

**Mechanisms of Soil Erosion Under Forest Vegetation –
Throughfall Kinetic Energy as a Function of Forest
Succession and Biodiversity in Subtropical Forests in China**

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1 Introduction and objectives

1.1 Biodiversity and Ecosystem Functioning

Biodiversity

Biodiversity can be defined as “the number abundance and composition of genotypes, populations, species, functional types and landscape units in a given system” (Scherer-Lorenzen, 2005). The term was first introduced to the scientific community by the end of the 1970s in the proceedings of a conference on conservation biology (Soulé and Wilcox, 1980).

About 10 years later, at the beginning of the 1990s, the term “Biodiversity and Ecosystem Functioning” (BEF) emerged due to growing concern about a global loss of biodiversity (Loreau et al., 2001; Scherer-Lorenzen, 2005) and enormous costs associated due to the loss of habitats and ecosystems (Pimentel et al., 1997). This circumstance raised the question of the relation of ecosystem properties to biodiversity.

As a consequence, the United Nations have proclaimed the decade 2011-2020 as the “United Nations decade on biodiversity” and expressed five strategic goals (Convention on Biological Diversity, 2011):

- (i) Strategic Goal A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society
- (ii) Strategic Goal B: Reduce the direct pressures on biodiversity and promote sustainable use
- (iii) Strategic Goal C: Improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity
- (iv) Strategic Goal D: Enhance the benefits to all from biodiversity and ecosystem services
- (v) Strategic Goal E: Enhance implementation through participatory planning, knowledge management and capacity building

Looking at forests we observe a continuous loss of biodiversity. During the last 8,000 years nearly half of the earth’s original forests have diminished and every year about 13 million hectares are lost. In tropical, temperate and boreal forests the majority of the world’s

terrestrial species can be found and they form the source of over three quarters of the world's accessible fresh water. Moreover, forests play a major role in the world's carbon cycling (Convention on Biological Diversity, 2011).

Ecosystem services and functioning

One basic question in biodiversity research deals with the relation of biodiversity and various ecosystem services (Scherer-Lorenzen, 2005). According to the "Convention of Biological Diversity" (Convention on Biological Diversity, 2011), ecosystem services are separated into four groups:

- 1) Provisioning services: e.g. the supply of goods (timber from forest, fish from the oceans, etc.)
- 2) Regulating services: e.g. the regulation of climate, filtering of air and water, storing of carbon, prevention of soil erosion
- 3) Cultural services: e.g. spiritual/ religious value, aesthetic value
- 4) Supporting services: e.g. formation of soils, processes of plant growth

Since soils control many of these services, at least to a certain extent, they play a major role in this ecosystem service approach. A prominent example is the function of a soil to provide plants with water and nutrients. In return, plants protect the soil against erosion. Any disturbance of this fragile interplay between soils and the surrounding ecosystem can lead to a downward-spiral, a fact that is known not only from dry ecosystems, where widespread disturbance and devastation resulted in the problem of desertification (Schlesinger et al., 1990).

The understanding of forest ecosystem functioning is therefore of primary interest in biodiversity and ecosystem research as forests provide the basis of most ecosystem services mentioned above (Nasi et al., 2002; Chazdon, 2008).

1.2 Soil erosion and forest vegetation

Soil erosion and its prevention is an important issue from both an ecological and economical point of view. Especially in subtropical China, where high rainfall intensities cause severe and continuous soil losses, soil degradation by erosion and its control is one of the major environmental problems and a central topic for the last decades (Thorp, 1936; Huang, 1987; Aldhous, 1993; Biggelaar et al., 2003; Kolb, 2003; Shi et al., 2004; Cai et al., 2005; Wang et al., 2005). The environmental impacts of soil erosion are numerous. Erosion causes enormous economic costs (Pimentel et al., 1995; Lal, 1998; Montgomery, 2007) due to reduced land productivity, off-site effects caused by deposits and pollutants from eroded sites affect human safety, food security and socio-economic development (Shi et al., 1998, 2000; Lin, 2002; Yu et al., 2006; Darilek et al., 2009). There is a broad consensus that vegetation is a key control for erosion processes (Thornes, 1990; Morgan, 2005). Therefore, afforestation is widely used as a measure of soil protection against soil erosion (Vertessy, 2001; Zhang et al., 2002; Huang et al., 2003). In China, total forest cover increased in the last 60 years mainly because of the proportion of afforestations having constant double-digit growth rates. Nevertheless, the proportion of natural forests is continuously declining (Song and Zhang, 2010).

Main effects of a plant cover regarding reduction or enhancement of erosion are modification of drop-size distribution, retention of direct raindrop impact (splash erosion), and changes in spatial distribution of throughfall amount at the ground surface (Chapman, 1948; Levia and Frost, 2006). Rainfall characteristics are altered when raindrops hit the plant canopy. Some will shatter producing smaller drops, while some will coagulate on leaves before falling to the ground as large drops. The kinetic energy (KE) of throughfall in subtropical forests is up to 2.7 times higher than under open field conditions (Vis, 1986; Brandt, 1988; Nanko et al., 2008a; Geißler et al., 2010a). For example, Brandt (1989) has shown that large drops from leaves may be significant sources of splash detachment in forests, indicating that drop size may overplay drop velocity (Massman, 1983; Styczen and Høgh-Schmidt, 1988; Salles and Poesen, 2000).

Splash detachment caused by raindrop impact is the initial process of soil erosion (Morgan, 2005). The KE of falling drops detaches soil particles that impact (Erpul et al., 2005) and initiates overland flow indirectly by decreasing the infiltration rate due to clogging of soil pores at the soil surface (Le Bissonnais and Singer, 1992; Salles and Poesen, 2000;

Singer and Shainberg, 2005). Therefore, a continuous and intact ground cover is considered as a central measure to prevent soil erosion in forests (e.g. Zhou et al., 2002; Ghahramani et al., 2011).

Based on the mechanisms mentioned above the process system of soil erosion under forest can be divided into two basic parts:

- (i) the alteration of rainfall into throughfall and
- (ii) the drop impact on the soil surface or on surfaces of shrubs and herbs vegetation or litter and potential overland flow generation (Fig. 1, dark blue arrows).

During the steps in this process system rainwater is lost by evapotranspiration, stemflow and infiltration (light blue arrows). This results in generally less than 80 % of the water arriving at the canopy falling down as throughfall (Levia and Frost, 2006) .

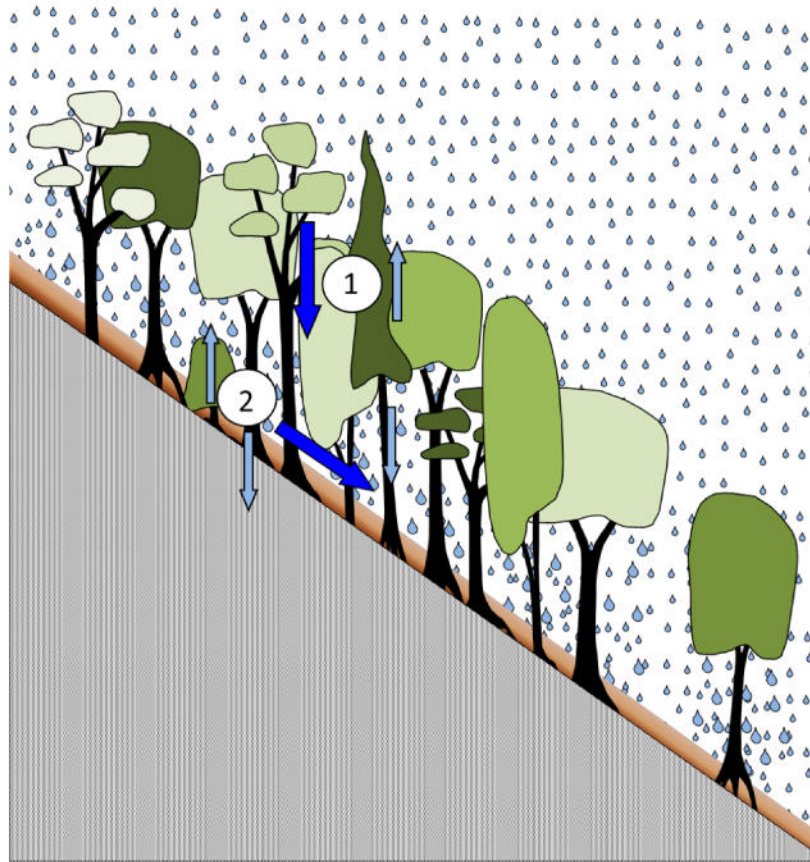


Fig. 1: Process system of soil erosion under forest separated in (1) drop interception and rainfall alteration by tree canopies and (2) drop interception, splash erosion and overland flow generation at the forest floor.

There is no doubt that mechanisms that control soil erosion under forest are very 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 documented for acacia forest in Indonesia (Wiersum et al., 1985), beech forest in New Zealand (Mosley, 1982) or tropical rain forest in Colombia (Vis, 1986).

One of the central issues regarding KE of throughfall in forests is its relation to forest stand variables, to specific species and to canopy architecture. Forest stand variables like tree density (Pressland, 1976; Stogsdill et al., 1989; Bochet et al., 2002) and tree morphological factors like tree height (Wainwright, 1999; Geißler et al., 2010a; Wakiyama et al., 2010), height of the first branch (Nanko et al., 2008b), canopy thickness (Levia and Frost, 2006; Nanko et al., 2006), 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 (Williamson, 1981; Hall and Calder, 1993; Nanko et al., 2006; Park and Cameron, 2008; Xu et al., 2009; Geißler et al., under review) are all supposed to influence throughfall KE in some way, although some studies neglect these dependencies (Vis, 1986; Brandt, 1989; Foot and Morgan, 2005). Yet, the contribution of the above mentioned factors to the generation of throughfall remains largely unclear.

