shrub species (www.bef-china.de), was established in 2009 at a distance of about 40 km from the study site. Here, artificial stands of defined species diversity levels were established by planting seedlings. During the first few years these experimental stands will thus reflect the conditions of young successional stages. In our analysis we restricted tree selection to a size range that could be achieved by the planted trees within 5 to 15 years.

The target trees served as the centre of a circular plot, in which all trees with a dbh ≥ 5 cm were measured. The plot radius was equal to half of the target tree's height (Ammer et al., 2005), with a minimum radius of 5 m. The relative position of the neighbours to the target tree was determined by recording the azimuth and horizontal distance from stem base to stem base. All neighbours were determined to species level. For all target trees and neighbours dbh, total tree height, and crown radii were measured. Crown radii were measured in the eight subcardinal directions (N, NE, E, etc.) by means of a crown mirror. The crown cover was visually estimated for all trees to fit within one of five equal percentage cover classes (1-20%, 21-40%, etc.).

We harvested the 40 target trees and cut 5 cm thick stem discs from the base and at breast height. We used the stem discs obtained from the base for age determination and those from breast height to measure the annual radial growth of the previous five years. In the lab, the stem discs were sanded with a belt sander using progressively finer grits from P60 to P400. Tree-ring widths were measured on the two radii forming the longest axis of the disc and on the two radii forming the axis perpendicular to it. Measurements were taken to the nearest 0.01 mm on a measuring table (Instrumenta Mechanik Labor (IML), Wiesloch, Germany) combined with a binocular (Wild, Heerbrugg, Switzerland), and were recorded by the IML software T-Tools pro. Mean annual radial growth was calculated as the average five-year radial growth measured in four directions divided by five.

For each group of trees, local slope inclination and aspect were recorded. Four topsoil samples (100 cm^3 each, upper 5 cm) were taken in the vicinity of each target tree and pooled to form one bulk sample. The soil samples were dried at 60 °C, sifted and grinded. For determination of pH(H_2O)-value, 10 g of dry soil were suspended in 25 ml of distilled water and shaken for 15 minutes. After 45 minutes the pH was measured by means of an electrode (WTW Mircoprocessor pH Meter pH96). The S-value and cation exchange capacity (CEC) as well as base saturation (BS) were measured using the method of Brown (1943).

2.3 Data analysis

Differences in growth and local environmental characteristics between the two species were tested with Student's t-test. In this analysis as well as in regression analyses (see below) data were $\log_{10}(x+1)$-transformed prior to meet the requirement of normal distribution and homoscedasticity.

Three different primary variables were used to quantify the tree size when calculating the competition indices: dbh, total height, and crown projection area. For all analyses the height of the neighbours was corrected for the slope position (z-axis) with trigonometric calculations (Pretzsch, 2009). The crown projection area (hereafter crown area) was calculated from the eight crown radii using the formula for a polygon. For the analyses, the crown area of all trees was weighted by the crown cover, estimated for the given tree, by multiplying the crown area with the following values: 1-20 %: 0.2, 21-40 %: 0.4, etc. Because the combination of several primary variables into one competition index makes the statistical qualities of an index difficult to understand (Weigelt and Jolliffe, 2003), we decided to use simple spatially explicit individual-based competition indices to describe the competition, experienced by each target tree, as a function of the relative size and proximity of the neighbouring trees (Table 1). CI1 to CI3 use the three primary variables dbh, height, and crown area, respectively, and are calculated with the simple size ratio. CI4 to CI6 were designed to reflect the asymmetry of aboveground competition, with the squared ratio enhancing the size differences between target trees and neighbours (Castagneri et al., 2008). In all competition indices the influence of a neighbour decreases linearly with its distance from the target tree.

Three approaches to identify potential competitors were compared. The first approach used height angles from the base of the target tree ("angular height method", Richards et al., 2008). Trees were included as potentially competing neighbours if their height (corrected for the slope position) was greater than a critical height determined from the horizontal distance (m) between neighbour and target tree ($dist_{tj}$) and the angle (a) from the ground at the base of the focal tree (Biging and Dobbertin, 1992; Richards et al., 2008; Pretzsch, 2009). This method is also called "reversed search cone method" (Pretzsch, 2009), and in this study we use the opening angle of the reversed search cone (b; degrees) where $b = 180° - 2a$, because this is more intuitive: The larger b is, the larger the search volume, i.e. the larger the number of potentially included neighbours. The second approach was a fixed radial distance (r; m) from the target tree. Any tree within this distance was included as a neighbour. In the third approach those trees were included whose mean crown radius overlapped with the mean crown radius of the target tree (Corral Rivas et al., 2005).

For each species, the performance of different competition indices and neighbour inclusion approaches to quantify the effects of competition on radial growth was tested using least squares linear regression analyses (Stoll and Newbery, 2005; Vanclay, 2006). For the first two neighbour inclusion approaches the adjusted coefficient of determination (R^2) was calculated for the relationship between mean annual radial growth of the last five years (in mm year^{-1}) and each competition index at a given opening angle or radial distance. Opening angles between 35° and 80° and radial distances between 2.0 and 6.5 m were tested in steps of 5° and 0.5 m, respectively. The adjusted R^2 values were then plotted against opening angle or radial distance. As the third approach uses a single set of competitors, only one linear regression was calculated per competition index.

Multiple regressions were used to test for competitive equivalence of conspecific and heterospecific neighbours. Mean annual radial growth was modelled as a function of two neighbour competition indices, one calculated from conspecific and the other from heterospecific neighbours. In the case of competitive equivalence both independent variables should be significantly related to radial growth, and the estimated regression parameters should be similar. Linear regressions were used to examine if the competition indices are related to the number of neighbouring trees.

Local species richness is defined as the number of species among all selected neighbours. To obtain estimates of local species richness that are unaffected by density, rarefaction analysis was based on Hurlbert’s (1971) formula, as implemented in the vegan package in R 2.10. (R Development Core Team 2009), using a fixed number of 5 individuals per group. To study diversity effects in the competition relationships, we related the competition index to local species richness and to rarefied species richness. To test for diversity effects on growth, we calculated the competition index per species by dividing the competition index of all species by the local species richness and rarefied species richness, respectively. Both the two species richness measures as well as the two ratios were then related to radial growth.

Finally, simple and multiple regression models were developed to predict the radial growth as a function of a selected set of biotic (competition index, initial target tree dbh (=dbh in 2003)) and abiotic (slope inclination, slope aspect (with aspect transformation according to Beers et al., 1966), chemical soil conditions) variables of the target trees and their local environment. In the stepwise multiple regressions the input variables were z-transformed prior to analysis, resulting in a model with intercept = 0. With the exception of the rarefaction analysis, all analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL).

3. Results

For both species, mean dbh was about 10 cm and did not differ significantly between species (Table 2). However, tree-ring analyses of the stem discs taken from the base of the target trees revealed that the age of *C. fargesii* varied from 11 to 26 years, whereas *Q. fabri* was significantly older, with an age range of 22 to 54 years (Table 2). The target trees of *C. fargesii* were also significantly taller than those of *Q. fabri* (mean height 11.5 m and 8.8 m, respectively). In both species, crown area was about 7 m^2 and did not differ significantly. The mean annual radial growth over the last five years was significantly higher in *C. fargesii* than in *Q. fabri* (3.5 and 1.0 mm, respectively; Table 2). In *C. fargesii* a weak positive relationship between age and dbh was found (adjusted $R^2 = 0.22$, $P = 0.02$). Neither the dbh of *Q. fabri* nor the other growth variables for both species were significantly related to age (all $P > 0.05$).

Table 1 Definitions of competition indices

Competition index	Formula	Source
$CI1_t$	$= \sum_{j=1}^{n} dbh_j / (dbh_t \times (dist_{tj} + 1))$	Hegyi (1974)
$CI2_t$	$= \sum_{j=1}^{n} h_j / (h_t \times (dist_{tj} + 1))$	Modified after Hegyi (1974)
$CI3_t$	$= \sum_{j=1}^{n} cpa_j / (cpa_t \times (dist_{tj} + 1))$	Biging and Dobbertin (1992)
$CI4_t$	$= \sum_{j=1}^{n} (dbh_j / dbh_t)^2 / (dist_{tj} + 1)$	Modified after Castagneri et al. (2008)
$CI5_t$	$= \sum_{j=1}^{n} (h_j / h_t)^2 / (dist_{tj} + 1)$	Modified after Castagneri et al. (2008)
$CI6_t$	$= \sum_{j=1}^{n} (cpa_j / cpa_t)^2 / (dist_{tj} + 1)$	Modified after Castagneri et al. (2008)

dbh_j neighbour tree diameter at breast height (cm); dbh_t target tree diameter at breast height (cm); $dist_{tj}$ horizontal distance (m) between neighbour (j) and target tree (t); h_j neighbour tree height (m); h_t target tree height (m); cpa_j neighbour tree crown projection area (m^2); cpa_t target tree crown projection area (m^2)

The profiles of the adjusted R^2 values showed considerable variation among the two species, the three different competition indices, the different neighbour inclusion approaches, and the opening angles / radii (Figs 1 and 2). Generally, the competition indices using crown area as the size variable and opening angles as the neighbour inclusion approach had the highest adjusted R^2 in both species. *C. fargesii* had maximum adjusted R^2 of 0.74 and 0.78 at opening angles of 50 to 60° with CI3 and CI6, respectively (Figs 1 and 3). *Q. fabri* reached maximal adjusted R^2 of 0.62 and 0.71 at an opening angle of 50° with CI3 and CI6, respectively. In *C. fargesii* the peak for the competition index using the simple dbh ratio (CI1) was at an opening angle of 55° (adjusted R^2 = 0.56). A different pattern occurred when the squared dbh ratio was used (CI4): for a wide range of opening angles (50 to 80°) high adjusted R^2 values of about 0.7 were found. In *Q. fabri* the R^2 values of CI1 and CI4 were well below those of CI3 and CI6 at any opening angle. In both species the competition indices using height as the size variable (CI2 and CI5) performed very poorly (Fig. 1). Compared to the search cone neighbour inclusion approach, the fixed radial distance approach exhibited a different pattern in the profiles of the adjusted R^2 values (Fig. 2). In the former, the R^2 values were highest at intermediate opening angles, whereas in the latter the R^2 values generally increased with radial distance and peaked at the largest distances (> 5.5 m). In *C. fargesii* the maximum R^2 values were 0.65 and 0.74 at a radius of 6.5 m for CI3 and CI6, respectively. *Q. fabri* had maximal R^2 values of 0.53 for CI3 at a radius of 5.5 m and of 0.62 for CI6 at a radius of 6 m

(Fig. 2). When only those neighbour trees were included whose mean crown radii overlapped with those of the target trees (third neighbour inclusion approach), the adjusted R^2 values were generally low (*C. fargesii*: CI3: $R^2 = 0.29$, $P = 0.009$; CI4: $R^2 = 0.26$, $P = 0.01$; CI6: $R^2 = 0.45$, $P = 0.001$; *Q fabri*: CI6: $R^2 = 0.17$, $P = 0.04$; all others not significant).

Table 2 Characteristics (mean and standard deviation (SD)) of 20 destructively sampled trees of *Castanopsis fargesii* and *Quercus fabri*, respectively, and of local biophysical environmental variables

	Castanopsis fargesii		Quercus fabri		
Variable	Mean	SD	Mean	SD	*P*
Age	16.3	5.0	39.1	8.8	<0.001
dbh (cm)	9.5	2.0	9.6	1.7	ns
Height (m)	11.5	1.3	8.8	1.6	<0.001
Crown area (m^2)	7.2	3.4	6.9	3.5	ns
Annual radial growth (mm)	3.5	1.5	1.0	0.5	<0.001
Local species richness	5.5	1.5	4.6	1.7	ns
Rarefied species richness	3.7	0.7	3.8	0.5	ns
Slope inclination (°)	33	7	31	7	ns
Slope aspect (°)	183	91	215	83	ns
pH (H_2O)	4.2	0.1	4.1	0.1	ns
S-value (mval/g dry soil)	3.2	1.3	2.9	1.4	ns
CEC (mval/g dry soil)	5.6	1.3	5.3	1.5	ns
BS (%)	54	10	50	15	ns

Based on these results, CI6 was selected for the further analyses for both species, with an opening angle of 55° in *C. fargesii* and 50° in *Q. fabri*. The relative proportion of the conspecifics' competition index in the total competition index ranged from 0 (i.e. no conspecific neighbour) to 85 % (i.e. almost all competition came from conspecifics) in *C. fargesii*, whereas it was 0 to 38 % in *Q. fabri*. When radial growth was modelled as a function of conspecific and heterospecific competition, both independent variables were significant in *C. fargesii* (Table 3), but the adjusted R^2 was somewhat lower than in the simple regression model (Table 4). In *Q. fabri*, however, conspecific competition was not significantly related to radial growth, and the adjusted R^2 was somewhat higher than in the simple regression model ($R^2 = 0.75$). With one exception, the competition index was not significantly related to the number of neighbouring trees (exception: CI6 calculated from conspecific neighbours of *C. fargesii*: $R^2 = 0.25$, $P = 0.014$).

Local species richness and rarefied species richness were not significantly different between the two species (Table 2). The competition index was not significantly related to both species richness measures (all $P > 0.05$). Radial growth was either only weakly or not significantly related to both species richness measures (Table 4). Using the competition index divided by local or rarefied species richness had only a marginal influence on model outcomes (data not shown).

None of the abiotic variables differed significantly between the two species (Table 2). Simple regression analyses showed that radial growth was either not significantly or only weakly related to the independent variables initial dbh, local slope inclination and aspect, pH (H_2O), S-value, CEC, and BS (Table 4). In the final multiple regression models of both species only one variable, the competition index, was included because the initial dbh of the target trees, as well as all other environmental variables, had only a marginal influence on five-year radial growth.

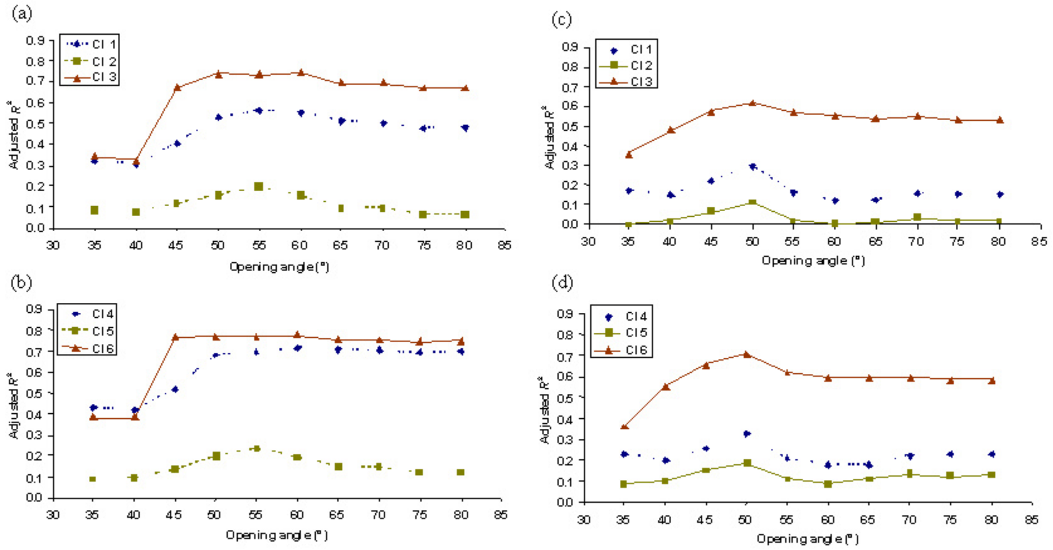

Fig. 1. Effect of opening angle (°) on adjusted R^2 values of regression models for *Castanopsis fargesii* (a and b) and *Quercus fabri* (c and d) fitted to predict mean annual radial growth as a function of competition, using six competition indices. (a) and (c): CI1 (dbh), CI2 (height), CI3 (crown projection area). (b) and (d): CI4 (dbh), CI5 (height), CI6 (crown projection area).