1.3 Literature overview: Kinetic energy of throughfall in forests – Factors and controls

Measurement of kinetic energy of throughfall in forests

As already addressed above, in soil erosion research a widely used parameter to estimate the erosive power of rainfall is KE (Morgan, 2005). According to the formula of KE, parameters needed to calculate rainfall KE are the size and the fall velocity of each individual drop (Salles et al., 2002):

$$KE = \frac{1}{2} m v^2$$

where m = drop mass and v = drop velocity.

The drop size distribution (DSD) of rainfall is known since the pioneering works of Laws (1941), Marshall and Palmer (1948) and Gunn and Kinzer (1949). Their works are primarily related to rainfall under open field conditions. As devices measuring rainfall KE directly

remain scarce, rainfall KE is commonly derived from rainfall intensity. Overviews are given by Morgan (2005), Salles et al. (2002) and van Dijk et al. (2002).

Consequently, the methods applied for measuring erosive power of throughfall under vegetation were originally designed for studying properties of open field rainfall. These are

- (i) the paper stain method (Wiesner, 1895; Brandt, 1988),
- (ii) the flour pellet technique (Bentley, 1904; Brandt, 1989),
- (iii) laser disdrometers (Hall and Calder, 1993; Nanko et al., 2008a) and recently
- (iv) a piezo-electric sensor (Wakiyama et al., 2010).

According to the measuring principle of these methods they can be sorted as follows:

- (i) measure DSD and assuming terminal velocity of falling drops (methods a and b),
- (ii) measure DSD and drop velocity and calculate KE according to the formula given above (method c),
- (iii) measure KE directly (method d).

The advantage of disdrometers is to measure rainfall events without interrupts. However, the number of replications is limited because of high technical and financial demands. The other methods lack basically temporal continuity (Nanko et al., 2008a) or are based on outdated assumptions. Taking into account these limitations, Mosley (1982) in New Zealand and Vis (1986) in Colombia used splash cups (Ellison, 1947) for estimating throughfall erosivity successfully. The major advantage of splash cups is their easy handling and the high number of replications that can be obtained at reasonable costs. As splash cups measure neither the drop size distribution nor the KE directly they have to be calibrated (Bisal, 1950; Cornelis et al., 2004; Scholten et al., 2011).

Components of throughfall

Forest canopies alter rainfall properties by redistributing rainfall into throughfall, stemflow and evapotranspiration (Levia and Frost, 2006). About 2/3 of the rainfall reaches the ground as throughfall (Vis, 1986; Brandt, 1988; Nanko et al., 2004; Wei et al., 2005; Reid and

Lewis, 2009; Ziegler et al., 2009). Its components are free throughfall, drip from leaves and branches (also called released throughfall, cf. Dunkerley, 2000) and the so-called splash from leaves which is caused by impacting drops spattering on leaves or branches. Each of these three components is supposed to have a unique drop size distribution (Nanko et al., 2006) (Fig. 2).

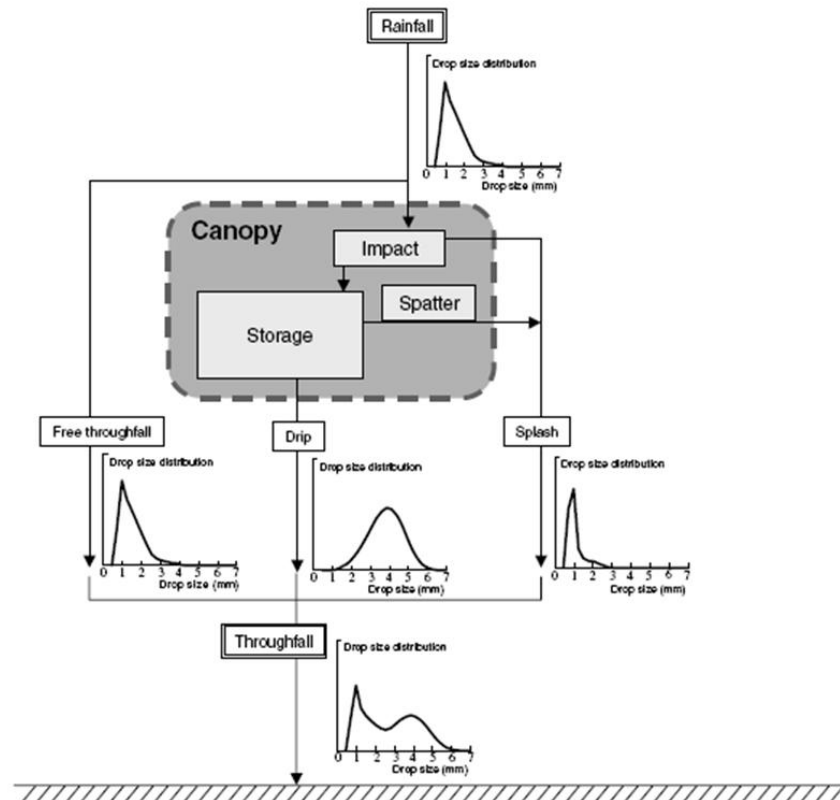


Fig. 2: Partitioning of rainfall into the components of throughfall with characteristic drop size distributions (modified after Nanko et al., 2006).

Free throughfall passes through the canopy without striking the plants surfaces. Released throughfall is rainfall which is intercepted by plant components and released when the storage capacity of these components is filled (Dunkerley, 2000). The erosivity of throughfall in total depends mainly on the relation between the components of throughfall. Like KE of rainfall KE of throughfall is commonly described in Joule per unit surface (J m^{-2}) or additionally with unit rainfall ($\text{J m}^{-2} \text{mm}^{-1}$).

Kinetic energy of throughfall in forests for different ecological zones

In the past, KE of throughfall in forests has been studied in several ecological zones around the world with an emphasis on tropical and subtropical regions. The first attempt was made by Chapman (1948). He came to the result of throughfall under a red pine plantation in North America being of higher erosivity than adjacent open field rainfall. Concluding, Chapman (1948) stated that the modification of the size of the drops by its pass through the canopy is responsible for this gain in KE. Moreover, he stated rainfall intensity having no influence on throughfall KE as plant canopies alter the drop sizes independently from rainfall characteristics.

In another study in Japan, Tsukamoto (1966) could confirm the results of Chapman and concluded throughfall having a typical drop size distribution. In a beech forest in New Zealand, Mosley (1982) was the first to use calibrated splash cups in forests for estimating throughfall erosivity. He could show the KE in the forest ($28.6 \text{ J m}^{-2} \text{ mm}^{-1}$) (Tab. 1) being 1.5 times higher than under open field conditions ($18.8 \text{ J m}^{-2} \text{ mm}^{-1}$) and mentioned a high variability of throughfall KE in the forest. Similar to Chapman (1948), Mosley states throughfall KE being independent of rainfall intensity as the canopy is responsible for the drop size distribution of throughfall.

Table 1: Kinetic energy (KE) of throughfall after different authors.

Source	KE ($\text{J m}^{-2} \text{ mm}^{-1}$)	Ratio rainfall / throughfall	Forest ecosystem
Mosley (1982)	28.6	1.5	temperate beech forest (New Zealand)
Imeson and Vis (1984)	30.8	1.34	tropical rainforest (Colombia)
Wiersum (1985)	-	1.5	forest plantation (Indonesia)
Vis (1986)	23.0 to 37.1	1.22 to 1.97	tropical rainforest (Colombia)
Brandt (1988)	16.9 to 40.2	1.24 to 2.64	tropical rainforest (Brazil)
Nanko et al. (2004)	24.6	2.23	subtropical forest plantation (Japan)
Nanko et al. (2008)	15.9 to 20.7	-	subtropical forest plantation (Japan)
Wakiyama et al. (2010)	16.9 to 21.0	-	subtropical forest plantation (Japan)

Wiersum (1985) could show an increase of the erosive power of throughfall by 57 % compared to open field rainfall in a forest plantation in Indonesia. According to his results a two-fold increase in drop sizes was responsible for this circumstance. Concluding, Wiersum (1985) states a direct soil cover being more important for erosion control than higher

vegetation and “a proper functioning forest ecosystem is more important for erosion control than just trees”.

In a Colombian forest ecosystem, Vis (1986) using splash cups and filter paper also confirmed a higher erosive power for throughfall compared to open field rainfall. Moreover, he could demonstrate that throughfall has a bimodal drop size distribution in contrast to open rainfall which shows a unimodal distribution. The values he obtained show increases in KE of throughfall between 22 % and 72 % compared to open rainfall (23.7 to 37.1 J m⁻² mm⁻¹).

Brandt (1988), applying the paper staining method, measured throughfall KE in a tropical rainforest in Brazil. By comparing forests with multiple vegetation layers Brandt (1988) showed that the presence of various vegetation layers strongly affects throughfall KE. Under a single layer canopy, KE of throughfall increased up to 1.84 times that of open field rainfall, while the change in KE under the multiple-layered canopy proved to be 0.4 times of that of rainfall. Brandt (1988) concludes that a lowering of KE of throughfall below the KE of rainfall is only achieved through the amount of rainfall intercepted.

In the 1990ies, highly sophisticated techniques became applied when measuring throughfall KE (Hall and Calder, 1993). In a Japanese cypress plantation in Japan, Nanko et al. (2004, 2008b) used laser disdrometers for measuring throughfall KE. By using this automatic technique Nanko et al. (2004) could show a six-fold decrease in drop counts in the forest compared to the open field. Nevertheless, throughfall had a 2.5 times higher KE (24.57 J m⁻² mm⁻¹) than adjacent open field rainfall (11.03 J m⁻² mm⁻¹). According to Nanko et al. (2004, 2008) a high number of large drops under forest vegetation is responsible for this circumstance.

Although several attempts have been made for estimating throughfall KE the studies are hard to compare and consistent datasets remain rather small. The biggest disadvantage of the above mentioned studies is the small number of replications on the (forest) plot and the event scale. Moreover, differently calibrated devices have been used and different assumptions have been made (see section 1.3). As rainfall parameters have proved to cause significant differences in throughfall KE (Nanko et al., 2006), a certain number of events should be sampled to account for this variability.

Biotic factors influencing throughfall generation

As mentioned above, height of the vegetation is one of the most important factors controlling throughfall KE (e.g. Chapman, 1948; Mosley, 1982; Vis, 1986; Styczen and Høgh-Schmidt, 1988; Brandt, 1988; Morgan, 2005). Height affects the velocity of falling drops and thus influences KE directly. Most recently the height effect could be shown by Wakiyama et al. (2010). They compared two forest stands of different age and showed that the 36-year old stand (average height = 17.4 m) produces a 1.24 times higher throughfall KE than the 21 year old stand (average height = 9.2 m). In another recent study, Geißler et al. (2010a) could show an asymptotic increase in the erosive power of throughfall with increasing successional stage of a forest stand.

Contrastingly, low canopies are supposed to decrease rainfall KE substantially. Under low crops, McGregor and Mutchler (1978), Quin and Laflen (1981) and Noble and Morgan (1983) could show a reduction of rainfall KE down to 10 % of open field KE. Other researchers focusing on shrubs and dwarf shrubs also report a substantial decrease of throughfall KE under low canopies (Bochet et al., 1998; Wainwright et al., 1999). During the first stages of forest succession the gain of height leads to a continuous increase in throughfall KE (e.g. Geißler et al., 2010b). This effect is supposed to diminish with increasing age of the forest stand as terminal velocity of drops is assumed to be reached at about 8 m depending on drop size (e.g. Stuart and Edwards, 2006).

To our knowledge only one study examined the effect of stand density on throughfall KE so far. In a small experimental plantation Geißler et al. (manuscript 3) could show the effect of higher throughfall KE with increasing interplant distances. This is supposed to be caused by a shift in the proportion of throughfall components.

Moreover, some studies mainly focusing on throughfall amount and water balance dealt with this issue. Basically, as mentioned above, a variation in plant spacing should affect the relation of the different elements of throughfall (free throughfall, release throughfall or drip) to each other. Stogsdill et al. (1989) examined the relationship between throughfall amount and stand density in a *Pinus taeda* plantation. Their results indicate an increase of throughfall amount after thinning operations. Moreover, they mention differences regarding forest age when focusing on throughfall for different densities. They state for young pines thinning (or wider planting distances) would create large inter-individual gaps. In these gaps, free throughfall occurs and a substantial increase (or change) in total throughfall would be

observed (Pressland, 1976; Stogsdill et al., 1989). Similar to this, Bochet et al. (2002) could show a decrease in the reduction of throughfall KE under dwarf shrubs with increasing distance to the plant.

The term canopy architecture summarizes mainly values for e.g. branch- and leaf inclination, height of the first branch and canopy thickness. Herwitz (1987) showed the importance of branch angles on throughfall generation and the formation of drip points. In general, higher inclined branches lead to a higher amount of water transferred on branches. Subsequently, this water is divided into stemflow and drip from branches. Van Elewijk (1989) could also prove an effect of branch slope on the amount of water transferred within a canopy. The general tendency is increased water flow on branches (and the formation of drip points) for higher inclinations with a maximum around 40 to 60°. The number of branches is supposed to be positively correlated with canopy storage capacity (Herwitz, 1985).

Contrary to these findings Foot and Morgan (2005) could not prove any effect of canopy architecture variables like leaf inclination or branch inclination on the amount and KE of throughfall. During their laboratory experiment, artificial plants were modified according to expected impacts on throughfall erosivity and were then exposed to a simulated rainstorm. As there were even no significant differences even between plots with plants and bare control plots, one is likely to assume that this experimental setup is insufficient to measure differences or dependencies of plant parameters in throughfall generation.

In another laboratory study, Nanko et al. (2008a) could demonstrate the effect of canopy thickness on throughfall KE. Thinner canopies tend to produce throughfall drops of higher KE than thicker canopies. Additionally, an enhanced amount of throughfall is documented. This is mainly due to lower canopy storage and a less likely re-interception of drops by lower parts of the canopy. The variable of interest in this case would be, besides canopy thickness itself, the height of the first branch (Nanko et al., 2008a). Canopy storage is a crucial point as the amount of water passing the canopy is one of the most important factors when considering throughfall KE (Levia and Frost, 2006). Herwitz (1985) for example studied canopy storage in a species-rich tropical rainforest and could show that canopy storage varies among species. This is consistent with the results of other researchers focusing on the water balance in forests (e.g. Schroth et al., 1999; Levia and Frost, 2006; Park and Cameron, 2008) or on water balance for small trees (Aston, 1979).

Leaf area index (LAI) is of major interest when considering throughfall amount and properties. It is basically summarizing effects of canopy thickness, leaf and branch count to a dimensionless number. In general, throughfall decreases with increasing LAI (Chen et al., 1997; Crockford and Richardson, 2000; Gómez et al., 2001; Levia and Frost, 2006). This could be followed by Park and Cameron (2008) only for lower rainfall intensities. For higher rainfall intensities, they state, LAI loses influence as the storage capacity is lowered and the effect of rainfall intensity is much bigger than that of LAI. Up to now no study focused especially on the relation of throughfall KE to LAI.

Another point of interest regarding throughfall properties is the shape, size and orientation of leaves. Leaf surfaces form the major storage device in a plant and they are supposed to have a substantial influence on throughfall properties, especially throughfall amount (Levia and Frost, 2006; Park and Cameron, 2008) and drop size distribution (Hall and Calder, 1993). The most obvious differences related to throughfall properties can be observed between leaves of deciduous resp. evergreen and coniferous trees. Several drip mechanisms like “launch drip”, “tipping bucket drip”, “induced drip”, “reservoir drip” and “needle drip” are reported in the literature (Armstrong and Mitchell, 1988). As the storage capacity of needles is much less than for most of the leaves, the average drop size under coniferous trees is generally smaller (Hall and Calder, 1993; Nanko et al., 2006). As mentioned above, a higher inclination of leaves (relative to the branch) is supposed to have a negative effect on throughfall amount (and therefore throughfall KE) as it controls the possibility of water to be stored on the leaf surface (van Elewijck, 1989).

In the past few studies focused on the influence of specific species. Throughfall KE in forests was believed to be independent of species (Vis, 1986; Brandt, 1989). Using a laser disdrometer Hall and Calder (1993) and later Nanko et al. (2006) found typical drop size distributions for several tree species. They found large differences which can be attributed to the leaf morphology. As mentioned above, needle leaved species generate finer throughfall drops than broad leaved species. Moreover, the study of Hall and Calder (1993) indicates that throughfall drop generation by different species also depends upon the nature of a rainfall event. In other words, species react different to rainfall events depending on the size or magnitude of the event.

A big proportion of throughfall erosivity is attributed to the amount of rainfall passing - or being released by - the canopy. Park and Cameron (2008) could show that the throughfall/

rainfall ratio is driven by the canopy traits of single species. Moreover they could show that the influence of plant parameters (crown length, LAI, canopy openness) varies with the total amount of rainfall, indicating that species react different to a variety of event magnitudes. Similar to others, Park and Cameron (2008) suggest the process of throughfall generation being the result of the interaction of a variety of variables – each having an influence which depends upon the nature of the rainfall event.

Abiotic factors influencing throughfall generation

As indicated for example by Park and Cameron (2008) and others external, meteorological factors may cover the influence of plants and their traits on throughfall KE. The crucial point is, again, canopy storage. The storage of water in the canopy is not only depending on the natural capacity of the canopy to store water, it also depends on rainfall intensity and wind speed which cause canopy vibration (Hall and Calder, 1993; Nanko et al., 2006; Geißler et al., manuscript 6). In a laboratory experiment Nanko et al. (2006) found throughfall DSD to be shifted to a dominance of smaller drops in case of severe canopy vibration. Moreover, they could show a different reaction of species to canopy vibration. The higher the storage capacity of a given species is, the more it is affected by external factors.

1.4 Objectives

The present study seeks to investigate the mechanisms of soil erosion in a broad leaved mixed forest. As the mechanisms enhancing or reducing soil erosion under forest vegetation are rather complex compared to open field conditions the processes have to be studied separately (see section 1.2). Accordingly, this study is focused on the alteration of rainfall into throughfall and the associated change in KE with the following underlying objectives:

- (i) to quantify the amount of throughfall KE for different successional stages from earliest succession (< 2yrs) to old growth forests (> 80yrs) compared to rainfall KE,
- (ii) to test for a species-specific effect on throughfall KE and its rationales,
- (iii) to study the influence of forest structural variables and biodiversity on throughfall KE,

(iv) to refine and calibrate splash cups as a highly precise and low tech tool for measuring KE of both rainfall and throughfall and to enable a large number of replications.

According to the objectives at first the methodological aspect of the development and calibration of splash cups has to be focused. Continuative, measurements in an established and highly diverse forest ecosystem have to be performed. In the Gutianshan National Nature Reserve (GNNR) in subtropical SE China, the multidisciplinary research group “Biodiversity and Ecosystem Functioning China” (BEF-China) seeks to investigate the relationship between ecosystem services and species conservation. In a first step, 27 comparative study plots (CSPs) have been randomly selected by the research group, stratified according to successional stages and biodiversity levels. There, a complete species inventory has been performed and basic variables describing forest structure have been measured (see section 2.1).