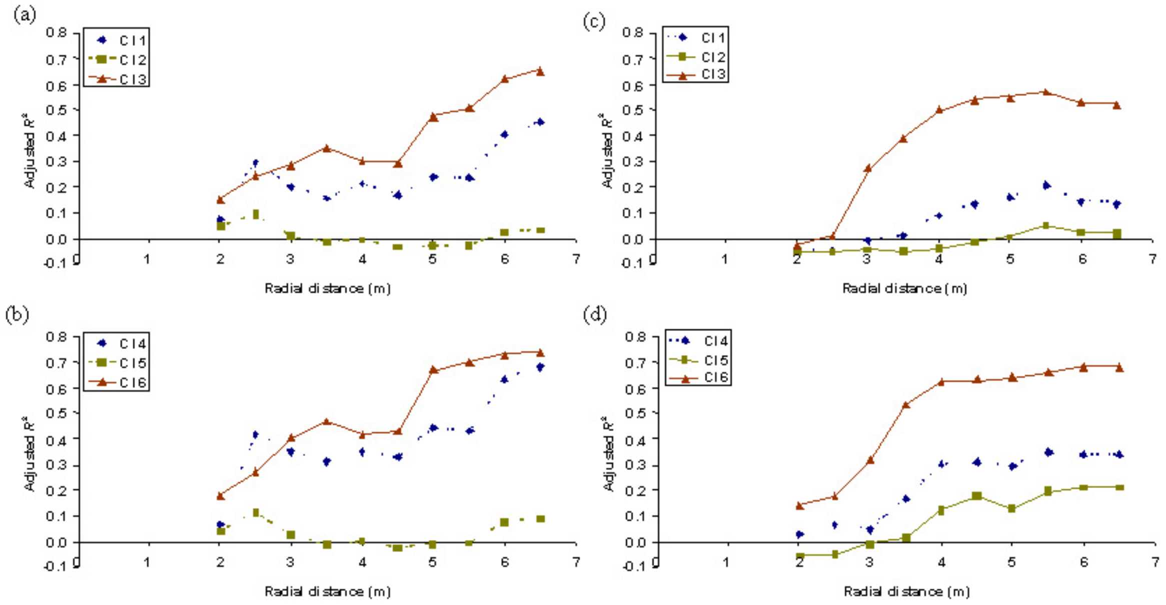

Fig. 2. Effect of neighbourhood radius (m) on adjusted R^2 values of regression models for *Castanopsis fargesii* (a and b) and *Quercus fabri* (c and d) fitted to predict mean annual radial growth as a function of competition, using six competition indices. (a) and (c): CI1 (dbh), CI2 (height), CI3 (crown projection area). (b) and (d): CI4 (dbh), CI5 (height), CI6 (crown projection area).

4. Discussion

Using relatively simple spatially explicit individual-based competition indices, we were able to explain up to 78 % and 75 % of the variation in the mean annual radial growth over the last five years in *C. fargesii* and *Q. fabri*, respectively. For the first time we are, thus, able to show that these indices are highly feasible to quantify the effect of local neighbourhood competition on diameter growth in a heterogeneous species-rich secondary EBLF. Although the majority of overstorey trees in this forest had a dbh within a relatively small range of 5 to 15 cm, tree-ring analyses of the 40 target trees as well as of the 12 large dominant overstorey trees (dbh > 25 cm) revealed that individuals of a wide age range (11 to > 80 years) were present in this forest stand. A long-term non-uniform forest management, thus, created a heterogeneous age structure in this managed forest. In addition, the mixture of woody species at the local scale is highly heterogeneous. Over all 40 tree groups the mean number of tree individuals per species was 1.9, i.e. every tree species was represented in the groups by fewer than two individuals. After eliminating density effects by rarefaction analysis the mean number of species per five individuals was 3.7 (Table 2). In a nearby 24-ha permanent EBLF plot located in the National Nature Reserve Gutianshan 159 species from 49 families were recorded with a dbh ≥ 1 cm (Lai et al., 2009). In the same reserve, Bruelheide et al. (in press) found 25 to 69 woody species > 1 m in height in 27 plots of 30 m x 30 m each from different successional stages. In EBLF of south-eastern China, thus, a high regional species richness corresponds to a high local species richness. Finally, EBLF are often characterised by a high variability in the topographic variables elevation, slope, aspect, and convexity (Lai et al., 2009; Legendre et al., 2009). In such a complex situation it is conceivable that simple competition indices could be inappropriate to explain a high proportion of the variation in individual-tree growth, and that, in addition to competition, various biophysical environmental factors could affect tree growth. Nevertheless, despite these potentially important factors the impact of competition in our study was obvious.

Table 3 Results of multiple linear regressions of mean annual radial growth (mm yr^{-1}) on conspecific and heterospecific competition indices for the two species *Castanopsis fargesii* and *Quercus fabri*. Adjusted R^2 and F is for the whole model, P gives the probability values for the parameter estimates (t statistic).

	Independent variable	Adjusted R^2	F	Parameter estimates	P
C. fargesii	$CI6_{conspecifics}$	0.72	25.34	-0.49	0.003
	$CI6_{heterospecifics}$			-0.52	0.002
Q. fabri	$CI6_{conspecifics}$	0.75	29.31	0.19	ns
	$CI6_{heterospecifics}$			-0.86	< 0.001

4.1 Performance of spatially explicit individual-based competition indices

We obtained adjusted R^2 values which are well above those typically found for models describing tree growth in response to competition (between 0.4 and 0.7, Corral-Rivas et al., 2005; Filipescu and Comeau, 2007; Castagneri et al., 2008; Dimov et al., 2008). Several mathematical and ecological reasons might help to explain this finding.

From our analyses it becomes obvious that the selection of the primary variable that quantifies the size of the trees is highly relevant for the quality of the models. We unveiled a clear ranking with the variable crown area performing best, stem diameter holding an intermediate position and height being completely inappropriate. Crown dimensions turned out to be appropriate to approximate the scale of the photosynthetic apparatus, which in turn determines the capacity of trees to produce dry matter (Smith, 1994). Crown dimensions strongly determine the individual’s ability to intercept light and to shade other trees, and crown responses are more rapid and more plastic than stem increment or height growth responses following changes in resource availability. Crown area is, therefore, known to be a very sensitive growth response variable to competition (Biging and Dobbertin, 1992; Simard and Zimonick, 2005; Getzin et al., 2008). However, to properly determine the crown area is more difficult and more time consuming than measuring dbh or height. Therefore, crown data are often not available in tree competition studies. In addition, on steep slopes the shape of tree crowns is often irregular, with an asymmetric expansion towards the downhill direction (Umeki, 1995), which makes the estimation of crown area by means of allometric relationships with stem dimensions difficult. In our study, two methodological operations considerably improved the suitability of crown data: recording eight crown radii (instead of only four) and calculating the crown area using the formula for a polygon instead of approximating it as an ellipse or using the mean radius to calculate the area of a circle (data not shown). It has to be considered, however, that total plant light interception and plant light harvesting efficiency is not only determined by characteristics at the crown level, but also at the shoot and leaf level (Niinemets, 2010). Due to the difficulties to investigate simultaneously the suites of traits at different hierarchical levels, the few existing studies are yet confined to tree seedlings and saplings (Niinemets, 2010).

Stem dimensions (dbh or basal area) are used in the formulation of many tree competition indices (Biging and Dobbertin, 1992, 1995; Corral-Rivas et al., 2005; Pretzsch, 2009). In our study, the model outcomes were sensitive to the mathematical specifications of the size ratio (see below) and to species identity when dbh was used as the size variable. Generally, radial growth and dbh are closely correlated (Pretzsch, 2009). In our study, this was not the case, primarily because of the small dbh range of the target trees. However, in both species, but particularly in *Q. fabri*, it becomes obvious that the current dbh is strongly affected by the past competition history of the trees. The dbh was only weakly (*C. fargesii*) or not at all (*Q. fabri*) related to age, because the older trees experienced one or more periods of severe growth suppression. Competition is generally known to affect height growth of trees only when it is extremely low or high (Ammer et al., 2005; Simard and Zimonick, 2005; Inoue et al., 2008). The lack of a relationship between height and radial growth supports the view that height growth is less sensitive to competition than diameter growth because it is a higher priority for carbon allocation (Simard and Zimonick, 2005; Pretzsch, 2009), and suggests that the intensity of local neighbourhood competition is currently at a level that closely regulates radial growth, but does not suppress height growth.

In comparison to the selection of the primary variable to quantify tree size, the mathematical specification of the relative size relationship was less important for the model outcome. Using squared size ratios always increased the adjusted R^2 values, but the differences were usually relatively small. An exception was the performance of the competition index using dbh as the size variable in *C. fargesii* (CI1 and CI4). With opening angles ≥ 50° CI4 performed almost as well as CI6 (using crown area). These results suggest that the mode of competition in this forest is primarily size-asymmetric, i.e. competition for light. This is best shown by using the crown dimensions to quantify the effect of competition on growth. In *C. fargesii*, dbh is a suitable size variable as long as the disproportionate effect of larger individuals on smaller individuals is accounted for by means of the mathematical specification of the relative size relationship. For *Q. fabri*, the clear differences between the size variables crown area and dbh remained, probably because of the stronger impact of the past competitive status on current dbh in this species. Grams & Andersen (2007) suggested that morphological adjustments are more important than physiological adjustments in obtaining limited resources when competition is size-asymmetric. In general, tree crowns respond with stronger lateral crown expansion towards space with high light availability (phototropic growth), resulting in crown asymmetry. Furthermore, the development of asymmetric crowns may be intensified by correlative inhibition (Takenaka, 2000). In a Chinese EBLF Lang et al. (2010) found that the crowns of four broad-leaved tree species were strongly displaced due to local neighbourhood competition.

In slope forests with a predominance of size-asymmetric competition the approach used to select competitors is of great importance. For a tree on a slope, the crowns of neighbouring trees in an uphill direction are situated at a higher position than those of the same-sized neighbours in a downhill direction and, thus, impose a stronger influence on individual-tree growth at a given height (Umeki, 1995). In contrast to the fixed radial distance approach, the search cone method takes this into account by giving more weight to tree height than distance. As a result, more neighbours are included in an uphill than in a downhill direction at a given opening angle, and larger neighbours are included even at larger distances. For both species, opening angles of 50 to 60° performed best. This corresponds to height angles of 60 to 65°, values which are often reported in the literature (Biging and Dobbertin, 1992, 1995; Pretzsch, 2009). Larger angles of inclusion of neighbouring trees, as suggested by Richards et al. (2008), either had no impact or decreased adjusted R^2 values.

In many studies it has been found that the optimal radial distances strongly depended on tree size dimensions (D’Amato and Puettmann, 2004). From our study, we can conclude that in younger EBLF radial distances of at least 5 m should be used; this corresponds roughly to half of the average canopy height (Ammer et al., 2005; Pretzsch, 2009). However, this conclusion has to be corroborated by studies on larger plots to allow for a further extension of the radial distances analysed. The third inclusion approach, which uses overlapping crown radii, and, thus, includes only the very local neighbours, was found to be unsuitable. This is confirmed by the performance of the two other approaches at the lowest opening angles or smallest radial distances.

Finally, individual-tree growth rates vary with age/size (Filipescu and Comeau, 2007). For the reasons given in section 2.2 we confined the analyses to overstorey trees with a relatively small dbh range, which might contribute to the high adjusted R^2 values obtained.

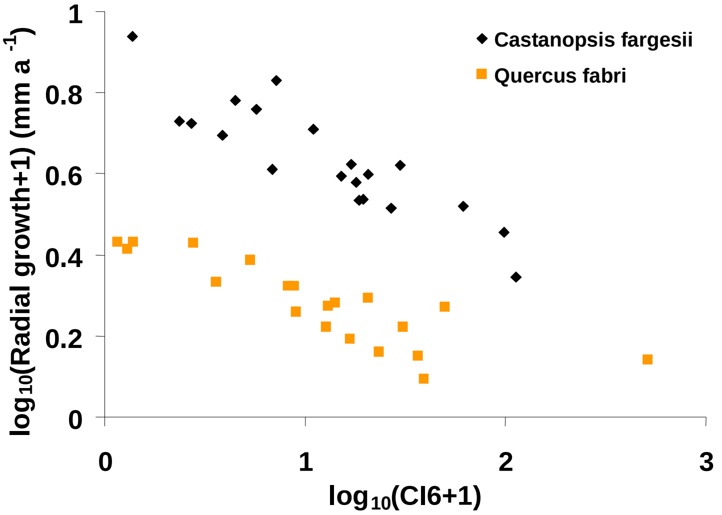

Fig. 3. Relationship between mean annual radial growth (mm a^{-1}) and CI6 with an opening angle of 55° in *C. fargesii* and 50° in *Q. fabri* (n = 20 each).

4.2 Competitive equivalence and diversity effects

In *C. fargesii* we found competitive equivalence of conspecific and heterospecific neighbours, which is in general accordance with Hubbell’s (2001) neutral model. In contrast, non-equivalent effects of con- and heterospecific neighbours were observed in *Q. fabri*. However, the differential effect of con- vs. heterospecific neighbours was contrary to the pattern which is often found, i.e. that conspecific neighbours are stronger competitors than heterospecific neighbours. In *Q. fabri*, the heterospecific neighbours had a strong negative effect on radial growth, whereas conspecifics did not significantly influence growth. One possible explanation for the difference between the two species might be that the gradient of competition effects of conspecifics was smaller in *Q. fabri* than in *C. fargesii*. We, thus, lack local neighbourhoods with very strong conspecific competition in the *Q. fabri* data. In tropical forests, decreased performance of trees surrounded by conspecifics has often been explained by species-specific herbivores and pathogens (Janzen, 1970; Connell, 1971). However, Schuldt et al. (2010) document a positive relationship between the degree of insect herbivory and plant diversity in a highly diverse EBLF, indicating a higher impact of generalist herbivores and, as a consequence, potentially less negative conspecific density-dependent effects. On the other hand, Zhu et al. (2010) found density-dependence in 39 out of 47 tree species in the same EBLF site. Thus, the mechanisms underlying the observed competition relationships still remain unclear.

Species richness per se was only weakly or not at all related to radial growth. Using the mean competitive effects per species by dividing the overall competition index by (rarefied) species richness only marginally affected model outcome. This means that the number of species in the local neighbourhood does not strongly influence the effect of competition on radial growth. An overall neutral effect of species richness on radial growth may be the result of very complex competition relationships in species-rich mixed forests with neighbourhood effects on growth that extend from significantly negative over too weak to be detectable to significantly positive (Zhao et al., 2006; Li et al., 2010). Alternatively, competitive equivalence of the different species (Hubbell, 2001) may explain these results. Future research in the newly established experimental tree plantations of BEF-China is designed to systematically analyse these relationships under controlled conditions in a broad range of EBLF tree and shrub species.