As this thesis is part of the BEF-China research group, results will contribute to the overall aim of linking various ecosystem services to biodiversity.

2 Overview on the manuscripts

2.1 BEF-China research in Gutianshan National Nature Reserve

(Manuscript 1, published in *Ecological Monographs* 81, 25-41)

The multidisciplinary DFG-research group 891 “Biodiversity and Ecosystem Functioning China” (BEF-China) covers different disciplines processed by nine subprojects (2008-2011) including ecology, zoology, soil science, forestry and statistics. The project seeks to investigate the relationship between ecosystem services like primary production, the prevention of soil erosion, element cycling and species conservation. The basic research approach consists of the combination of a long-term biodiversity experiment with studies in existing forests.

Manuscript 1 introduces into the project and summarizes basic results of the species inventory in the GNNR in the eastern part of Zhejiang Province in SE China (Fig. 3).

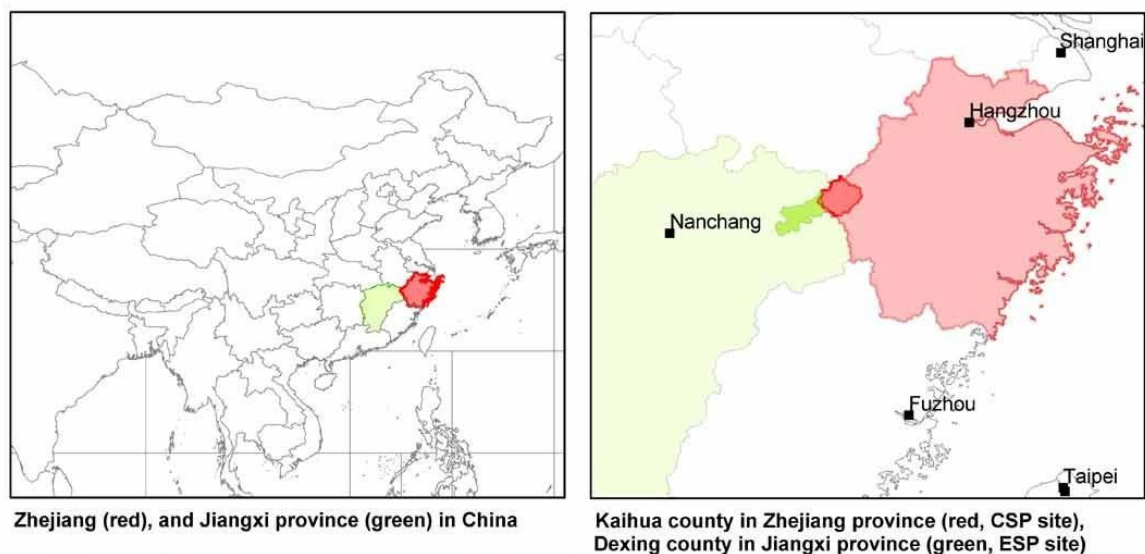


Fig. 3: Locations of the study sites of BEF-China.

In 2008, 27 CSPs were established in the nature reserve (Fig. 4). The plots (each 900 m² in size) were selected randomly according to succession in five successional stages (<20, <40, <60, <80, and ≥ 80 yrs.). Individuals of all adult species and shrubs > 1 m height were counted. Additionally, all woody recruits in each central subplot (100 m²) were counted.

Moreover, a number of environmental variables (e.g. LAI, elevation, slope, aspect, soil moisture, pH, C, N and C/N ratio) and biotic structural variables (height and cover of tree and shrub layers) were measured on the CSPs by the different subprojects (Fig. 5).

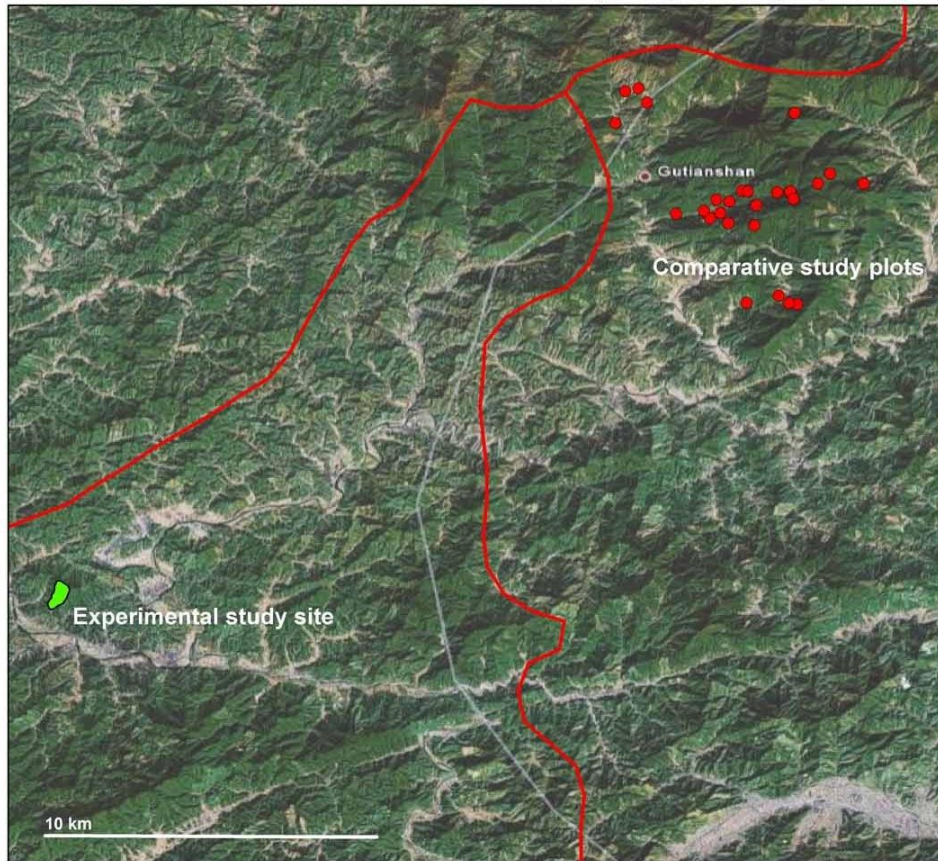


Fig. 4: Location of the experimental study site (green area) and the CSPs (red dots).

Adult species richness varied from 25 to 69 species per plot and in total 148 woody species from 46 families were recorded. The results show a clear successional gradient in species composition. Applying the rarefaction method, adult richness per 100 individuals increased with successional stage. No evidence was found abiotic variables or rare species being responsible for this circumstance. Local species richness and composition seems to be mainly caused by diffuse, random immigration over time. No species were found to depend on or to dominate specific successional stages and immigration rates were more or less constant during succession. The results show that young forests are not entirely different from old forests regarding species composition or richness. Consequently, results obtained from

young, experimental forest stands could be transferred to conditions in virtually all other successional stages.

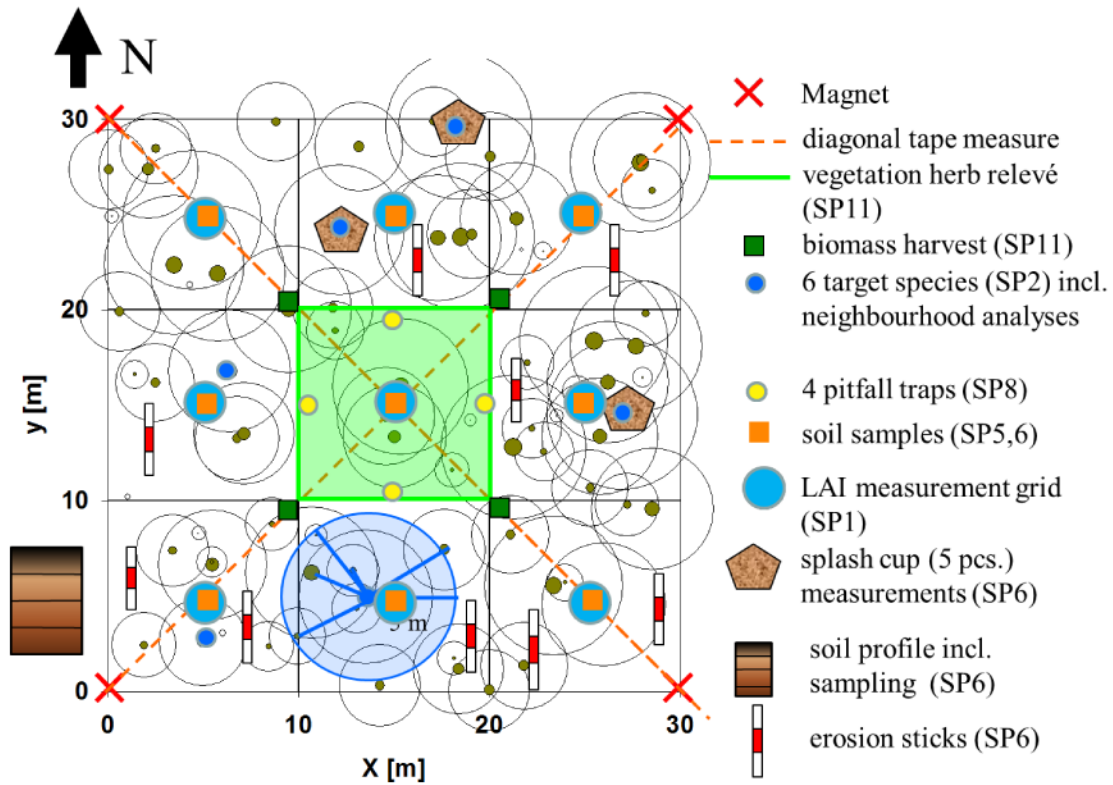


Fig. 5: Measurements on the CSPs undertaken by the different subprojects of BEF-China.