4.3 Impact of other biophysical environmental factors

Local neighbourhood competition is by far the most important single factor affecting radial growth among the factors considered in our study. Initial tree size has often been found to be an explanatory variable as good as or even better than competition indices. For example, in a naturally established population of *Pinus sylvestris* the variables initial size (i.e., cross-sectional area of the stem base at the beginning of the growth interval), age, and competition index accounted for 62 % of the variation in five-year basal area growth (Stoll et al., 1994). However, initial size had by far the greatest effect on growth ($R_{partial}^2 = 0.56$). Stoll et al. (1994) attributed the relatively low competition effect to the low population density, due to which only initial competitive interactions were given. Inoue et al. (2008) demonstrate that the dominant factor affecting stem volume growth shifts during stand development in younger plantations: initial tree size was the dominant factor before canopy closure, whereas local neighbourhood competition had the greatest impact after canopy closure. This is confirmed by our analysis from a naturally regenerated forest stand where canopy closure had been achieved several years earlier. In addition, the range in initial dbh was relatively small in the 40 target trees, which makes it more difficult to observe an effect. Slope inclination has been shown to significantly affect the stature of a tree in terms of crown displacement and stem inclination (Umeki, 1995; Lang et al., 2010). In our study, we only observed a weak negative relationship between slope inclination and radial growth in *Q. fabri*. High morphological plasticity of EBLF tree species might be the reason for the low sensitivity of radial growth towards the topographic conditions in these highly variable environments (Lang et al., 2010).

4.4 Management implications

The results of our study suggest that relatively simple spatially explicit individual-based competition indices are a useful tool for assessing competition in younger secondary mixed-species EBLF, provided that the appropriate primary variable that quantifies the size of the trees is selected. As individual-tree diameter growth appears to be strongly influenced by local neighbourhood conditions, tree growth can be closely regulated by thinning and harvesting operations. However, to meet the various objectives of sustainable forest management such as reducing pest damage or fire risks, biodiversity conservation, carbon sequestration, or soil erosion control, selection harvest systems should be applied.

In recent years, great efforts have been made in China to maintain younger secondary EBLF, to convert single-species conifer stands into mixed-species stands or to use species mixtures in reforestation (Wang et al., 2007; Lei et al., 2009; Li et al., 2010). However, up to now only few studies dealt with mixture effects in Chinese EBLF. In a three-year pot experiment with eight EBLF tree species Li et al. (2010) found that the relationships between tree growth and competition varied with species identity and time. Our results indicate that there may be high competitive equivalence among different species. Clearly, more research is needed to elucidate the effects of species mixtures in these forests.

Acknowledgements

We thank Yurong Zhou and Jonas Daldrup for help with the fieldwork and Teng Fang (Gutianshan NNR) for help with species identification. We are very grateful for the support we received within the BEF-China research group. Funding for this study was provided by the German Research Foundation (DFG FOR 891/1) and by the National Science Foundation of China (NSFC 30710103907 and 30930005).

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PAPER IV

Mechanisms promoting tree species coexistence:
Experimental evidence with saplings of subtropical forest ecosystems of China

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Keywords: biomass allocation, branch demography, complementarity, crown architecture, density, facilitation, niche differentiation, species composition, species identity, species richness

Journal of Vegetation Science DOI 10.1111/j.1654-1103.2012.01403.x.

Abstract

Questions: The maintainence of a diverse sapling pool is of particular importance for the regeneration and persistance of species-rich forest ecosystems. However, the mechanisms of coexistence of saplings have rarely been studied experimentally. We thus ask:
Do species richness, species composition, species identity and stand density have effects on the coexistence, growth patterns and crown architecture of tree saplings?
Location: Jiangxi Province, Southeast China
Methods: In a field experiment, we manipulated the local neighbourhood of saplings of the four early-successional subtropical species (*Schima superba*, *Elaeocarpus decipiens*, *Quercus serrata* and *Castanea henryi*) with regard to species richness (1, 2 and 4 species), species composition (monocultures, six two-species combinations and one four-species combination) and stand density (low, intermediate and high). We tested for treatment effects and the impact of species identity on growth variables, biomass allocation, crown architectural traits and branch demography.
Results: Species richness was a poor predictor of all response variables, but enhanced pruning and branch turnover. In contrast, species composition proved to be of great importance for growth, biomass allocation, crown architecture and branch demography. Local neighbourhood interactions of saplings were characterised by complementary or facilitative as well as by competitive mechanisms. Intraspecific competition was higher than interspecific competition for two species (*C. henryi*, *Q. serrata*) depending on the respective species combination. To a high degree the competitive ability of species can be explained by species identity. Competition for light likely played a major role in our experiment, as evidenced by the strong response of crown architecture and branch demography to the manipulated predictor variables.
Conclusions: Effects of species composition and species identity on growth rates and crown architectural variables of tree saplings point to niche separation as a mechanism of species coexistence, while effects of species richness were not yet prominent at the sapling life stage.

1 Introduction

The question as to which mechanisms maintain and promote species coexistence has increasingly raised interest in the light of biodiversity loss and species extinction (Barot 2004; Hillebrand & Matthiessen 2009). Two theories play a key role in the current discussion on plant species coexistence: neutral theory and niche theory. According to neutral theory, functional equivalence (i.e. co-occurring species do not have to be different in rates of growth, dispersal or speciation), together with stochastic events, is a sufficient explanation for species coexistence (Hubbell 2005; Rosindell et al. 2011). Niche theory, by contrast, implies that coexistence is explained by the interspecific differentiation in response to exploitative competition for environmentally limiting resources (DeClerck et al. 2005; Kraft et al. 2008) or in response to species-specific pathogens (Petermann et al. 2008; more general: Loreau & Hector 2001; Silvertown 2004; Levine & HilleRisLambers 2009). Niche partitioning may occur in space, in time or with regard to the quality of resources. As a result, in species combinations resources may be used in a complementary and more efficient way than in monocultures, and interspecific competition is reduced compared to intraspecific competition (Kahmen et al. 2006).

For trees, the most important above-ground resource is light (Denslow 1987; Canham et al. 1994). Since light harvesting efficiency is significantly affected by biomass allocation to leaves, foliage distribution and branching frequency (Niinemets 2010), the separation in niche space with regard to light harvest should be evidenced by species-specific growth patterns, biomass allocation or plant architecture. In addition to abiotic factors competitive interactions strongly influence individual tree growth. In particular, crown dimensions and architecture are known to respond sensitively to local neighbourhood interactions (Biging & Dobbertin 1992; Getzin et al. 2008; Schröter et al. 2011). However, to explain the spatial development of crowns in detail, information on single branches of individual trees is needed, since the process of crown expansion depends on the spatial development of branches and branch demography, which in turn is affected by local neighbourhood interactions (Franco 1986; Stoll & Schmid 1998; Sumida et al. 2002).

In this study, we experimentally analyse mechanisms of species coexistence of individual trees at the sapling stage, making use of the local neighbourhood approach (Pretzsch 2009). The maintainence of a diverse sapling pool is important to ensure the regeneration and persistence of species-rich forests (Bruelheide et al. 2011). We refer to tree saplings as young tree individuals that have survived the critical seedling phase and whose local neigbourhood is characterised by strong competition caused by a high density of similar-aged individuals. Important factors of this local neighbourhood which might affect the individual performance of tree saplings are species richness and species composition, species identity, stand density and the size of the tree saplings. The focus on individual tree growth patterns, biomass allocation and architectural traits is particularly promising in woody species, because these species have easily identifiable, large individuals with biomass accumulation in long-lasting structures.

We planted saplings of four early-successional subtropical species in monoculture as well as in two- and four-species combinations. In order to determine whether niche separation is the mechanism that enables the coexistence of these species in an early stage of their life, we tested for species richness, species composition and species identity, as well as for density and initial diameter size effects. Specifically, we tested the following hypotheses:

(H1) Species richness of the local neighbourhood affects the growth and morphology of saplings.

(H2) The species composition of the local neighbourhood affects growth and morphology of saplings.

(H3) The species identity of the target sapling is an important predictor of its growth and morphology.

(H4) Density affects growth and morphology of saplings.

2 Materials and Methods

2.1 Study area and experimental design

Our experiment was set up near Xingangshan, Jiangxi province, South-east China (29° 06’ 33’’ N/ 117° 55’ 24’’ E). The study area is characterised by a subtropical monsoon climate with an average annual precipitation of approximately 2,000 mm and a mean temperature of 15.1 °C. The natural vegetation is a subtropical broad-leaved forest with a dominance in abundance of evergreen species (Bruelheide et al. 2011). Nevertheless, the number of occuring deciduous and evergreen species is almost balanced (Lou & Jin 2000). The subtropical broad-leaved forest ecosystems of South-east China represent a global hotspot of phytodiversity (Barthlott et al. 2005).

The experimental area was a former agricultural field, which was ploughed, harrowed and divided into four blocks prior to setting up the experiment in March 2009. Four highly abundant, early-successional species were chosen for the experiment: *Schima superba* Gardn. et Champ., *Elaeocarpus decipiens* Hemsley (evergreen), *Quercus serrata* Murray and *Castanea henryi* (Skan) Rehd. et Wils. (deciduous) (Yu et al. 2001). We manipulated species richness and species composition of tree saplings on plots of 1 m² size. Three plot-related species richness levels were established: monocultures, two-species combinations and four-species combinations. The four monocultures of each species, all six possible two-species combinations, and one four-species combination made a total of eleven species compositions. In addition to enabling the analysis of species richness effects, the comparison of all possible species combinations also makes it possible to identify the effects of intraspecific versus interspecific competition (Massey et al. 2006) as well as competitive dominance of specific species. Species identity was treated as another predictor variable in the experiment. Finally, the species richness and species composition treatments were fully crossed with a density treatment. The low density treatment comprised only one individual per plot, whereas the experimental plots with high and intermediate density each contained 16 individuals, planted in an array of four by four. Planting distances between saplings in the high and intermediate density treatment were 15 and 25 cm, respectively. The high, intermediate and low densities in this experiment refer to 44,000, 25,000 and 10,000 saplings per ha, respectively. In the nearby Gutianshan Nature Reserve, densities of 16,000 individuals per ha were found in an early successional secondary forest stand (< 20 years; Bruelheide et al. 2011). In the species combinations, each species was represented by the same number of individuals in both the peripheral rows (i.e. 12 individuals) as well as in the center (i.e. four individuals). To avoid edge effects, all analyses were performed using the four central individuals. All treatment combinations were replicated four times, once in each of the four blocks. The total number of plots was 132 (11 species compositions x two densities (high, intermediate) x four blocks + 11 low density x 4 species in 4 blocks = 88 + 44 plots). All treatment combinations were randomly assigned to plots within blocks. The experiment was run until September 2010 when destructive harvest took place. Individuals of the intermediate density treatment of one block were harvested in July 2010.

2.2 Field measurements

Sapling mortality

Over the course of the experiment, 223 out of 1,452 saplings died (15.4 %; number of dead saplings per species: *C. henryi* 92, *S. superba* 95, *Q. serrata* 18, *E. decipiens* 18). Since 96 % of these dead individuals died during the first growing season (March to October 2009), post-planting stress was assumed to be the main reason for sapling mortality. Consequently, only data of saplings that survived this phase of establishment were incorporated in the analyses.

Sapling growth

Total height of saplings (i.e. length from ground to apical meristem) was measured in November 2009 and September 2010. Stem diameter at base height was measured 5 cm above ground in N-S and E-W direction with a caliper, and the mean value was used in the analyses. The position of the diameter measurements was marked permanently with white paint. Measurements were taken in March 2009 (initial stem diameter), November 2009 and September 2010. Growth rates of absolute height and diameter were calculated as: (value (September 2010) - value (November 2009))/ 11.

Above-ground biomass

To analyse biomass allocation patterns with regard to stratification (i.e. height layers) and to different constitutents (stem, branches and leaves), the four central individuals per plot were harvested in September 2010 in 50 cm strata starting from ground. Saplings were divided into stem, branches and leaves for each stratum. Biomass was dried at 70° C for 48 h and weighed to 0.01 g precision. Biomass data were logarithmically transformed prior to analyses.

To analyse the vertical above-ground biomass distribution, we calculated the cumulative biomass fraction *C*, i.e. the proportion of cumulative above-ground biomass, summed up from the ground to the height strata *hs* (50, 100, 150, 200, 250 cm). For each individual we fitted the coefficient of vertical biomass distribution as the linear regression coefficient β of *C* over *hs* (see Jackson et al. 1996; Vonlanthen et al. 2010). The coefficient of vertical biomass distribution indicates the steepness of declining *C* with increasing *hs*. Higher coefficient values, in turn, indicate biomass more evenly distributed over the total height of the tree.

Crown architecture

All crown architectural parameters were determined in June and September 2010. A branch was defined as a primary furcation longer than 1 cm. The height of the first branch was measured, and crown length was calculated as the difference between total sapling height and height of the first branch. The length of the first and the longest branch was measured as the distance from the stem to the longest tip of the respective branch.

Branch demography

Branches were counted bi-monthly during winter 2009/10 (November, January, March) and monthly from April to June 2010 and in September 2010. Branch turnover and pruning are interpreted as a measure of adaption ability to changes in neighbourhood conditions over time. Branch turnover was calculated as the sum of all changes in branch number (no matter whether positive or negative) from November 2009 to June 2010. Pruning was defined as the sum of all negative changes in branch number (November 2009 to June 2010) and describes the dieoff of branches over time.

2.3 Statistical analyses

The overall aim of this study was to disentangle neighbourhood effects on growth, biomass allocation, crown architecture and branch demography of saplings. Firstly, the complete dataset was used to test for (H1) by fitting mixed effects models (Model 1) including species richness and density as factorial variables and the initial diameter as fixed effect. The initial diameter was used to account for differences in size at the beginning of the experiment. Secondly, all two species combinations were analysed for species composition (H2). Mixed effects models (Model 2a) were fitted using species composition, density and initial diameter as fixed effect. The analyses with Model 2b were performed for the high density treatment data divided by species to exclude density effects and to test for composition effects on the individual-level of each species. Model 2b contained species composition and initial diameter as fixed effects. Thirdly, mixed effects models (Model 3) for all monocultures were calculated to test (H3). They were fitted by the predictor variables species identity, density and initial diameter as fixed effects.

Random effects for all models were plot nested in block. Model simplification was performed by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($p < 0.05$). Since all density treatments were included in the analyses of Models 1, 2a and 3, the complete data from the June 2010 measurements was used to ensure a balanced data set. Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances). The significant categorical variables were further examined by a Tukey post-hoc test. For the sake of clarity and more comprehensive analyses, the models presented here did not account for the presence and absence of species (for these models see supporting information S1). Since a test for a phylogenetic signal (K statistics) in the observed growth and crown architectural traits was not significant, we did not consider phylogeny in the statistical analyses (see supporting information S2).

In addition, we calculated Pearson correlation coefficients between height and diameter growth rates and crown architectural variables. If not indicated otherwise, values are given as mean with standard deviation.

All statistical analyses were performed using R 2.12. (R Development Core Team, 2010) using the packages “nlme” for the analyses of mixed effects models (Pinheiro et al. 2010), “multcomp” for post-hoc Tukey tests (Hothorn et al. 2008) and “picante” for the K statistics (Kembel et al. 2010).

3 Results

3.1 Height and diameter increment

The mean sapling height at the time of planting was 33 cm ± 13 cm, compared to a mean height of 124 cm ± 39 cm at the end of the experiment. *S. superba* (6.74 ± 2.17 cm month^{-1}) had the highest mean absolute height growth rate, followed by *E. decipiens* (6.31 ± 2.27 cm month^{-1}), *Q. serrata* (5.57 ± 2.34 cm month^{-1}) and *C. henryi* (3.63 ± 2.67 cm month^{-1}). Species richness had no significant impact on the absolute growth rate of sapling height. However, species composition significantly affected absolute growth rates ($p = 0.03$). Model 2b revealed that the height growth rate of *C. henryi* ($p = 0.019$) and *Q. serrata* ($p = 0.046$) individuals was affected by species composition. Individuals of both species were significantly higher in combination with *E. decipiens* compared to monocultures. The absolute height growth rate was also influenced by species identity ($p < 0.001$). Neither density nor the initial stem diameter of saplings affected height growth.

The mean absolute growth rates of diameter per month were: *E. decipiens* (0.7 mm ± 0.5) > *S. superba* (0.6 mm ± 0.3) > *Q. serrata* (0.5 mm ± 0.3) > *C. henryi* (0.3 mm ± 0.3). Absolute diameter growth rates were neither affected by species richness nor by species composition. However, species identity was a highly significant predictor of diameter growth ($p = 0.008$). The diameter growth rate of *C. henryi* was significantly lower than that of *S. superba* and *E. decipiens* ($p < 0.05$). In addition, density had a significant influence on absolute diameter growth rate ($p < 0.001$). The diameter growth of saplings was significantly enhanced in the low density treatment compared to both the intermediate and high density treatment ($p < 0.001$). In contrast, the initial stem diameter had no significant effect on diameter growth.

Both absolute height and diameter growth rates were positively correlated with crown length (Pearson correlation coefficient, $r = 0.84 / 0.50$, respectively), the length of the longest branch ($r = 0.40 / 0.51$) and the number of branches ($r = 0.49 / 0.45$).

3.2 Above-ground biomass

Model 1 revealed no significant effect of species richness on above-ground biomass or on the coefficient of vertical biomass distribution. Species composition, in contrast, significantly influenced biomass increment ($p = 0.009$) and allocation to different constituents ($p < 0.01$). Results of Model 2b showed that of *C. henryi* individuals accumulated significantly more biomass in combination with *E. decipiens* than in the monoculture ($p < 0.001$) and in combination with *S. superba* ($p = 0.023$, Fig. 1A). The biomass of leaves of *C. henryi* individuals was significantly lower in monocultures than in combination with *E. decipiens* ($p = 0.005$) or in the four species combination ($p = 0.025$, Fig. 1B). Similar to *C. henryi*, the stem and total biomass of *Q. serrata* individuals was higher in combination with *E. decipiens* than in monoculture ($p < 0.01$) and in combination with *C. henryi* ($p < 0.05$, Fig. 1C/D). Species identity was a significant predictor of all biomass-related variables (all $p < 0.001$). In general, results of post-hoc Tukey tests revealed that the biomass of all constituents of *C. henyri* was significantly lower than that of the other species (Table 1).

Stratum-related biomass allocation patterns of different constituents proved to be quite stable over density treatments for each species (Fig. 2). Species identity effects were evident for the coefficient of vertical biomass distribution ($p < 0.001$). Increasing density had negative effects on all biomass constituents ($p < 0.05$), whereas no density effects on the vertical biomass distribution were found. Regarding the total above-ground productivity within the low density treatment, the four species ranked as follows: *S. superba* (157.2 ± 134.7 g) > *E. decipiens* (135.2 ± 145.99 g) > *Q. serrata* (97.0 ± 92.3 g) > *C. henryi* (42.0 ± 43.4 g).

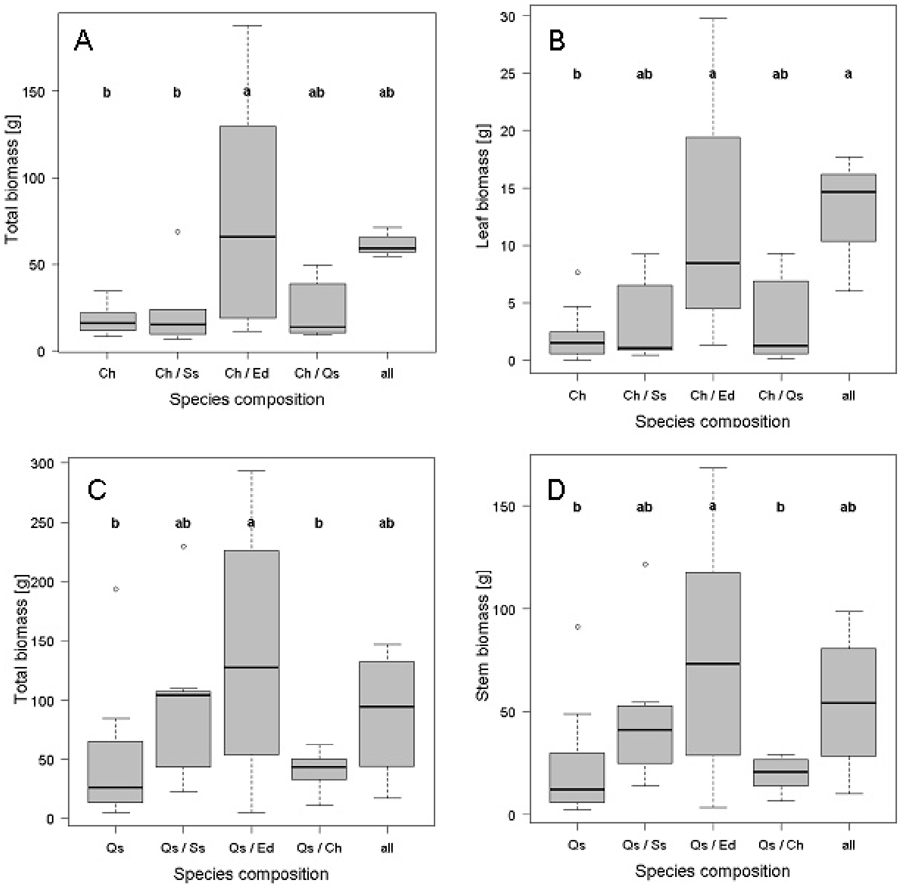

Fig. 1. Boxplots of the individual total biomass (A) and leaf biomass (B) of *C. henryi,* and of total biomass (C) and stem biomass (D) of *Q. serrata* in the different species compositions. Significances of post-hoc Tukey tests of the explanatory variable "species composition" tested by Models 2b are indicated by different letters. Species codes: Ch: *C. henryi*; Ed: *E. decipiens*; Qs: *Q. serrata*; Ss: *S. superba*.

Table 1. Mean values of above-ground biomass allocation to different constituents (dry weight per plant [g] and standard deviations) for the four species. Different letters show significant post-hoc Tukey results.

Constituents	***C. henryi***	***E. decipiens***	***Q. serrata***	***S. superba***
Total	13.9 ± 10.8 ^{a}	34.5 ± 33.6 ^{b}	37.8 ± 25.6 ^{b}	56.7 ± 33.7 ^{b}
Stem	20.2 ± 22.8 $^{\mathbf{a}}$	69.9 ± 68.6 $^{\mathbf{b}}$	47.9 ± 45.8 $^{\mathbf{b}}$	57.3 ± 42.8 $^{\mathbf{b}}$
Branches	13.6 ± 14.6 $^{\mathbf{a}}$	44.7 ± 62.2 $^{\mathbf{b}}$	18.5 ± 22.2 $^{\mathbf{a}}$	32.5 ± 36.3 ^{b}
Leaves	8.2 ± 11.0 ^{a}	20.6 ± 30.3 $^{\mathbf{ab}}$	30.1 ± 28.0 $^{\mathbf{b}}$	67.4 ± 61.9 $^{\mathbf{c}}$

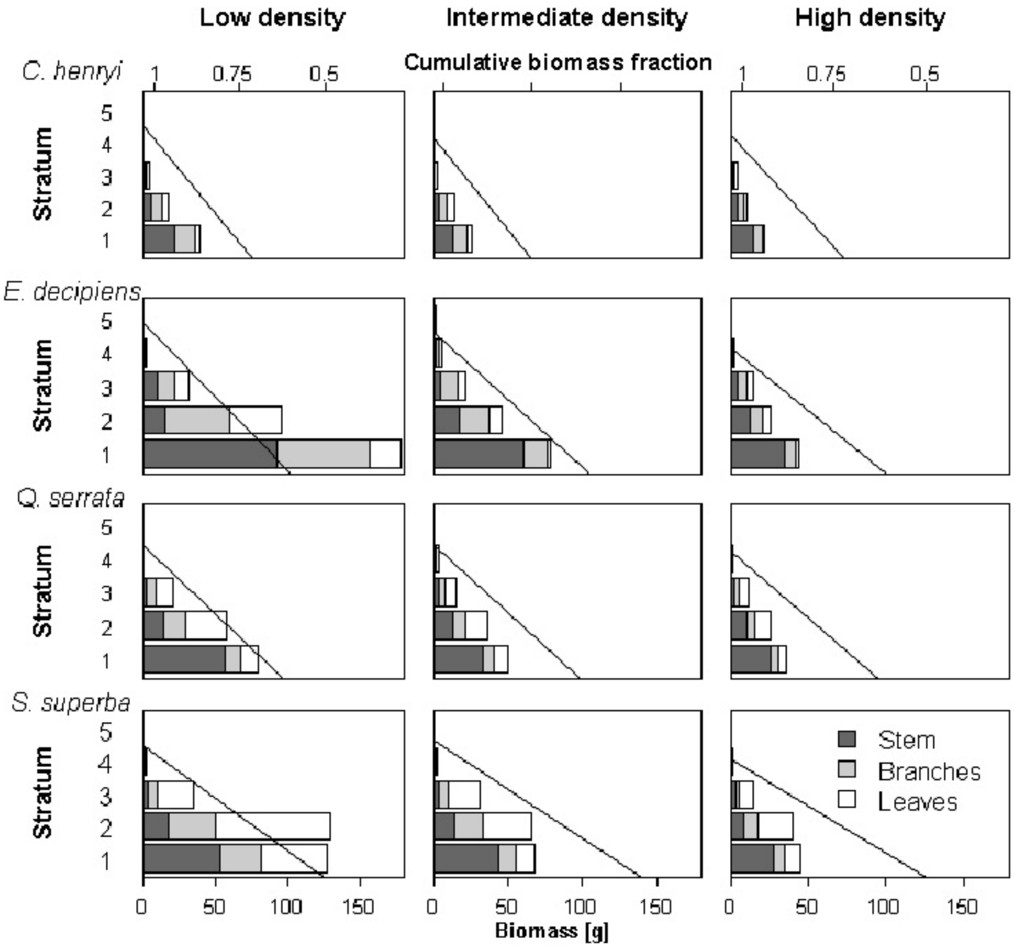

Fig. 2. Allocation patterns of the biomass constituents (stem, branches, leaves) per individual over different strata. Mean biomass values per strata are shown for species of the different density treatments (barplots). Each stratum comprises 50 cm in height. The black line represents the mean coefficient of vertical biomass distribution for the respective species and density treatment.

3.3 Crown architecture

Species richness had no effect on crown architecture, whereas species composition proved to be a significant predictor for all crown architectural variables ($p < 0.05$ for all variabels). Model 2b results show that species composition had a significant effect on crown length of *C. henryi* and *Q. serrata* and on the length of the longest branch of *S. superba*. The crown length of *C. henryi* was significantly enhanced when growing with *E. decipiens* compared to both the monoculture and the combinations *C. henryi – S. superba* and *C. henryi – Q. serrata* ($p < 0.05$). Moreover, the crown length of *C. henryi* was higher in the four-species combination compared to the monoculture ($p < 0.05$). The crown length of *Q. serrata* was significantly higher when grown with *E. decipiens* compared to the monoculture ($p = 0.008$) and the *Q. serrata – C. henryi* combination ($p = 0.020$). In addition, the crown length of *Q. serrata* was enhanced in the four-species combination compared to the *Q. serrata* monoculture ($p = 0.028$) and combination with *C. henryi* ($p = 0.042$). The length of the longest branch of *S. superba* was significantly enhanced when grown in combination with *C. henryi* compared to the monocultures, the combinations *S. superba – E. decipiens* and *S. superba – Q. serrata,* and the four-species combination (all $p < 0.05$).

3.4 Branch demography

Species richness had no effect on the number of branches (developed at the end of the experiment) but influenced branch turnover ($p = 0.043$) and pruning ($p < 0.001$; Fig. 3).

Branch turnover was significantly enhanced in the four species combination compared to the two species combination (p = 0.047). Pruning was higher in the four species combinations than in the two species combinations and monocultures (p < 0.001). Species composition significantly affected the number of branches, branch turnover and pruning. Species identity significantly affected branch demography (all variables; Table 2).

Table 2. Crown architecture and branch demography. Values are means for species and density treatments. Different letters show significant differences of post-hoc Tukey tests.

Crown characteristic	**Species means**				**Density means**		
	C. henryi	***E. decipiens***	***Q. serrata***	***S. superba***	**Low**	**Middle**	**Dense**
Height of first branch [cm]	8.94	6.17	13.36	13.15	4.52^{a}	9.85^{ab}	10.91^{b}
Crown length [cm]	72.89	106.15	76.02	80.97	94.76	89.78	82.08
Length of first branch [cm]	38.91^{a}	21.64^{b}	24.42^{b}	36.24^{a}	26.05^{ab}	36.16^{b}	24.12^{a}
Length of longest branch [cm]	52.65	62.14	43.85	52.82	65.05^{b}	58.01^{b}	48.13^{a}
Number of branches #	6.89^{a}	21.32^{c}	16.54^{b}	9.56^{a}	17.64^{b}	13.64^{ab}	12.82^{a}
Branch turnover *	15.48^{ab}	30.72^{c}	22.31^{bc}	14.14^{a}	27.12^{b}	22.85^{b}	19.05^{a}
Pruning °	6.23^{a}	6.85^{b}	4.99^{b}	4.16^{b}	6.77	6.01	5.09

All branches exceeding 1 cm in length, counted in June 2010.

* Sum of all changes in branch number (positive and negative) from November 2009 to June 2010.

° Sum of all negative changes in branch number (November 2009 to June 2010).

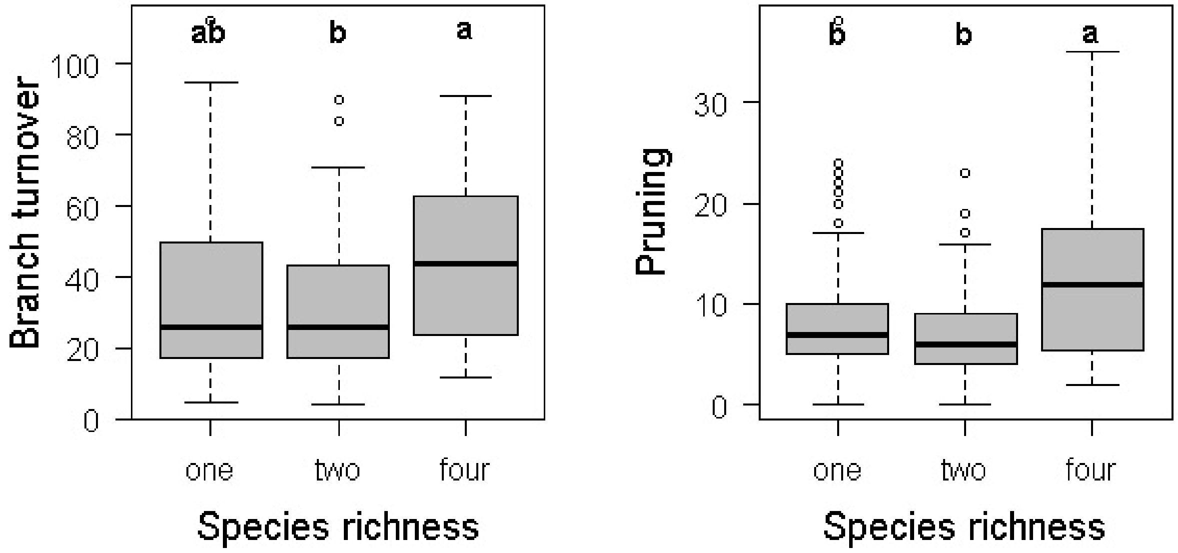

Fig. 3. Boxplots of branch turnover and pruning for species richness levels. Branch turnover is the sum of all positive and negative changes in branch number, whereas pruning is the sum of branch losses over the duration of the experiment. Significances of post-hoc Tukey tests of species richness tested by Model 1 are indicated by different letters.