A subset of the several values mentioned in this manuscript has been used in this thesis (manuscripts 3, 4, 5, 6). Besides the data mentioned in this manuscript numerous other studies have been conducted in the GNNR and are still going on.

2.2 A new splash cup to measure the kinetic energy of rainfall

(Manuscript 2, published in *Journal of Plant Nutrition and Soil Science*, doi: 10.1002/jpln.201000349)

In the past several attempts have been made to measure KE of throughfall under vegetation canopies. Most of the methods applied in previous studies either lack temporal continuity or the possibility to achieve a certain number of replications due to high technical

and financial demands. Splash cups are a cheap and easy to operate low tech tool for measuring rainfall and throughfall KE efficiently with a high number of replications. Manuscript 2 reports on the measurement principle and measurement procedure and gives results of the calibration using a laser disdrometer.

The splash cup technique measures the soil or unit sand lost by comparison of a given amount of material prior to the erosive event and the remaining material thereafter. Splash cups have successfully been used throughout the last decades since Ellison (1947) presented the first prototype to conduct research on the detachment of soil particles by raindrops. Since then modifications have been presented following two lines of research:

- (i) measurements on the detachment of soil particles from a given cup and
- (ii) measurements on soil particles collected in a given cup that have been detached from natural ground.

Ellison (1947) originally used soils with different textures to assess the detachability of soil material in relation to standard sand. Since then, most splash cups were designed to measure the amount of soil splashed from the soil surface to a target (Morgan, 1978; Salles and Poesen, 2000; van Dijk et al., 2003; Legout et al., 2005). However, these methods are not appropriate for estimating differences in KE of rainfall or throughfall because the results are confounded by the erodibility of the soil. Further, measurements of particle detachment with splash cups face some technical requirements that are similar to rainfall simulation, especially concerning the steadiness of boundary conditions and the need to guarantee that all detached particles leave the measuring unit.

To ensure that the Tübingen splash cups (T splash cups) meet the requirements to minimize the rim-, size-, and wash-off effects (Bisal, 1950; Poesen and Torri, 1988; Erpul et al., 2005; Leguédois et al., 2005) and to be applicable to ecosystem research worldwide, the objective was to develop a splash cup that

- (i) measures sand loss as a function of KE and, thus, can be calibrated,
- (ii) has a constant soil moisture over a reasonable period of time,
- (iii) keeps soil moisture actively constant under natural rainfall and under evaporation conditions,

(iv) is sensitive to very low rainfall intensities, and

(v) has acceptable uniformity over a wide range of rainfall intensities and durations.

Furthermore, the splash cups must be easy to transport and to install under any kind of frost-free field conditions, maintenance-free during measurements, durable under harsh climatic conditions as well as inexpensive and fast to install and collect in order to allow for a large number of measurements at a time.

Like in other studies (e.g., Vis, 1986; Cornelis et al., 2004), the T splash cups (Fig. 6) were successfully calibrated and the relation between loss of sand and KE of rainfall is very close (Fig. 7).

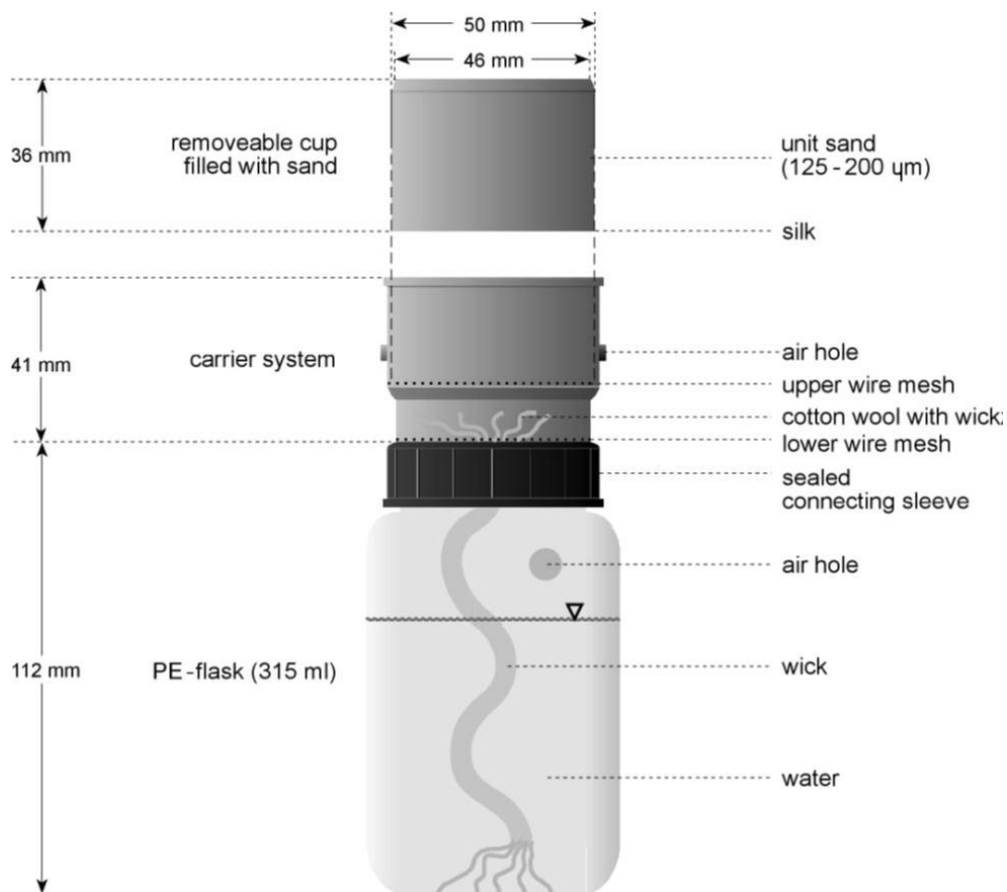


Fig. 6: The Tübingen splash cup (T splash cup).

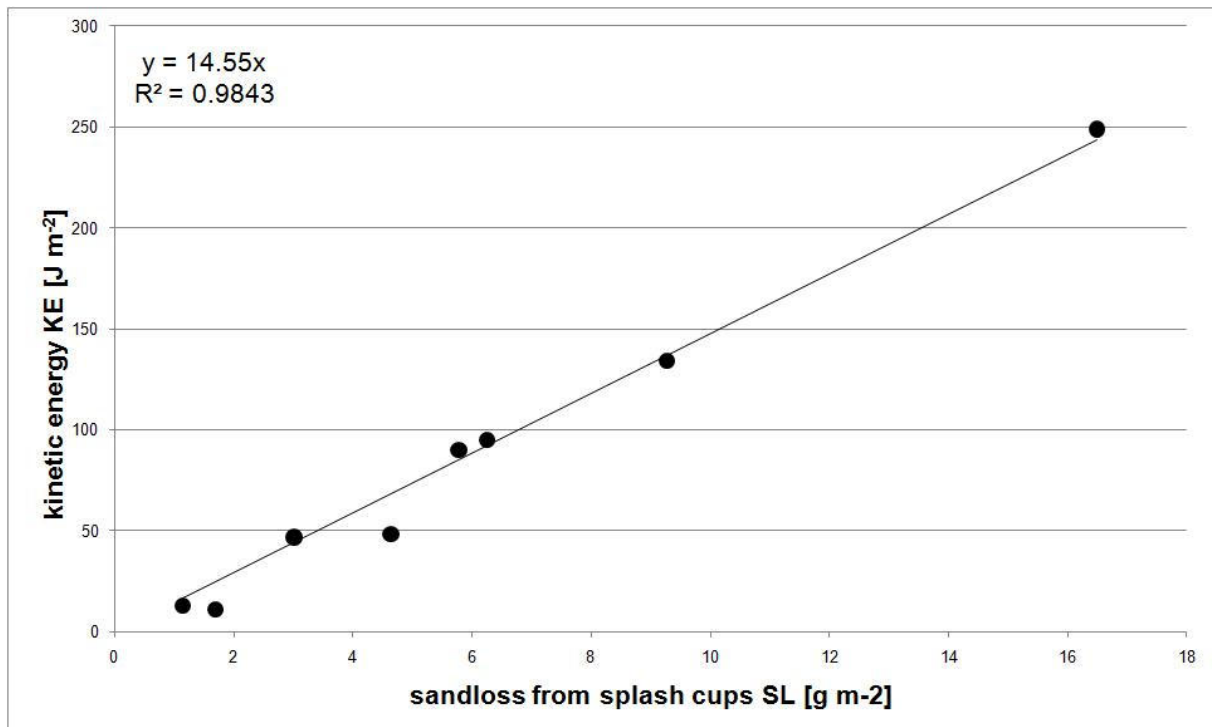


Fig. 7: Calibration curve for converting sand loss into kinetic energy.

Accordingly, the loss of sand converted to KE shows good correlations with the standard variables characterizing rainfall events (amount, average of the highest intensities per event) over a range of values. This is consistent with the results of other investigations (e.g., Wiersum, 1985) and shows the reproducibility and reliability of the measurements with the T splash cups. It is further supported by the low standard deviation of the measurements in the open field.