4. Discussion

4.1 Effects of species richness

Our study analysed for the first time species richness effects on the branch demography of tree saplings. The increase in pruning and branch turnover with higher species number proved the high dynamics in the four species combinations. Sapling individuals may adapt their crown architecture to changes in their local neighbourhood by modifying their branching arrangement (Sumida et al. 2002). These changes may be caused by the species-specific crown architecture of neighbouring saplings and differences in leaf occurence. We interpret the observed highly dynamic branch demography as an effect of proceeding niche differentiation with regard to light harvesting in this relatively complex neighbourhood of the four species combination.

Contrary to our expectations, we found no significant effect of species richness on the other growth and crown architectural parameters. This finding may be attributable to two factors. Firstly, it is well conceivable that diversity effects may evolve at a later stage of sapling development. Lang et al. (2010) analysed older tree individuals (20 – 100 years) of an overlapping species pool (*S. superba*, *Castanopsis eyrei* Champ. ex Benth., *Q. serrata*, *C. henryi*) in the same study region. The authors found that crown area was affected by functional diversity. They concluded that this was due to niche separation in terms of height stratification, timing of leaf occurrence and crown density (Lang et al. 2010). Secondly, species richness effects on tree growth responses (for example attributable to niche complementarity) might only become apparent at higher levels of diversity (Papaik & Canham 2006). The occupied niche space should increase with higher species number and thereby make niche complementarity more likely to occur.

4.2 Effects of species composition

The effects of species composition on growth, biomass allocation, crown architectural and branch demographic variables indicated that the species identity of neighbouring saplings is an important determinant of sapling growth (H2) in our experiment. This finding is in accordance with studies that demonstrate the importance of neighbour tree identity for growth (e.g. Massey et al. 2006; von Oheimb et al. 2011) and crown formation (Frech et al. 2003; Massey et al. 2006; Lintunen & Kaitaniemi 2010) of individual trees.

We hypothesise that several mechanisms - depending on the species involved - determine effects caused by species composition. These are evidenced by differences in the growth performance of less productive species (here: *C. henryi*, *Q. serrata*; deciduous) in the monocultures compared to combinations containing both highly productive (here: *E. decipiens, S. superba*; evergreen) and less productive species.

When growing together with *E. decipiens*, the two species *Q. serrata* and *C. henryi* grew taller and produced more biomass than when growing in monoculture or with other species. These results indicate that intraspecific competition of *C. henryi* and *Q. serrata* individuals was higher than the species' interspecific competition with *E. decipiens*. Massey et al. (2006) also demonstrated that height growth of saplings may increase in heterospecific plots. However, due to a higher branching of the saplings within homospecific plots, the authors did not detect any effect of species composition on above-ground biomass. In our study, the reduced competition experienced by *C. henryi* and *Q. serrata* was caused to a greater extent by the species identity of the competitor, i.e. by *E. decipiens*, than by the fact that it was growing with any heterospecific neighbour. Based on the observed high productivity of *E. decipiens* in the low density treatment, we would have expected a reduced performance of less competitive species in combinations with *E. decipiens*. In addition, the biomass of *E. decipiens* individuals was not affected by species composition. Thus, the increased growth of

C. henryi and *Q. serrata* in combination with *E. decipiens* indicate the existence of complementary or facilitative mechanisms.

The enhanced crown length of *C. henryi* and *Q. serrata* in combinations with *E. decipiens* points to complementarity of crown architecture. Complementary effects and, thus, reduced interspecific competition for light within the four-species plots compared to high intraspecific competition in monocultures also resulted in longer crowns in both species. In contrast, *C. henryi* had shorter crowns in combination with *S. superba,* than in combination with *E. decipiens*. This indicates - together with the enhanced length of the longest branch of *S. superba* in combination with *C. henryi* - negative competitive effects of *S. superba*. The effects of species composition on crown architectural variables highlight the importance of competition for light as a structuring factor of neighbourhood interactions.

4.3 Effects of species identity

Species identity was a strong predictor throughout the whole experiment. We found all the response variables analysed to be affected by species identity, which confirms our H3. Our findings approve the results of other studies that described species-specific relative growth rates (Dekker et al. 2008; Suter et al. 2010) and crown architecture (Takyu 1998). Branching frequency, foliage distribution, and biomass allocation to leaves significantly affect light harvesting (Niinemets 2010). Energy gain by increased light harvesting is likely to be converted to growth, and thus, sapling growth and survival was found to be related to architectural traits (Takyu 1998; Sterck et al. 2003; Dekker et al. 2008). In our study, height and diameter growth were also found to be related to the vertical and horizontal crown dimensions.

When ranking the observed species according to their productivity, the two evergreens performed better than the two deciduous species. In contrast to our results, seedlings (< 0.5 years) of evergreen species in the same study region have been found to accumulate less biomass and to show a reduced phenotypic plasticity with regard to shade than deciduous species in a greenhouse experiment (Böhnke & Bruelheide 2011). However, the saplings in our experiment were older, and, thus, effects of their growth performance during the seedling stage were of minor importance. The advantages of evergreen leaves, i.e. longer photosynthetic season, lower costs of replacing leaf nutrients and tougher laminae to endure frost, drought and herbivory (Givnish 2002), might also have contributed to the better performance of the evergreen species in our experiment.

Our results indicated a close relationship between species identity and branch demography. Species identity effects on branch demography were pronounced, since each of the four species had a different branch development strategy. The number of branches was low for *C. henryi* and *S. superba*. Whereas *S. superba* had the lowest degree of pruning and thus was able to invest more in stem biomass, *C. henryi* displayed high branch mortality, combined with long branches and smaller height increments. In contrast, *Q. serrata* had an intermediate number of branches and degree of pruning. High turnover rates and branch numbers of *E. decipiens* combined with large height and diameter growth suggest that this species may be able to adapt quickly to changes in the local light environment and, thus, to optimize its foraging for light by means of a highly flexible biomass allocation to branches. The differences between species in branch demography may be seen as niche separation with regard to light harvesting.

4.4 Effects of density

We found a negative effect of density on diameter growth rates but no density effects on height growth, thus partly confirming H4. Our findings are in agreement with competition studies, according to which diameter growth was often found to be influenced by the local neighbourhood (Biging & Dobbertin 1992; Canham et al. 2004; von Oheimb et al. 2011). The significant reduction of biomass in all constituents of saplings of the high density plots indicated that competition increased with increasing stand density.

In addition, density significantly affected crown architecture. A positive effect of reduced stand density on crown area was found for mature trees by Yu et al. (2003) and Hein et al. (2008). However, while the number and length of branches of loblolly pine increased with decreased density (Yu et al. 2003) this was not the case in Douglas fir (Hein et al. 2008). Thus, effects of density on crown architecture might be species-specific and generally depend on the distances to the neighbours which a tree individual may encounter in a respective stand.

Conclusion

In general, our results support the model of niche separation in terms of light harvesting of the species analysed. The species identity of neighbours as well as that of a target tree itself largely determines the outcome of neighbourhood interactions. Our study proved the complexity of local neighbourhood interactions and coexistence mechanisms in an early life stage of tree individuals.

Acknowledgements

We are grateful to Andreas Schuldt for ongoing and fruitful discussion on the ideas of this manuscript. We would like to thank Walter Durka for his support for the analyses of phylogenetic signal. The work and help of Mr Qi and Mrs Fang in collecting data and maintaining the experiment is greatly acknowledged. We would like to thank the whole research group BEF China and especially the group of PhD students for the successful and cooperative teamwork. This study was funded by the German Research Foundation (DFG FOR 891/1). We are grateful for this support.

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Supplementary material:

Online Appendix S1: Test of phylogenetic signal in the traits
Online Appendix S2: An alternative analysis of our results

Electronic Appendix S1:

An alternative analysis of our results.

The explanatory variable species richness may be captured as a factorial variable (Sf), as a linear or as a loglinear variable. It may also be represented by a contrast of monocultures versus species combinations (mono). We tested for all these different species richness variables in Models A. In Models B, we tested for the effect of species presence (used as contrast of presence versus absence) and all two-way interactions, and in Models C for the species composition (comp, factorial variable). Due to the experimental design it was not possible to test for all these effects within one model. In addition, full models contained the fixed effects: species identity (ID), density and the initial diameter of the saplings (init dia). Random effects were plot nested in block. Model simplification was performed by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($p < 0.05$). The table shows results of the most parsimonious models. AIC values are given to compare the goodness of fit of the Models A-C for each response variable. Species names are given as: *Castanea henryi* (CH), *Elaeocarpus decipiens* (ED), *Quercus serrata* (QS), *Schima superba* (SS).

	Absolute growth rate												Biomass					
	Height						Diameter						Total					
Model	A		B		C		A		B		C		A		B		C	
AIC	1214.09		1213.69		**1209.23**		**213.13**		217.16		253.01		735.67		**735.21**		745.30	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
Sf	3.08		-		-		-		-		-		-		-		-	
Comp	-		-		7.71	***	-		-		2.92	**	-		-		8.72	***
CH	-		27.36	***	-		-		14.78	***	-		-		37.00	***	-	
ED	-		8.29	**	-		-		-		-		-		5.56	*	-	
QS	-		-		-		-		-		-		-		0.05		-	
SS	-		10.71	**	-		-		-		-		-		11.83	***	-	
ID	34.46	***	22.12	***	16.68	***	17.68	***	12.68	***	10.21	***	31.78	***	17.46	***	11.79	***
Density	-		-		-		19.33	***	20.69	***	20.62	***	12.57	***	17.31	***	17.59	***
init dia	7.50	**	8.75	**	5.33	*	-		-		-		32.90	***	33.36	***	31.16	***
ED:QS	-		-		-		-		-		-		-		-		-	
ED:SS	-		8.43	**	-		-		-		-		-		16.84	***	-	

	Biomass																	
	Stem						Branches						Leaves					
Model	A		B		C		A		B		C		A		B		C	
AIC	2951.39		2908.83		**2883.17**		**773.20**		777.27		786.46		786.58		**785.59**		790.99	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
Sf	-		-		-		-		-		-		-		-		-	
Comp	-		-		4.48	***	-		-		6.32	***	-		-		16.66	***
CH	-		13.41	***	-		-		16.74	***	-		-		71.60	***	-	
ED	-		9.95	**	-		-		14.61	***	-		-		4.06	*	-	
QS	-		0.16		-		-		6.58	*	-		-		-		-	
SS	-		0.08		-		-		1.53		-		-		39.34	***	-	
ID	15.58	***	9.79	***	8.56	***	21.43	***	10.45	***	7.72	***	68.07	***	35.58	***	25.31	***
Density	4.76	**	5.75	**	6.24	**	22.78	***	26.74	***	25.93	***	16.54	***	20.15	***	21.45	***
ini dia	43.34	***	44.62	***	41.50	***	27.22	***	27.44	***	25.28	***	12.02	***	11.54	***	11.60	***
ED:QS	-		5.70	*	-		-		-		-		-		-		-	
ED:SS	-		8.38	**	-		-		12.41	***	-		-		9.30	**	-	

	Biomass					
	Coefficient of vertical biomass distribution					
Model	A		B		C	
AIC	**418.10**		426.11		438.77	
	F-value	p	F-value	p	F-value	p
Sf	-		-		-	
Comp	-		-	-	3.64	***
CH	-		4.56	*	-	
ED	-		3.26		-	
QS	-		-	-	-	
SS	-		8.12	**	-	
ID	8.74	***	5.54	**	4.33	**
Density	-		-	-	-	
init dia	-		-	-	-	
ED:QS	-		-	-	-	
ED:SS	-		6.61	*	-	

	Crown architecture																	
	Height of first branch						Crown length						Length of first branch					
Model	A		B		C		A		B		C		A		B		C	
AIC	**1321.58**		1321.97		1328.21		3095.30		3066.12		**3040.28**		2939.80		**2922.8**		2898.29	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
mono	4.99	*	-		-		-		-		-		-		-		-	
Sf	-		-		-		-		-		-		-		-		-	
Comp	-		-		2.35	*	-		-		7.40	***	-		-		3.70	***
CH	-		-		-		-		3.99	*	-		-		14.18	***	-	
ED	-		-		-		-		44.40	***	-		-		5.56	*	-	
QS	-		-		-		-		6.65	*	-		-		6.72	*	-	
SS	-		10.91	*	-		-		5.03	*	-		-		-		-	
ID	7.28	***	3.91	*	4.23	**	26.46	***	9.92	***	10.26	***	15.94	***	7.54	***	6.88	***
Density	6.55	**	8.21	***	6.41	**	4.69	*	5.41	**	5.13	**	3.64	*	3.80	*	3.71	*
init dia	-		-		-		32.59	***	32.02	***	30.69	***	-		-		-	
ED:SS	-		-		-		-		10.43	**	-		-		-		-	
ED:CH	-		-		-		-		-		-		-		7.18	**	-	
CH:ED	-		-		-		-		-		-		-		-		-	
CH:SS	-		-		-		-		-		-		-		-		-	

	Crown architecture						Branch demography											
	Length of longest branch						Number of branches						Branch turnover					
Model	A		B		C		A		B		C		A		B		C	
AIC	2977.40		2972.59		**2937.85**		2239.14		2235.40		**2221.45**		1106.78		**1103.30**		1108.04	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
mono	-		-		-		-		-		-		-		-		-	-
Sf	-		-		-		-		-		-		5.76	**	-		-	-
Comp	-		-		3.08	**	-		-		14.73	***	-		-		14.26	***
CH	-		-		-		-		37.53	***	-		-		20.70	***	-	-
ED	-		10.4701	**	-		-		59.54	***	-		-		87.86	***	-	-
QS	-		11.6678	***	-		-		16.22	***	-		-		6.48	*	-	-
SS	-				-		-		20.36	***	-		-		7.01	**	-	-
ID	11.72	***	4.42	**	3.83	*	72.01	***	28.65	***	25.48	***	56.28	***	23.00	***	20.92	***
Density	5.67	**	5.59	**	6.09	**	6.81	**	7.58	***	7.26	**	6.85	**	10.42	***	7.07	**
init dia	20.78	***	20.50	***	19.87	***	24.57	***	24.04	***	23.36	***	11.28	***	10.49	**	11.23	**
ED:SS	-		-		-		-		-		-		-		-		-	-
ED:CH	-		-		-		-		-		-		-		-		-	-
CH:ED	-		-		-		-		-		-		-		5.91	*	-	-
CH:SS	-		-		-		-				-		-		6.92	**	-	-

	Branch demography					
	Pruning					
Model	A		B		C	
AIC	**836.34**		844.87		851.45	
	F-value	p	F-value	p	F-value	p
mono	-	-	-		-	
Sf	9.53	***	-		4.41	***
Comp	-	-	0.00		-	
CH	-	-	17.81	***	-	
ED	-	-	4.23	*	-	
QS	-	-	1.67		-	
SS	-	-	5.62	**	-	
ID	9.67	***	11.22	***	5.44	**
Density	7.13	**	3.54		6.90	**
init dia	-	-	-		4.21	*
ED:SS	-	-	-		-	
ED:CH	-	-	-		-	
CH:ED	-	-	-		-	
CH:SS	-	-	7.48	0	-	

Electronic Appendix S2

Test of phylogenetic signal in the traits

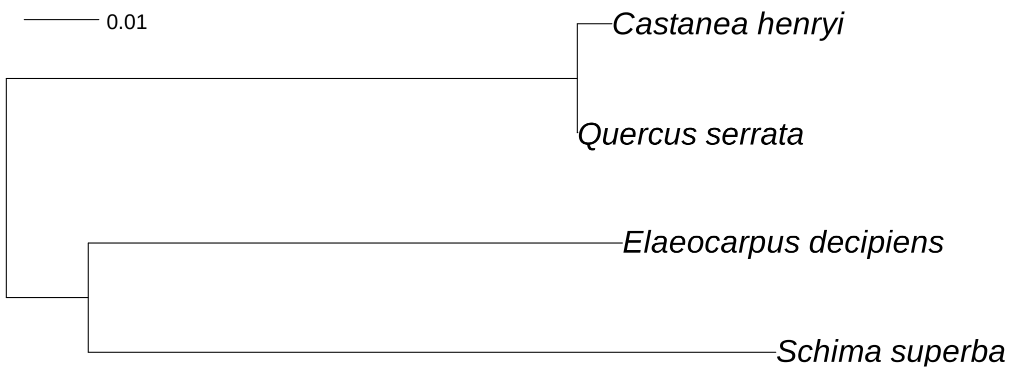
To confirm that the analysed trait data of our four observed species are statistically independent and not influenced by the phylogenetic relatedness of the species, we run a test of phylogenetic signal in the species traits. K statistics were calculated, which describe the strength of phylogenetic signal compared with an expectation based only on the phylogenetic tree topology and branch lengths and assuming Brownian motion character evolution (Blomberg et al. 2003). A K value less than one indicates that the phylogentic signal is less than expected under Brownian motion evolution, whereas a K value greater than one implies a strong phylogenetic signal. The significance of the phylogentic signal can be tested by comparing the observed patterns of the variance of independent contrasts of the trait to a null model of shuffling taxa labels across the tips of the phylogeny (Kembel 2010). The analyses were done by means of the R-package picante (Kembel et al. 2010).

For the construction of the phylogenetic tree, sequences of rbcL and matK where downloaded from NCBI Genbank (http://www.ncbi.nlm.nih.gov/; Tab 1) for the species of interest or of closest available relatives (for C. henryi) and aligned with ClustalW in Bioedit. Based on the combined alignment consisting of 1094bp a phylogenetic hypothesis was generated using Maximum likelihood (Fig. 1) in MEGA5 (Tamura et al. 2011) applying the Tamura-Nei model of base substitution, uniform mutation rates, complete deletion of gaps and tree inference by nearest-neighbour-interchange. Branch lengths in the ML tree are a direct measure of the number of base substitutions.

Table 1. Accession numbers of sequences used.

	*rbc*L	*mat*K
Castanea henryi	M94936 (*Castanea sativa*)	EF057123
Elaeocarpus decipiens	HQ427154	HQ415261
Quercus serrata	HQ427171	HQ427319
Schima superba	HQ427230	HQ427375

Fig. 1 Maximum Likelihood tree based on combined rbcL and matK sequences.



As indicated in Table 2 we could not detect a significant signal of phylogeny in the analysed traits of the present study. Although the K values for crown length and the biomass of branches were close to one, the comparison to the null model revealed no significant effect of phylogeny. Thus, we assumed that our data points were statistically independent and we did not consider phylogenetic structure in the further statistical analyses. However, we are aware that the power to detect phylogenetic signals was found to be low for trees including fewer than 20 taxa (Blomberg et al. 2003).

Table 2. Results of the test of phylogenetic signal in the observed traits.

Trait	K	Observed variance of PICs	Mean variance of PICs of null modell	p-value of PIC variance
Height of first branch	0.11	2299.40	2788.25	0.63
Crown length	1.13	4387.18	50984.34	0.11
Length of first branch	0.08	23106.70	16224.61	0.52
Length of longest branch	0.12	9314.27	12637.06	0.40
Number of branches	0.10	10359.05	9853.72	0.53
Branch turnover	0.23	5817.04	12610.89	0.24
Pruning	0.16	187.85	332.94	0.44
Total biomass	0.11	62621.75	68832.84	0.69
Biomass of stem	0.13	83436.53	97420.59	0.59
Biomass of branches	0.93	4705.89	45150.05	0.07
Biomass of leaves	0.24	58293.25	149750.79	0.36

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PAPER V

Impact of tree saplings on the kinetic energy of rainfall – The importance of stand density, species identity and tree architecture in subtropical forests in China

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Keywords: BEF-China, soil erosion experiment, throughfall kinetic energy, splash cups, soil erosion, splash erosion

Agricultural and Forest Meteorology 156 (2012) : 31-40.

Abstract

In order to estimate the influence of plant architectural traits on the erosivity of throughfall we studied throughfall kinetic energy (KE) under tree saplings in a plantation-like experiment in the humid subtropics. Our analyses of rainfall and throughfall KE are based on measurements using calibrated splash cups. Two experiments were carried out, one focusing on density effects and the other testing for species-specific effects and effects of species mixtures. The major architectural traits were measured to characterize sapling morphology. Mixed effects models were used for statistical analysis. In both models, rainfall KE was identified as the most important effect on throughfall KE. Overall, rainfall KE per area was reduced by 59% below the canopy of the studied saplings. We found a significant effect of sapling density on throughfall KE. This is primarily due to the relation between free throughfall and released throughfall. As free throughfall possesses a far higher KE than released throughfall originating from saplings, lower sapling density results in higher total throughfall KE. We also showed that the influence of density on throughfall KE decreases with increasing sapling height due to lateral canopy growth of the saplings.

Throughfall KE was significantly different among species. We attribute this to species-specific differences in crown architectural traits. These traits have opposite influence on throughfall KE and interact with each other. Depending on its magnitude, one crown trait can possibly superimpose contrary effects of others.

1. Introduction

Soil erosion is an important issue from both an ecological and a financial point of view. In subtropical China, where high rainfall intensity causes severe and continuous soil losses, soil degradation caused by erosion and means of controlling it have for a long time been viewed and discussed as a major environmental problem (Aldhous, 1993; Biggelaar et al., 2003; Cai et al., 2005; Huang, 1987; Kolb, 2003; Shi et al., 2004; Thorp, 1936; Wang et al., 2005). The environmental impacts of soil erosion are numerous. Along with enormous economic costs (Lal, 1998; Montgomery, 2007; Pimentel et al., 1995) due to reduced land productivity, off-site effects from runoff sediments and pollutants from eroded sites affect human safety, food security, and social and economic development (Darilek et al., 2009; Lin et al., 2002; Shi, 1998, 2000; Yu et al., 2006).

It is commonly accepted that vegetation is a key control mechanism for the type and intensity of erosion (Morgan, 2005; Thornes, 1990), and afforestation is widely used as a measure of soil protection against soil erosion (Song and Zhang, 2010; Zhang et al., 2000). The key mechanisms of plant cover in reducing or enhancing erosion have been known since 1948 to be the modification of drop-size distribution, retention of raindrop impact (splash), and changes in spatial distribution of rainfall at the ground surface (Chapman, 1948). Rainfall characteristics are modified when raindrops hit the plant canopy. Some will shatter, producing smaller drops, while others will coalesce on leaves before falling to the ground as large drops. The kinetic energy (KE) of throughfall in subtropical forests can be up to 2.7 times higher than under open field conditions (Brandt, 1988; Geißler et al., 2010b; Nanko et al., 2004; Nanko et al., 2008a; Vis, 1986). Splash detachment caused by raindrop impact is the initial process of soil erosion. The KE detaches soil particles that impact (Erpul et al., 2005) and initiate overland flow indirectly by decreasing the infiltration rate as soil pores at the soil surface become clogged (Le Bissonnais and Singer, 1992; Salles and Poesen, 2000; Singer and Shainberg, 2004).

Brandt (1989) has shown that large drops from leaves may be significant sources of splash detachment in forests, indicating that drop size may be more important than drop velocity (see also Massman, 1983; Salles and Poesen, 2000; Styczen and Høgh-Schmidt, 1988). Throughfall under vegetation can generally be separated into free throughfall and released throughfall, as throughfall has a bimodal drop size distribution (Hall, 2003; Nanko et al., 2006; Nanko et al., 2008a). Free throughfall passes the canopy without striking plant surfaces, while released throughfall has been intercepted and drops are released from leaves and branches (Nanko et al., 2006; Dunkerley, 2010). The properties of free throughfall can therefore be equated de facto with properties of open field rainfall (e.g. intensity, amount, kinetic energy). In turn, the properties of released throughfall strongly depend on vegetation features, stand characteristics (see below) and varying meteorological factors (Nanko et al., 2006).

It can be assumed that mechanisms that control soil erosion under forest canopies are dynamic in space and time, and soil loss may even increase with height growth of trees due to changes of the KE of rain. This has been demonstrated for acacia forest in Indonesia (Wiersum, 1985), beech forest in New Zealand (Mosley, 1982), tropical rain forest in Colombia (Vis, 1986) or a forest plantation in Japan (Nanko et al., 2006; Wakiyama et al., 2010).

One of the central issues regarding throughfall KE in forests is its relation to forest stand variables, to specific species and to canopy architecture. Forest stand variables such as tree density (Bochet et al., 2002; Pressland, 1976; Stogsdill et al., 1989) and tree morphological factors such as tree height (Geißler et al., 2010a; Wainwright et al., 1999; Wakiyama et al., 2010), height of the first branch (Nanko et al., 2008b), canopy thickness (Levia and Frost, 2006; Nanko et al., 2010), leaf area index (LAI; Gómez et al., 2001; Park and Cameron, 2008), branch and leaf traits (Herwitz, 1985, 1987; van Elewijk, 1989), and ultimately species identity (Hall and Calder, 1993; Nanko et al., 2006; Park and Cameron, 2008; Williamson, 1981; Xu et al., 2009) are all thought to influence throughfall KE in some way, although some studies neglect these dependencies (Brandt, 1989; Foot and Morgan, 2005; Vis, 1986). Yet, the contribution of the above mentioned factors to the generation of throughfall remains largely unclear. The role of young trees in reducing the risk of soil erosion is of major interest (e.g. Zheng et al., 2008). Questions include e.g. the influence of certain species on different aspects of soil amendment and -protection (Wishnie et al., 2007), and of sapling density (Hartanto et al., 2003) on soil erosion processes. Throughfall KE is one major component of this process as it influences splash erosion, the initial process of soil erosion (Morgan, 2005).

It is important to improve our knowledge of the impact and extent of these factors on throughfall KE, as this relationship is one of the major aspects of the atmosphere-plant-soil relationship in soil erosion science and ecology. Further, design and management of soil erosion control in forests depends largely on knowledge of the role of stand density, tree architecture and species identity.

Therefore, the aim of this study was to analyze the throughfall KE under tree saplings in relation to planting density and to tree species identity, using four tree species that are typical of subtropical forests in China. Two experiments were carried out in an experimentally established tree plantation, and throughfall KE was measured using calibrated T Splash cups (Scholten et al., 2011).

The objectives of this study are

(i) to quantify the amount of KE of rainfall absorbed by tree saplings,

(ii) to study the effect of different planting densities on throughfall KE,

(iii) to test for species identity effects on throughfall KE,

(iv) to test for species-specific differences in crown architecture and relate them to throughfall KE.

2. Material and Methods

2.1. Study area

The study was conducted in the eastern part of Jiangxi Province, P.R. China (N29° 06.293 E117° 55.286). The study area is characterized by a subtropical monsoon climate with a mean annual precipitation of 1963 mm and a mean temperature of 15.1 °C. The rainy season with high intensity monsoon rainfall events (> 100 mm h-1, project-owned climate station) is from May until mid-August. The soils of the region are mainly Cambisols and in the lower parts of the landscape Acrisols and Ferralsols. The natural vegetation is a subtropical broad leaved forest with a dominance of evergreen species (Bruelheide et al., 2011).

2.2 Experimental Design

The experiment was established in March 2009, on a former agricultural field with a total area of 5400 m^2. The field was divided into four blocks. Within each block, 1 m² plots were positioned randomly and planted with 16 tree saplings (4 x 4) each. The saplings were planted at two densities: the planting distance between saplings was 25 cm (low density) and 15 cm (high density). The low and high densities in this experiment correspond to 25,000 and 44,000 saplings per ha, respectively. In the nearby Gutianshan Nature Reserve, densities of 16,000 individuals per ha were found in an early successional secondary forest stand (< 20 years; Bruelheide et al. 2011). We chose four species that are very abundant in the study region and represent early-successional species of different functional groups: evergreen (*Schima superba* Gardn. et Champ. and *Elaeocarpus decipiens* Hemsley) vs. deciduous

(*Quercus serrata* var. *brevipetiolata* and *Castanea henryi* (Skan) Rehd. et Wils). The saplings were planted in either monoculture or a four-species mixture. In the four-species mixture, each species was represented by the same number of individuals in both the peripheral rows (i.e. 12 individuals) as well as in the center (i.e. four individuals). The assignment of species to the planting positions for the central and the peripheral individuals was random. All treatments were replicated four times, once in each of the four blocks. At the time of the measurements (spring and summer 2010) the tree saplings were 2 yrs old and had a maximum height of 1.2 m. The experiment was, thus, designed to simulate an early stage of succession in a humid subtropical forest ecosystem in China.

Generally, five splash cups were placed per plot in positions 1B, 2A, 2B, 2C and 3B (see Fig. 1). If any of the four tree saplings surrounding a splash cup was dead, splash cups were placed in the remaining positions (1A, 1C, 3A, 3B). In cases where the number of dead individuals meant that no more than 3 splash cups could be positioned per plot, the plot was abandoned. Splash cups were positioned at equal distances in the grid to ensure constant distances between splash cups and tree stems, since distances affect quantities and throughfall KE measured below the canopy (Nanko et al., 2008b; Nanko et al., 2011).

Experimental design (A): Tree density effects on throughfall KE

In the density experiment we focused on the two evergreen species *S. superba* and *E. decipiens*. We used plots with monocultures of both species planted at the two densities. Each treatment combination (species x density) was replicated four times (*S. superba* x low density only two times).

Experimental design (B): Tree species effects on throughfall KE

The species identity experiment was conducted to test for species-specific differences of tree saplings on throughfall generation. We used monocultures of the four species *S. superba*, *E. decipiens*, *Q. serrata* and *C. henryi.* We also tested the effect of the four-species mixture. Again, every treatment (four monocultures and the four-species mixture) was replicated four times (i.e. once per block – monocultures of *S. superba* and *C. henryi* only two times).

An overview of all replicates is given in Table 1.

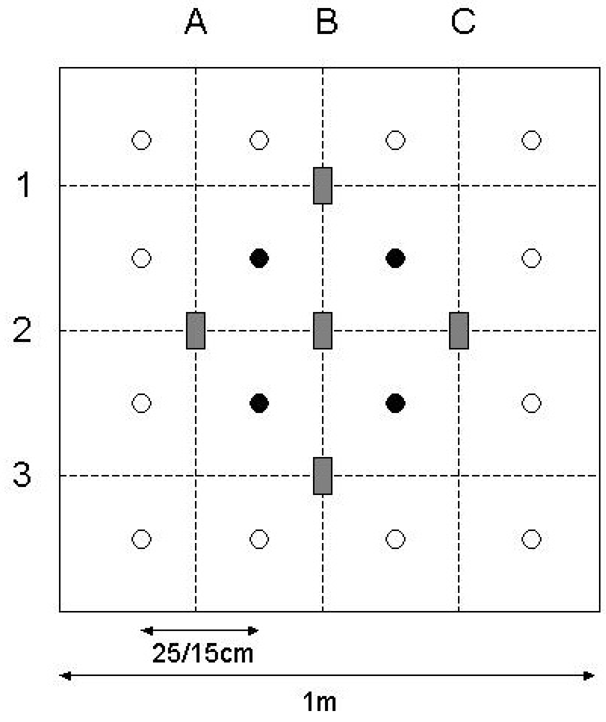

Fig. 1 Schematic design of an experimental plot (1 m^2 in size). Saplings are represented by circles, splash cups by grey boxes. The optimal positioning of splash cups is shown. Filled circles symbolize the four individuals in the centre of the plot for which additional measurements of crown architecturewere carried out.