During the measurements, the sand surface was not lowered substantially. Therefore, the relationship between loss of sand and KE of rainfall is best described with a simple linear correlation. However, for higher KE the slope of the calibration function is supposed to be different due to a higher and more pronounced rim effect (Bisal, 1950). Due to the small size of the cups we suppose that the rim effect has substantial influence on the results with T splash cups only for far higher KEs than those observed in Tübingen and in subtropical China or for longer measuring intervals at both high rainfall amounts and intensities. Since the initial water content is a crucial point in splash erosion studies (Poesen and Savat, 1981), much effort was spent on the construction of a hydraulic contact that reacts fast on difference between the actual water content and the saturated water content of the unit sand over a reasonably long period of time. Due to the good drainage performance of the T splash cups

and the hydraulic contact of unit sand in the carrier system and water in the reservoir (cf. Fig. 6), the wash-off effect (Kinnell, 1974) could not be observed in the field. The same is true concerning the relationship between soil moisture and size. The holes in both carrier and plastic flask provide sufficient drainage of excess water during higher rainfall intensities. During phases of evaporation, water deficit in the carrier system is balanced immediately ensuring constant moisture conditions up to one week without rain. The size effect was minimized by the dimension of the cup and by the equivalent diameter of the unit sand. According to the investigations of Legu dois et al. (2005), we chose unit sand of 125-200 μm particle size because the splash lengths are greatest in this fraction ranging from 5-23 cm. This determines the diameter of the cup as well, in our case set to 4.6 cm.

Concluding we can state that the T splash cup is a high-precision device to measure the loss of sand due to the impact of raindrops (splash effect). It suits perfectly the specific needs for biodiversity experiments under natural conditions in forest ecosystems where a large number of replications under very diverse vegetation are required. Referring to the very durable construction and the ease of operation we can point out that the T splash cups are designed to work unattended under rough field conditions like steep slopes and remote areas accessible on foot only. Another advantage is the easy calibration of the T splash cup measurements with laser precipitation monitors (disdrometers). Thus, they record the KE of rainfall per area and can be used to calibrate soil erosion models. Further, the T splash cup can cope with high intensity rainfall which is typical for subtropical regions. This allows a wide range of applications in the future not only under natural conditions but also in rainfall simulation studies.

2.3 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

(Manuscript 3, submitted to *Agricultural and Forest Meteorology*, 8th of March 2011)

Throughfall in forest ecosystems is generally of a higher KE than open field rainfall. Most important determinants are the change in drop sizes and the height effect. This has been shown for several forest ecosystems around the world and most recently for a succession sequence in a forest ecosystem in SE China (manuscript 4) and two plantations of contrasting age in subtropical Japan (Wakiyama et al., 2010).

Studies focusing on the influence of younger trees (e.g. forest rejuvenation or young plantations) on throughfall KE remain scarce and a possible species specific impact in throughfall KE has only been documented for larger trees (Hall and Calder, 1993; Nanko et al., 2008) or for Mediterranean dwarf shrubs with strongly contrasting habits (Bochet et al., 2002; Xu et al., 2009).

Biotic parameters like branch count and branch inclination or leaf characteristics are supposed to strongly influence throughfall properties but results either show specific impacts (Herwitz, 1987; van Elewijk, 1989) or neglect them (Foot and Morgan, 2005). Especially for afforestation issues and ecosystem restoration attempts it is necessary to gain knowledge about the impact of specific species and the rationales for this.

The measurements 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. This is clearly 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”, were rainfall KE and throughfall KE are balanced.

Experiment A

The first part of the experiment showed the effect of sapling density. The higher density of the saplings resulted in a 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 is supposed to be a result of a shift in the proportion of throughfall components (Fig. 8).

For the high density planting, the main component of total throughfall is “released throughfall”, and “free throughfall” is supposed to play a minor role. Consequently, the gain in sapling height results only in a slight increase of throughfall KE which is mainly caused by drip from leaves and branches. For the low density planting the effect of height is more obvious. It was, however, contrary to the pattern which is often found, i.e. that throughfall KE increases with increasing tree height. This is supposed to 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 is not yet closed. In canopy gaps a higher throughfall

KE and amount (free throughfall) can be observed (Pressland, 1976; Stogsdill et al., 1989; Bochet et al., 2002). 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 the low density planting than for the high density planting (cf. Raat et al., 2002).

It can be stated that any effects revealed in this experiment are supposed to be caused by shifts in the proportion of throughfall components. This shift causes differences in the amount and therefore also KE of throughfall.

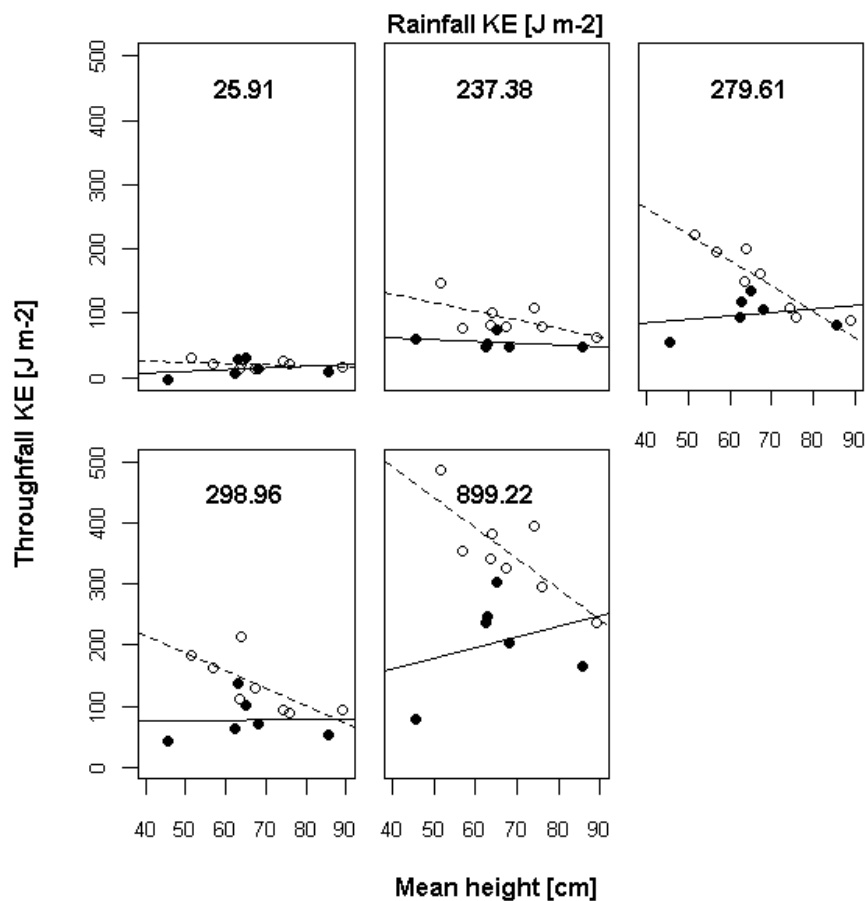


Fig. 8: Effect of sapling height on throughfall KE in five different rainfall events. Open circles represent the low density plots (dashed regression line), black dots the high density plots (black regression line).

Experiment B

In the second part of the experiment (species identity) species specific effects on throughfall KE could be identified (Tab. 2). From generalizable patterns of relative species effects on throughfall KE across rainfall events we can deduce species specific influential crown traits. Differential crown architectural traits may influence KE of throughfall contrarily and interact with each other.

The effect of specific species on throughfall KE showed that detailed measurement of architectural traits (esp. height, number of branches and angle of the first branch) 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 focusing on the soil erosion potential below these. Besides canopy closure, which prevents highly erosive raindrops to hit the soil, canopy storage appears to be important as it controls the amount of water (and therefore influencing KE directly) being able to fall from the leaves as drips.

Table 2: Effects influencing throughfall KE. Results of simplified mixed effects models, including block as random intercept for both experiments.

Fixed effects	F-value	p-value	
Kinetic energy of rainfall	499.35	<.0001	***
Density	50.28	<.0001	***
Mean sapling height	5.17	0.0266	*
Density * Mean sapling height	13.1	0.0006	***
Kinetic energy of rainfall* Density	33.24	<.0001	***
Kinetic energy of rainfall* Mean sapling height	2.15	0.1475	
KE of rainfall* Density* Mean sapling height	8.32	0.0055	**

2.4 Splash erosion potential under tree canopies in SE China

(Manuscript 4, published in CATENA, doi:10.1016/j.catena.2010.10.009)

During the last decades several researchers focused on the difference between rainfall erosivity and throughfall erosivity in forests. The general result was a substantial increase in erosivity under vegetation canopies, first mentioned by Chapman (1948). The question if throughfall erosivity was dependent on specific species has been negated for a long time,

before Hall and Calder (1993) and Nanko et al. (2008a) could show species specific throughfall erosivity using laser disdrometers. Manuscript 4 reports on splash cup measurements in a natural secondary forest ecosystem in subtropical SE China with special focus on the successional sequence and two selected tree species (*Schima superba*, *Castanopsis eyrei*) which are highly abundant in the study region (Bruelheide et al., 2011).

The results show that splash cup measurements yield precise and reproducible results under both open field conditions and forest vegetation. Under open field conditions the measured sand loss corresponded well with rainfall amount, average rainfall intensity, maximum rainfall intensity and the average of the five highest five minute intensities. The comparison of two devices for the measurement of precipitation (tipping bucket rain gauge and Vaisala sensor) demonstrate that measurements of the Vaisala sensor (drop size detection) corresponded much better to sand loss of splash cups in terms of rainfall amount and erosivity than to measurements of the tipping bucket rain gauge. The erosion potential of throughfall drops in forests was considerably higher (2.59 times) than under open field conditions (Fig. 9) and the spatial variability of the erosion potential was much more diverse in forests caused by free throughfall and drip.



Fig. 9: Sand detachment from splash cups under open field (a) and under forest vegetation (b) (black line = 1 cm).