The density experiment (henceforth experiment A) was conducted before leaves of the deciduous species were fully developed (22 March – 10 April 2010) and thus includes only the two evergreen species. Hypothesizing that released throughfall (which has a greater proportion compared to free throughfall in the dense plantings) is more related to specific species than free throughfall, we concentrated only on high density plots in the species identity experiment (henceforth experiment B). This was conducted after the leaves of the deciduous species had fully developed (15 May – 21 June 2010) and included both evergreen and deciduous species.

For comparison and reference, an open field measuring station was placed between block two and block three in the center of the experiment, i.e. less than 80 m away from the furthest throughfall KE measuring site. During every rainfall event three splash cups and one rainfall collecting bottle measured rainfall KE and rainfall amount. Values obtained from the splash cups were averaged thereafter. The standard deviation between measurements with splash cups in the open field is generally very low (Vis, 1986; Geißler et al., 2010b).

2.3 Measurement of throughfall KE

The methods applied for measuring the erosive power of throughfall under vegetation were originally designed for studying the properties of open field rainfall, and especially for measuring rainfall KE. These include the paper stain method (Wiesner, 1895), the flour pellet technique (Bentley, 1904) and disdrometers (Hall and Calder, 1993; Joss and Waldvogel, 1967; Nanko et al., 2004; Nanko et al., 2008a). With the exception of disdrometers, these techniques were not able to determine species-related changes in throughfall characteristics. Most of the methods lack temporal continuity as they only represent a very short time span of a rainfall event (Nanko et al., 2008a). The advantage of disdrometers is that they measure rainfall events without interruption. Usage is, however, costly and technically demanding so that only a limited number of replications can normally be obtained. Mosley (1982) in New Zealand and Vis (1986) in Colombia successfully used splash cups to estimate throughfall erosivity. The major advantage of splash cups is that they are easy to handle and that a large number of replications can be obtained at a reasonable cost. Moreover, they are able to measure the whole event rather than a short time span.

To measure throughfall KE we used “T Splash cups” which have a diameter of 4.6 cm and a surface of 16.62 cm². The loss of sand from the cups is converted into KE per area using a calibration function (Scholten et al., 2011).

Tab. 1: Experimental design. Overview of treatments and replicates in experiment A and B.

Experiment A

Density	**Species composition**	**No of replicated plots**	**No of measured rainfall events**	**Total no of replicates**
low	*E. decipiens*	4	5	20
low	*S. superba*	4	5	20
high	*E. decipiens*	4	5	20
high	*S. superba*	2	5	10

Experiment B

Density	**Species composition**	**No of replicated plots**	**No of measured rainfall events**	**Total no of replicates**
high	*C. henryi*	2	6	12
high	*E. decipiens*	4	6	24
high	mix	4	6	24
high	*Q. serrata*	4	6	24
high	*S. superba*	2	6	12

2.4 Measurements of co-variables

A set of co-variables characterizing the tree saplings' morphology was measured in March and June 2010. Total sapling height was measured as the distance from the ground to the apical meristem. Crown length was calculated as the difference of total height and the height of the first living first-order branch (i.e. branch arising from a trunk).

For experiment B, specific branch-related parameters were sampled to specify sapling crown architecture and to check for species-specific differences. For the four central individuals (see Fig. 1) the total number of branches (only first-order branches with a length > 1 cm were considered) and the length and angle of the first branch were determined. The first branch is very important for sapling architecture since it defines where and how the first prolonged lateral growth is possible. The angle of the first branch was estimated in three classes (class 1: 0-30° from horizontal, class 2: 30-60°, class 3: 60-90°).

2.5 Statistical analysis

All statistical analyses were performed using R 2.12. (R Development Core Team, 2010) using the packages "nlme" for the analyses of mixed effects models (Pinheiro et al., 2010) and "multcomp" for post-hoc Tukey tests (Hothorn et al., 2008). For the analysis of the splash cup measurements mean values of throughfall KE per plot and area were used.

We tested the effect of density and species identity on mean throughfall KE using mixed effects models with block as random effect. To avoid overparametrization we tested for collinearity of all predictor variables (correlations between variables was not allowed to exceed $R = 0.8$). The full models contained a number of main effects: besides the effect of density (only experiment A) both models contained mean rainfall KE as a characteristic of the rainfall event and a set of variables that described the saplings (species identity, mean height of saplings). We were also interested in the two-way and three-way interactions. Model simplification was done by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictor variables were left ($p < 0.05$). Model residuals did not show violation of modeling assumptions (normality and homogeneity of variances).

We constructed additional mixed effects models for different growth parameters with species as fixed, and block as random factor to analyze the morphological differences between species (total height, crown length, height of first branch, number of branches, length and angle of first branch). If species identity was significant, differences between species were further examined by a Tukey post-hoc test.

3. Results

3.1 Effectiveness of young trees in reducing KE of rainfall

Overall tree saplings reduced KE of rainfall per area by 59 %. The average ratio of rainfall KE to throughfall KE for five rainfall events was 0.43 (n = 70) for experiment (A). For six rainfall events in experiment (B) the average ratio of rainfall KE to throughfall KE was 0.40 (n = 96). For the high-density planting, the ratio was 0.33 (n=40), whereas the low-density planting showed a ratio of 0.51 (n=30) between rainfall KE and throughfall KE. In the experiment B, the ratios were 0.50 (species mixture) (n=24), 0.35 (*E. decipiens*) (n=24), 0.27 (*S. superba*) (n=12), 0.42 (*C. henryi*) (n=12) and 0.41 (*Q. serrata*) (n=24).

3.2 Effect of tree density on throughfall KE

In the experiment A rainfall KE together with the factor density and the interaction between both were the most important effects on throughfall KE ($p < 0.0001$, Tab. 2). The higher the rainfall KE, the higher the throughfall KE (effect size: 0.31 ± 0.02, obtained from R summary). Throughfall KE was significantly higher in the low-density than in the high-density plots. However, this was also affected by the magnitude of the rainfall event, since differences between the two density treatments became more pronounced with higher rainfall KE (Fig. 2). The effect of sapling height was significant ($p = 0.0266$), as was the interaction between planting density and mean sapling height ($p = 0.0006$). The influence of sapling height varied between the two density treatments: Height was negatively related to throughfall KE in the low density plots, but was either not significantly or only weakly related to throughfall KE in the high density plots. This differentiated reaction became more pronounced with higher rainfall KE (Fig. 3), as shwon by the significant threefold interaction ($p = 0.0055$). Species identity of the two evergreen species did not enter the final model, as it showed no significant effect on throughfall KE.

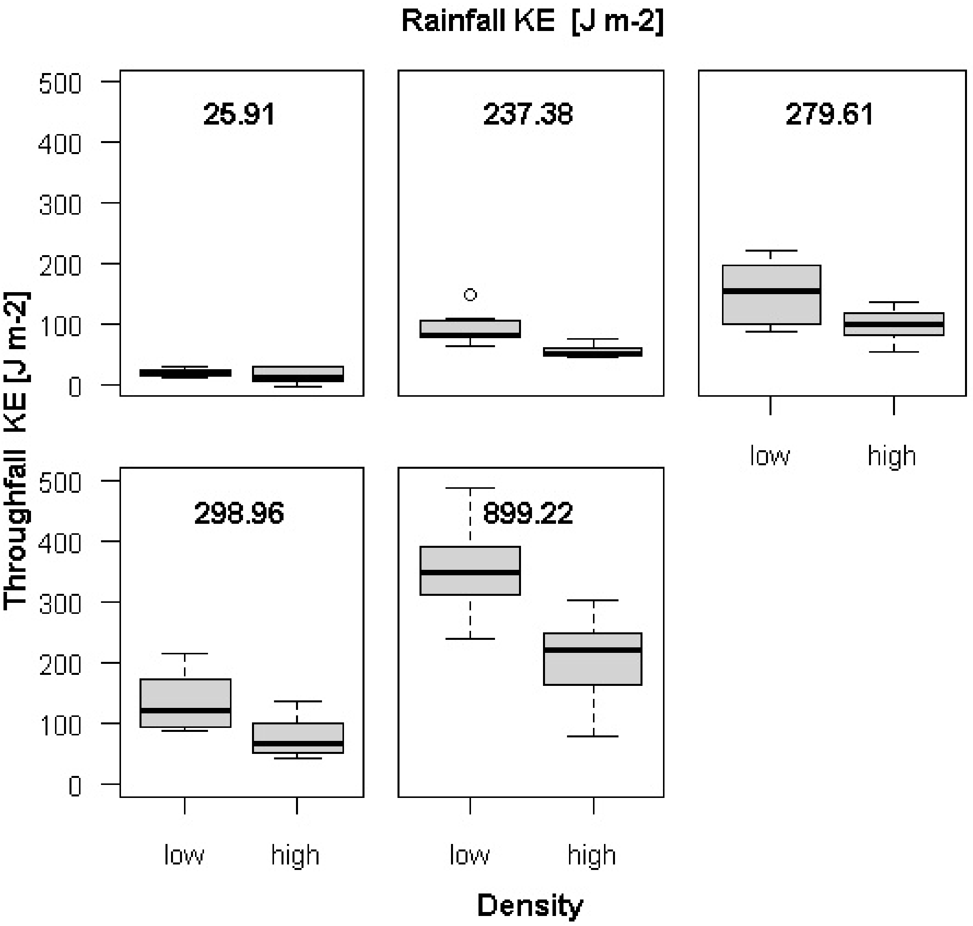

Fig. 2: Effect of tree density on throughfall KE in five different rainfall events. Rainfall events are classified by their rainfall KE. White open circles indicate outliers, black solid lines indicate the median of the values. The grey area is delimited by the lower and upper quartile.

Tab. 2 Effects influencing throughfall KE. Results of simplified mixed effects models, including block as random intercept for experiment A.

Fixed effects	**F-value**	**p-value**	
KE of rainfall event	499.35	<.0001	***
Density	50.28	<.0001	***
Mean sapling height	5.17	0.0266	*
Density* Mean sapling height	13.10	0.0006	***
KE of rainfall event* Density	33.24	<.0001	***
KE of rainfall event * Mean sapling height	2.15	0.1475	
KE of rainfall event * Density* Mean sapling height	8.32	0.0055	**

Significances are given as asterisks: $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***.

3.3 Effect of species identity on throughfall KE

In the species identity experiment B, rainfall KE also had a significant effect on throughfall KE (Tab. 3). Additionally, a significant increase in mean throughfall KE with sapling height was observed ($p = 0.0001$, effect size: 0.79 ± 0.44). Furthermore, we found a significant effect of species identity on throughfall KE ($p < 0.0001$). In general, throughfall KE was lowest below the evergreen species *S. superba*, and highest below the two deciduous species *C. henryi* and *Q. serrata* (Fig. 4). Both mean sapling height and species identity interacted with the rainfall KE. The effect of the four-species mixture on throughfall KE took an intermediate position between the overall effects of different functional groups. Similar to the results of the density experiment, the variability of throughfall KE seemed to increase with rainfall KE.

Tab. 3 Effects influencing throughfall KE. Results of simplified mixed effects models, including block as random intercept for experiment B.

Fixed effects	F-value	p-value	
KE of rainfall event	326.54	<.0001	***
Mean sapling height	14.59	0.0001	***
Species identity	9.84	<.0001	***
KE of rainfall event * Mean sapling height	6.20	0.0246	*
KE of rainfall event * Species composition of plot	4.16	0.0048	**

Significances are given as asterisks: p < 0.05 *; p < 0.01 **; p < 0.001 ***.

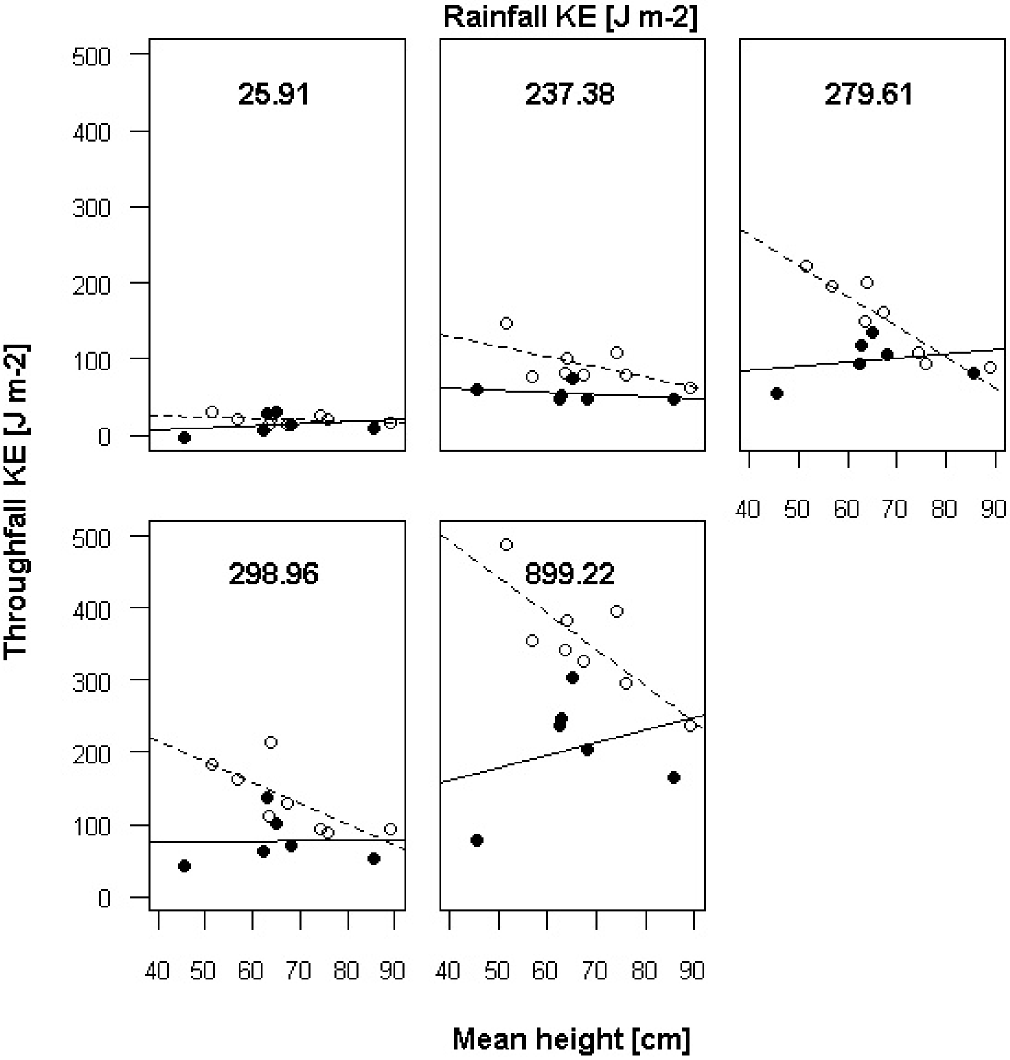

Fig. 3 Effect of sapling height on throughfall KE in five different rainfall events. Open circles represent the low density plots (dashed regression line), black dots the high density plots (solid regression line).

3.4 Architecture of species in the experiment

The total height of *Q. serrata* saplings (mean: 54.9 cm ± 13.5) was significantly lower than the total heights of the other species (Tab. 4). Height of the first branch, crown length and length of the first branch did not differ significantly between species. However, considerable differences were found between species in the number of branches and in the angle of the first branch. The mean number of branches ranged from 5 per sapling in *C. henryi* to 19 in *E. decipiens*. While *S. superba* had a mean angle of the first branch from the horizontal of 45°, a mean angle of 72° was observed in *C. henryi*. Fig. 5 depicts schematic drawings of the observed species based on the measured mean values. The morphological characteristics of the four-species mixture were generally characterized by mean values which lay in the middle of the single species values' range (Tab. 4). Pearson correlations between all architectural variables revealed high correlations between sapling height and the length of the longest branch (r = 0.67) and crown length (r = 0.78). Crown length and the length of the longest branch were also highly correlated (r = 0.85).

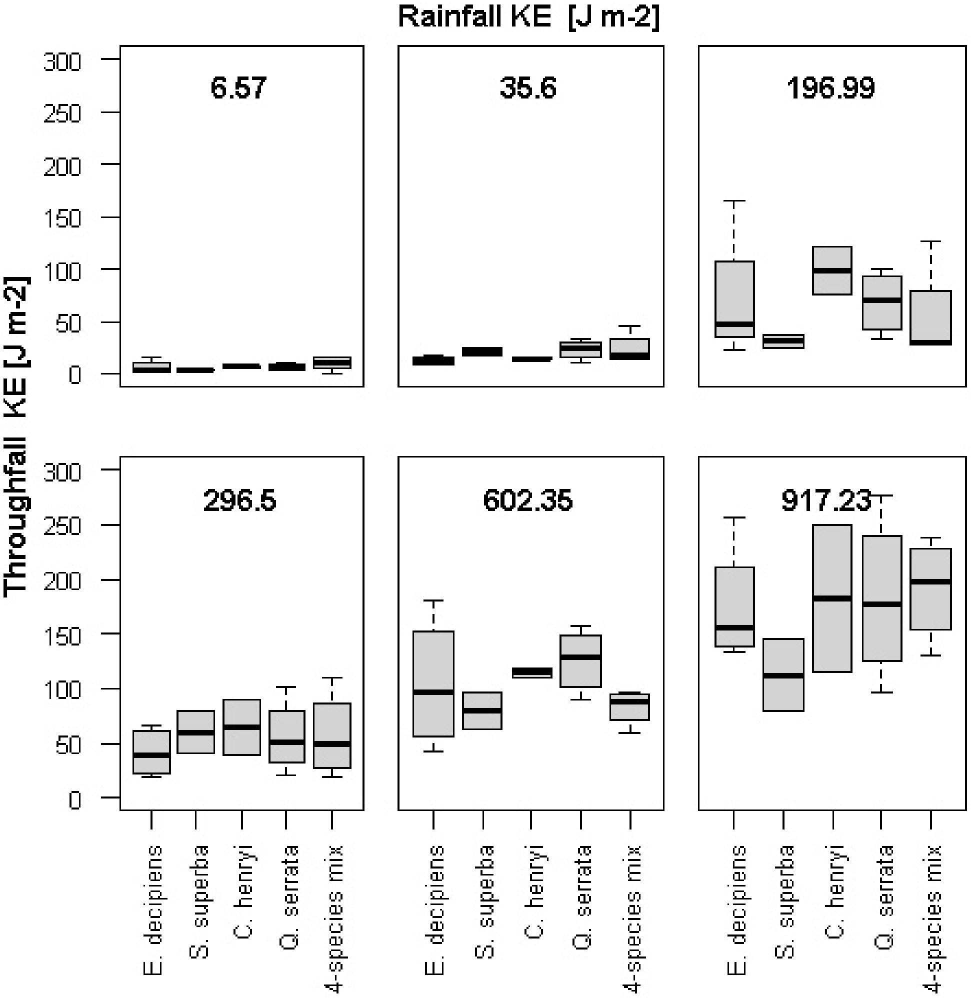

Fig. 4: Effect of species identity on throughfall KE for six different rainfall events.

4. Discussion

4.1 Tree saplings reduce rainfall erosivity

Our experiment demonstrated that tree saplings reduce rainfall KE effectively and substantially, irrespective of treatments and species. Throughfall KE is generally less than half of rainfall KE. There are two main reasons for this. On the one hand, the amount of water reaching the splash cups is reduced because of interception by, and subsequent evaporation from, the saplings (Levia and Frost, 2006); on the other hand, the KE is reduced a result of the low height of the saplings. Drops under tree saplings of up to 1.2 m in height are far from reaching terminal velocity, which is normally achieved at about 8 m above ground (Morgan, 2005). The height of the saplings is below an imaginary "threshold", where rainfall KE and throughfall KE would be balanced. This is consistent with the results of other studies which deal with throughfall KE (Bochet et al., 1998; McGregor and Mutchler, 1978; Noble and Morgan, 1983; Quinn and Laflen, 1981; Styczen and Høgh-Schmidt, 1988; Wainwright et al., 1999). As we measured neither throughfall amount nor evaporation from the saplings, the relative contribution of sapling height and reduced throughfall amount to reducing throughfall KE remains unclear.

Nevertheless, a substantial difference was observed during field work in the amount of sand which was splashed out of the different splash cups. Some splash cups were clearly influenced by open field rainfall which has more than twice the erosive power of average throughfall. The ratios between open field rainfall KE and throughfall KE for experiment A (dense=0.33; wide=0.51) show clearly that the differences between these KE values must have been caused by the two main components of throughfall, i.e. free throughfall and released throughfall (Dunkerley, 2010; Nanko et al., 2006). Therefore, we infer that the differences measured in both experiments are mostly caused by shifts in the proportion of the two main components of throughfall and that these, thus have a strong influence on the average values.

4.2 Planting distance between tree saplings affects throughfall KE

In experiment A we showed the effect of sapling density. The higher sapling density significantly reduced throughfall KE. Similar to other effects, the influence of planting density on throughfall KE becomes increasingly pronounced for higher rainfall KE. The threefold interaction between rainfall KE, height and density might be due to a shift in the proportion of throughfall components.

For the high density planting, the main component of total throughfall was released throughfall, and free throughfall played a minor role (Stogsdill et al., 1989; Levia and Frost, 2006). Consequently, the increase in sapling height resulted only in a slight increase of throughfall KE, which was mainly caused by drip from leaves and branches. For the low density planting, the effect of height was more obvious. It was, however, contrary to the pattern which is often found, i.e. that throughfall KE increases with increasing tree height. This might be caused by a shift in the relative proportion of the throughfall components as a result of sapling growth. In the low density plots with smaller saplings the canopy was not yet closed. In canopy gaps a higher throughfall KE and amount (free throughfall) can be observed (Bochet et al., 2002; Pressland, 1976; Stogsdill et al., 1989). During growth, these gaps between individual saplings are closed due to lateral crown expansion, and less highly erosive free throughfall reaches the ground, thereby reducing the density effect. The heterogeneity of the canopy also affects the variability of throughfall KE. Generally, the variability of throughfall KE is higher for low density planting than for high density planting (cf. Raat et al., 2002).

Species identity was identified as an effect of minor impact and did not enter the model. This might be due to the magnitude of other effects such as rainfall KE, density and sapling height masking species-specific effects.

Our results show that any effects revealed in this experiment may be caused by shifts in the proportion of throughfall components. This shift causes differences in throughfall amount and therefore also throughfall KE.

4.3 Species identity and crown architecture influences throughfall KE

In the species identity experiment we found species-specific effects on throughfall KE. From generalisable patterns of relative species effects on throughfall KE across rainfall events, we can deduce influential species-specific crown traits. These traits have opposite influence on throughfall KE and interact with each other. Depending on its magnitude, one crown trait can possibly superimpose contrary effects of others.

S. superba generally had the lowest throughfall KE among the observed species and events. However, the morphological characteristics of this species in terms of total height, height of the first branch and number of branches suggest that *S. superba* may have a higher throughfall KE than the other three species (Herwitz, 1985; Nanko et al., 2008b). On the other hand, the first branch of *S. superba* had the narrowest angle from the horizontal and was the second longest. These two branch parameters promote lateral extension and result in an increased crown width. Wider crowns of *S. superba* in turn yield a higher canopy cover than compared to the other species. This may lead to less free throughfall reaching the soil surface or, in other words, substantially reduced total throughfall KE.

E. decipiens, the second evergreen species, also showed a relatively low throughfall KE. Individuals of *E. decipiens* were taller than those of other species and had relatively short first branches. These first branches had a higher inclination than e.g. *S. superba,* which should result in a reduced canopy closure. In strong contrast, *E. decipiens* had the lowest height of the first branch (and, thus, the longest crown), and the highest number of branches. A long and dense crown results in a high canopy storage capacity (Herwitz, 1987). Moreover, due to the dense crown, released throughfall was very likely to be re-intercepted by lower parts of the crown (Nanko et al., 2008b). Higher canopy storage and a high probability of re-interception of released throughfall under *E. decipiens* thus lead to reduced throughfall KE. The effects which tend to reduce throughfall KE were weaker than effects which tend to increase throughfall KE in this case.

For most rainfall events the deciduous tree species ***Q. serrata*** had higher throughfall KE compared to the above mentioned evergreen species. Architectural traits that support a reduction of rainfall KE were the low total height, a medium to high number of branches and a relatively low inclination of the first branch. However, the length of the crown and the first branch tended to be low in *Q. serrata.* Both parameters resulted in a fairly open canopy where a high amount of erosive free throughfall was able to reach the ground.

The second deciduous species, ***C. henryi***, also generated a relatively high KE below its crown. This species had the lightest crown, indicated by the very low number of branches and the wide angle of the first branch from the horizontal, both of which lead to a low canopy storage capacity(Herwitz, 1985). In addition, steeply inclined branches lead to a higher amount of stemflow (van Elewijck, 1989), strongly reducing the amount of water able to fall from leaves and branches as drops.

A number of studies have shown that the crown architecture of individual trees is influenced by the species identity of their neighbours (Lintunen and Kaitaniemi, 2010; Massey et al., 2006; Thorpe et al., 2010), and, therefore, tree species may develop architectural traits in mixed-species stands that are rarely or never observed in monocultures (Pretzsch and Schütze, 2009). In our study, however, the mean values of crown parameters of the mixed-species plots were within the range of the values observed in the monocultures. This was true for the throughfall KE for most of the rainfall events. We were, thus, unable to identify any specific mixture effects on throughfall KE.

5. Summary and Conclusions

In summary, we can say that planting density and specific species have a substantial effect on throughfall KE. The former may be deduced from the proportion of throughfall components to each other and the latter by taking the detailed sapling architecture into account.

We found that only two years after planting, the saplings developed a substantial canopy which considerably reduced throughfall KE. The rapid establishment of a canopy is assumed to be a crucial factor in reducing soil erosion potential below tree saplings.

We also showed that the effect of density on throughfall KE decreases as sapling height (and therefore crown width) increases. This proves the importance of canopy closure on the extent of throughfall KE below tree saplings.

The effect of specific species on throughfall KE showed that detailed measurement of architectural traits leads to a better understanding of processes of throughfall generation. In our opinion, all canopy characteristics of a given tree species should be taken into account when focussing on the soil erosion potential below individuals of these species.

Besides canopy closure, which prevents highly erosive raindrops from hitting the soil, canopy storage also appears to be important as it controls the amount of water (and therefore has a direct influence on KE) able to fall from the leaves as drips.

Finally, the T splash cups proved to be a valuable and reliable method for the detection of differences in throughfall KE, even at this spatial scale.

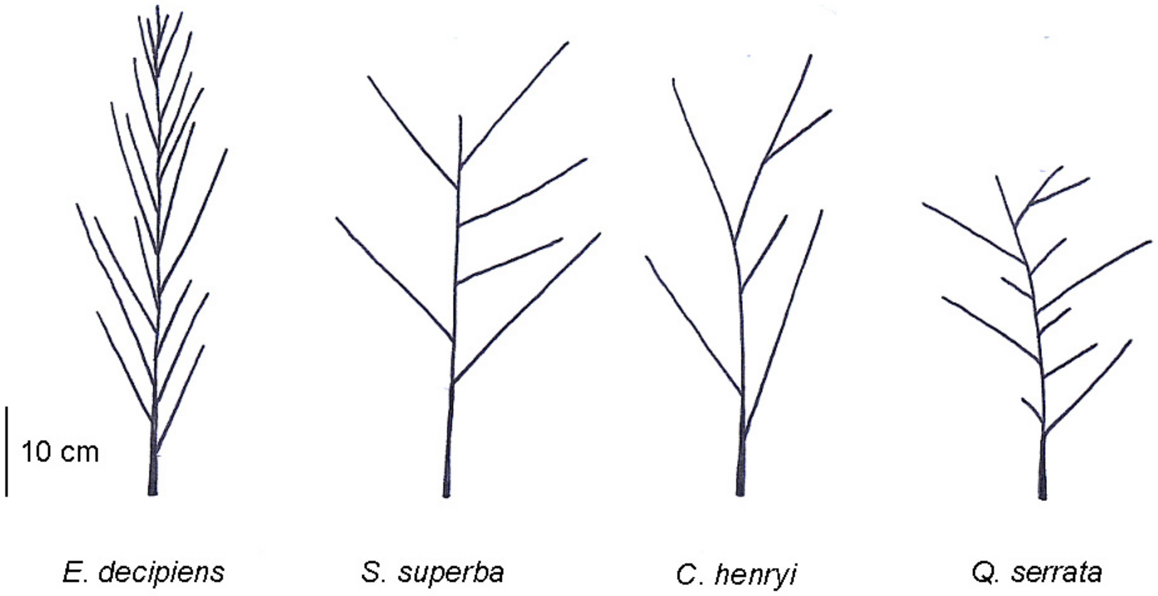

Fig. 5 Schematic drawing of species-specific sapling architecture. Mean values of total height, height of the first branch, number of branches, length and angle of the first branch are derived from the data (Tab. 2). Branching pattern was adapted according to field observations.

Acknowledgements

We are indebted to Susanne Nietzel, Jessica Henkner and Matthias Breitinger for their field assistance. We are grateful to Henrik von Wehrden, who provided helpful additional statistical advice. We also thank the Deutsche Forschungsgemeinschaft (German Research Foundation, DFG FOR 891/1) and the National Science Foundation of China (NSFC) for funding the BEF-China project. We also thank two anonymous reviewers for their valuable comments on the manuscript and their constructive suggestions. Moreover, we thank Linda Froome for improving the language quality of the article.

Tab. 4: Morphological characteristics of saplings of four tree species planted in monocultures and in a four-species mixture. Results for mixed effects models, including block as random intercept. Significant differences in post-hoc Tukey test are indicated by different letters. Branch angles are given in degree to the horizontal, calculated from mean values of three classes (see text).

	Fixed effect: Species			**Mean values**				
response variable	**F-value**	**p-value**		***E. decipiens***	***S. superba***	***C. henryi***	***Q. serrata***	**4-species mix**
Height [cm]	13.18	0.0015	**	**82.5 ± 17.5** ^{b}	**78.6 ± 9.4** ^{b}	**74.3 ± 18** ^{b}	**54.9 ± 13.5** ^{a}	**77.7 ± 11.2** ^{b}
Crown length [cm]	3.70	0.0546		76.0 ± 16.8	61.0 ± 5.0	65.1 ± 12.6	45.5 ± 6.1	58.5 ± 19.4
Height of 1st branch [cm]	1.70	0.2421		6.5 ± 2.5	17.6 ± 4.4	9.1 ± 5.5	9.5 ± 9.3	19.3 ± 13.7
Number of branches	8.34	0.0059	**	**18.8 ± 4.9** ^{a}	**6.6 ± 3.7** ^{bc}	**5.3 ± 1.4** ^{c}	**11.8 ± 1.0** ^{bc}	**13.8 ± 2.7** ^{a}
Length of 1st branch [cm]	1.14	0.4041		22.0 ± 19.9	36.4 ± 6.5	42.4 ± 11.2	23.7 ± 6.8	25.7 ± 11.8
Length of longest branch [cm]	1.50	0.2904		48.9 ± 6.7	37.9 ± 4.4	55.0 ± 26.9	35.7 ± 6.1	47.6 ± 11.8
Angle of 1st branch [°]	5.65	0.0185	*	**56 ± 10** ^{ac}	**45 ± 0** ^{bc}	**71 ± 5** ^{a}	**47 ± 15** ^{ab}	**53 ± 11** ^{abc}

Significances are given as asterisks: $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***.

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