By placing the splash cups under certain tree species it could be demonstrated that the erosivity of throughfall may depend on the species and also on the successional stage of the forest stand. The splash cup measurements made clear that the erosivity and amount of throughfall depends on the forest structure (age, cover, height). Moreover, it could be shown

that the ratio rainfall erosivity and throughfall erosivity is variable between different events (cf. Nanko et al., 2006). *Schima superba* generated throughfall drops of higher erosivity than *Castanopsis eyrei*. We assume that one reason for this finding is the larger size of the leaves resulting in larger throughfall drops and particularly drip (Fig. 10). The erosion potential is also a function of stand height because throughfall drops are much more likely to reach terminal velocity under intermediate and old growth forests. Therefore we conclude that the potential of throughfall to detach soil by splash is also related to the age of the specific forest stand: young forests have the lowest and old forests the highest erosion potential. Our study showed that splash cups are an appropriate method for comparing rainfall and throughfall erosivity. Despite the valuable and encouraging results presented in this paper a comparison with other studies remains challenging. This is due to the necessity of standardization of measuring equipment being one general difficulty of experimental studies in soil erosion (Stroosnijder, 2005). Differences caused by the measurement technique like cup size or grain size of the unit sand are typical. Further, varying external meteorological factors (Nanko et al., 2006) have to be taken into account.



Fig. 10: Leaf samples of *Castanopsis eyrei* (a) and *Schima superba* (b) (black line = 5 cm) (Kröber, 2010).

2.5 Estimation of throughfall erosivity in a highly diverse forest ecosystem using sand-filled splash cups

(Manuscript 5, Journal of Earth Sciences, doi: 10.1007/s12583-010-0132-y)

Manuscript 3 showed the dependency of splash erosion potential on the successional stage of the forests studied. Moreover, a species specific erosion potential could be shown using splash cups as a low-tech approach. Using an enlarged data set, manuscript 5 extends these results to two additional species and confirms the basic results of manuscript 4.

Simultaneous measurements under open field conditions and in forest stands of three successional stages in a humid subtropical forest ecosystem showed remarkable differences in sandloss. Throughfall in all varied between 57 % and 70 % of total precipitation. The average sandloss under vegetation (44.69 g m⁻²) was 2.59 times higher than that under open field conditions (17.24 g m⁻²). There was a non-linear increasing sandloss with increasing successional stage: the difference between the young successional stage and the intermediate successional stage (16.71 g m⁻², factor 1.51) was much higher than that between the intermediate successional stage and the old successional stage (1.45 g m⁻², factor 1.03) (Fig. 11).

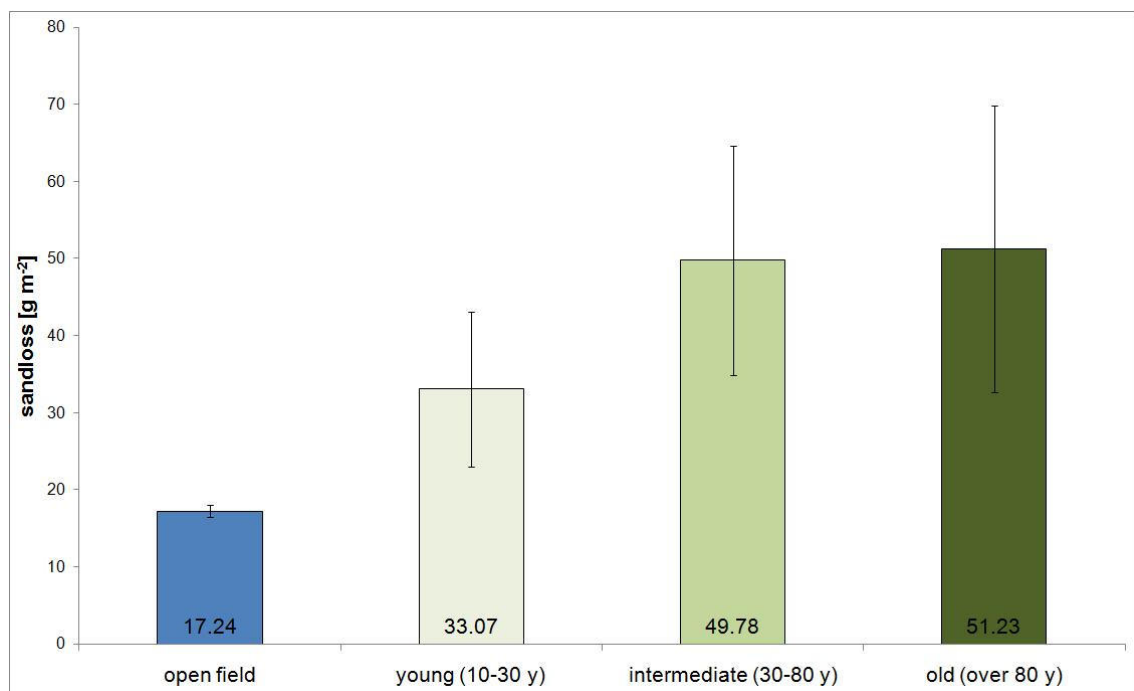


Fig. 11: Throughfall erosivity as measured by splash cups under open field conditions and three successional stages (solid lines = standard deviation).

The resulting standard deviations between the measurement replicates can be considered in two ways:

- (i) for open field conditions the standard deviation is much lower than that for all successional stages, and
- (ii) the difference in standard deviation between the young successional stage and the intermediate successional stage was much higher than that between the intermediate and the old successional stage.

The standard deviation found under two common species (*Schima superba*, *Castanopsis eyrei*) was much higher than that under open field conditions. Nevertheless, there were distinct differences in splash potential represented by sandloss between *Schima superba* (55.54 g m^{-2}) and *Castanopsis eyrei* (42.18 g m^{-2}), although the average amount of throughfall was quite similar (24.77 mm for *Schima superba* and 23.22 mm for *Castanopsis eyrei*) (Fig. 12).

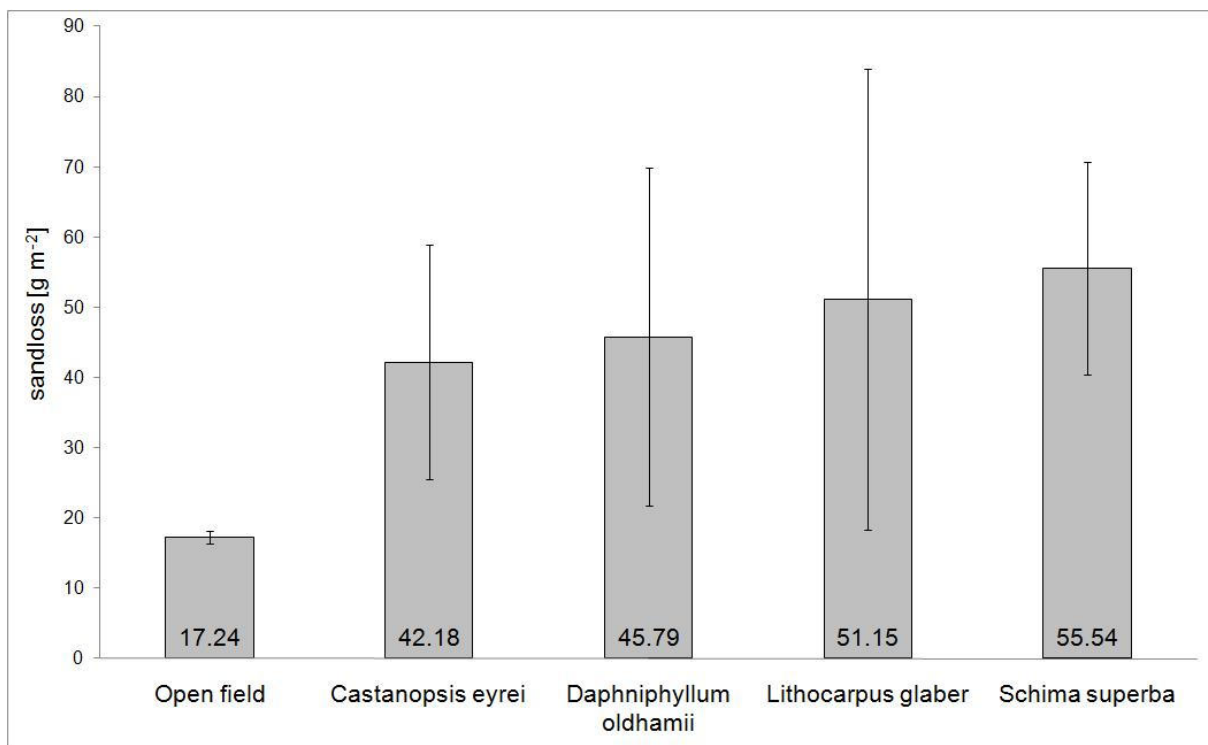


Fig. 12: Erosive power of throughfall as measured by splash cups for four tree species (solid lines = standard deviation).

The erosion potential of throughfall drops in forests was considerably higher (2.59 times) than that under open field conditions and the spatial variability of the erosion potential was much more diverse in forests, caused by free throughfall and drip. By placing the splash cups under certain tree species it could be demonstrated that the erosivity of throughfall depended on the species and also on the successional stage of the forest stand.

Schima superba, for example, generated throughfall drops of higher erosivity than *Castanopsis eyrei*. We assume that this is, amongst others, an effect of the larger size of the leaves of *Schima superba* which generates larger throughfall drops. The erosion potential is also a function of stand height because throughfall drops are much more likely to reach terminal velocity under old growth forests. Therefore, we conclude that the potential of throughfall to detach soil by splash is also related to the age of the specific forest stand: young forests have the lowest and old forests the highest erosion potential. This highlights the importance of a shrub, herb and litter layer in forest ecosystems to guard against soil erosion.

2.6 Biodiversity and throughfall kinetic energy in forest ecosystems in the humid subtropics of SE China – Effects of tree canopy structure, traits, and diversity

(Manuscript 6, in preparation, June 2011)

Relating throughfall KE to forest stand variables has been the objective of only few studies in the past. In general, factors like tree height (e.g. Wakiyama et al., 2010; Geißler et al., manuscript 4, manuscript 5), planting density (Pressland, 1976; Geißler et al., manuscript 3), canopy architecture (Herwitz, 1987; van Elewijk, 1989; Nanko et al., 2008), LAI (e.g. Levia and Frost, 2006; Geißler et al., manuscript 3), leaf traits and ultimately species identity (Hall and Calder, 1993; Nanko et al., 2006; Geißler et al., manuscript 3) are all supposed to influence throughfall properties resp. throughfall KE. Moreover, external meteorological factors have shown to have a substantial influence when comparing events of different magnitude.

The influence of biodiversity (resp. the number or composition of different species and functional groups) on throughfall KE or soil erosion as a whole has not been documented yet and studies are very rare. Using calibrated splash cups (Scholten et al., 2011) in a randomized design, throughfall KE was studied over a range of events in a highly diverse forest ecosystem in SE China (Geißler et al., manuscript 1). The dataset was analyzed using a mixed model

approach (Seltman, 2010). Prior to the analysis, the data were sorted by five hierarchical blocks in the order of their expected impact on throughfall KE, namely (1) event characteristics, (2) age/ height of the vegetation, (3) diversity measures, (4) crown openness and (5) leaf traits.

The results of the events measured show that the relation between rainfall KE and throughfall KE is highly variable in time depending on the amount and intensity of rainfall (Fig. 13). This indicates that canopy storage has a substantial effect on throughfall KE. In low amount and low intensity events there is in general a higher chance of rainfall to be intercepted and accumulated on leaves and branches. Contrastingly, higher event magnitudes and intensity result in a lower storage capacity of the canopy. Calder et al. (1996), Levia and Frost (2006) and Nanko et al. (2006) explain this circumstance with larger raindrops hitting the canopy during high magnitude events, preventing a storage on leaves and branches and allow a subsequent release of small throughfall drops. However, in low magnitude events, water can converge on leaves and fall to the ground as large drops gaining high values of KE. This results in a large difference in KE between open field and forest (e.g. event 9). In high magnitude events, the permanent impact of large drops prevents the water to converge on leaves and water is released from the canopy more easily resulting in much smaller drops with less KE. The same process system described here is responsible for higher throughfall volumes in tropical than in temperate regions where generally precipitation events larger in magnitude and intensity occur (Levia and Frost, 2006). Although wind speed is also supposed to affect this process system through canopy vibration (Nanko et al., 2006), no relationship ($R^2 = 0.047$) could be found in our data.

As expected, rainfall amount as the most important variable concerning throughfall KE. Rainfall amount showed a highly significant positive effect on throughfall KE which is quite logical (e.g. Levia and Frost, 2006) as there is generally a strong linear relationship between rainfall amount (mm) and KE (J m^{-2}) (e.g. Scholten et al., 2011). Numerous researchers found a dependency of throughfall amount on rainfall amount (e.g. Stogsdill et al., 1989; Filoso et al., 1999; Carlyle-Moses, 2004). This suggests throughfall KE is largely controlled by rainfall amount arriving at the canopy. Over the rainfall events measured rainfall amount was the variable describing by far most of the variability of throughfall KE.

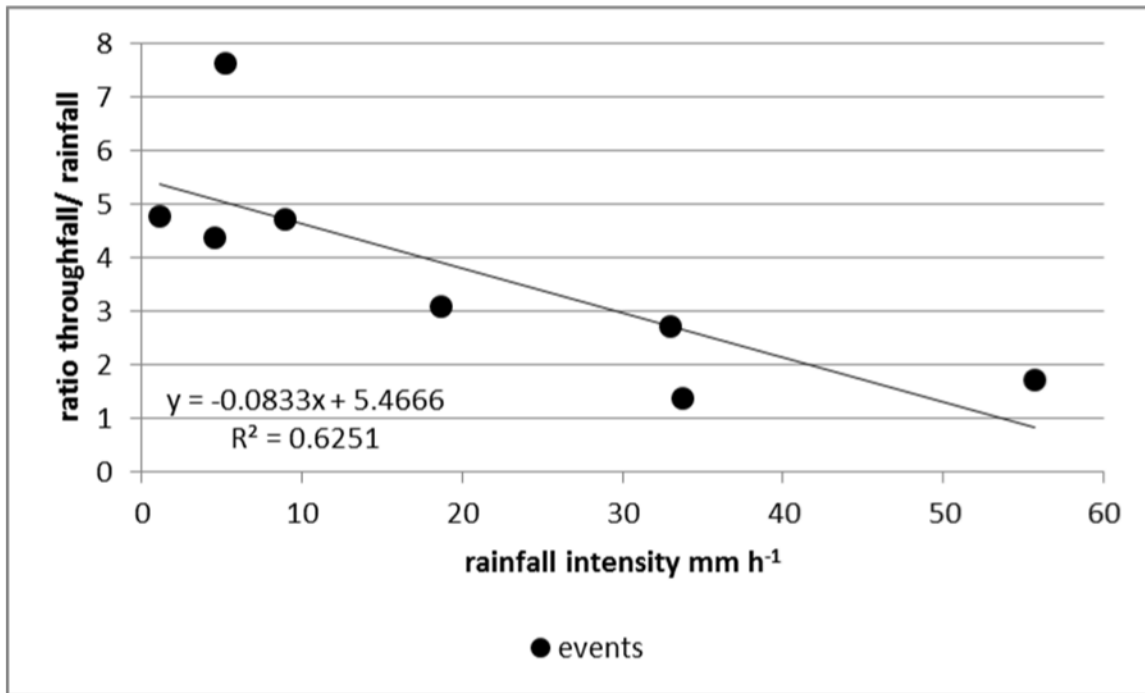


Fig. 13: Ratio between throughfall kinetic energy and rainfall kinetic energy in relation to rainfall intensity.

The weighted mean height of the vegetation proved to have a significant effect on throughfall KE as well. The height effect has been recognized by Chapman as early as 1948 and confirmed thereafter by numerous authors (e.g. Tsukamoto, 1966; Mosley, 1982; Wiersum, 1985; Vis, 1986; Brandt, 1988; Brandt, 1989; Nanko et al., 2004; Nanko et al., 2008b). Nevertheless, weighted mean height is only marginally significant (at the 0.5 level) although it is supposed to be a rather strong effect on throughfall KE. The cause for this circumstance is probably the vertical layering of the forest which is incorporated in weighted mean height through the coverage values for every layer. This is also the substantial difference to many other studies of throughfall KE which were performed mainly in (young) forest plantations, where height of the vegetation in a given plot remains rather constant (Chapman, 1948; Tsukamoto, 1966; Nanko et al., 2008a; Wakiyama et al., 2010). Through vegetation layering the height effect gets less clear than one would expect (Wiersum, 1985).

The interaction between rainfall amount and weighted mean height of the vegetation also showed to be significant. This indicates that during forest growth the relation of rainfall KE to throughfall KE changes (which affects the measured values for KE). For example in a dense young forest cover values are the highest (74 % in our case) decreasing with increasing age or height of the vegetation (down to 50 % in our case). This again affects canopy storage.

The slightly positive relationship between throughfall KE and biodiversity can be attributed to the increase of species richness with growing stand age in the forests studied. With increasing forest age species accumulate through random immigration of recruits during succession (Bruehlheide et al., 2011). Due to the gain of height with increasing forest age one would expect a substantially higher throughfall KE in species rich (and therefore mostly late successional) forests. However, throughfall KE remains rather constant with increasing species richness (Fig. 14). This means that species rich forests achieve to keep throughfall KE low, although maximum falling height of the drops is generally higher. However, in species rich forest ecosystems plant biomass and total plant cover is much higher than in species poor forests (Loreau et al., 2001; Scherer-Lorenzen, 2005; Hooper et al., 2005; Balvanera et al., 2006). Additionally, in species rich forests, ecological niches are better exploited and consequently throughfall drops are much more likely to be reintercepted by lower vegetation layers. Brandt (1988) and Wiersum (1985) have shown that a highly structured forest ecosystem keeps throughfall KE at low values despite of a total gain in height of the forest stand.

From block 5, LAI showed to have a significant negative effect on throughfall KE. With increasing LAI throughfall KE decreases. Basically, LAI is a measure of crown thickness and canopy openness. Therefore, higher LAI values should result in higher canopy storage, e.g. a smaller amount of throughfall or throughfall KE reaching the forest floor (e.g. Park and Cameron, 2008). Again, on the one hand this implies differences in throughfall KE being largely controlled by an alteration of the spatial distribution of the amount of throughfall. On the other hand also throughfall KE is lowered independently of rainfall amount under thicker canopies through the process of re-interception. Falling drops in thick canopies are much more likely to be re-intercepted and splitted by lower parts of the canopy (Nanko et al., 2008b) which has a negative effect on throughfall KE.

The significant negative impact of the proportion of coniferous species (block 5: leaf traits) on throughfall KE can be attributed to differences between throughfall drop generation and leaf shape. Drops released from needle shaped leaves generally have less KE than drops from broad leaved species as the storage capacity of needle shaped leaves is relatively small (Armstrong and Mitchell, 1988; Nanko et al., 2006). According to this, regarding KE of throughfall a certain proportion of coniferous species in a specific forest has beneficial effects for the forest ecosystem by lowering throughfall erosivity.

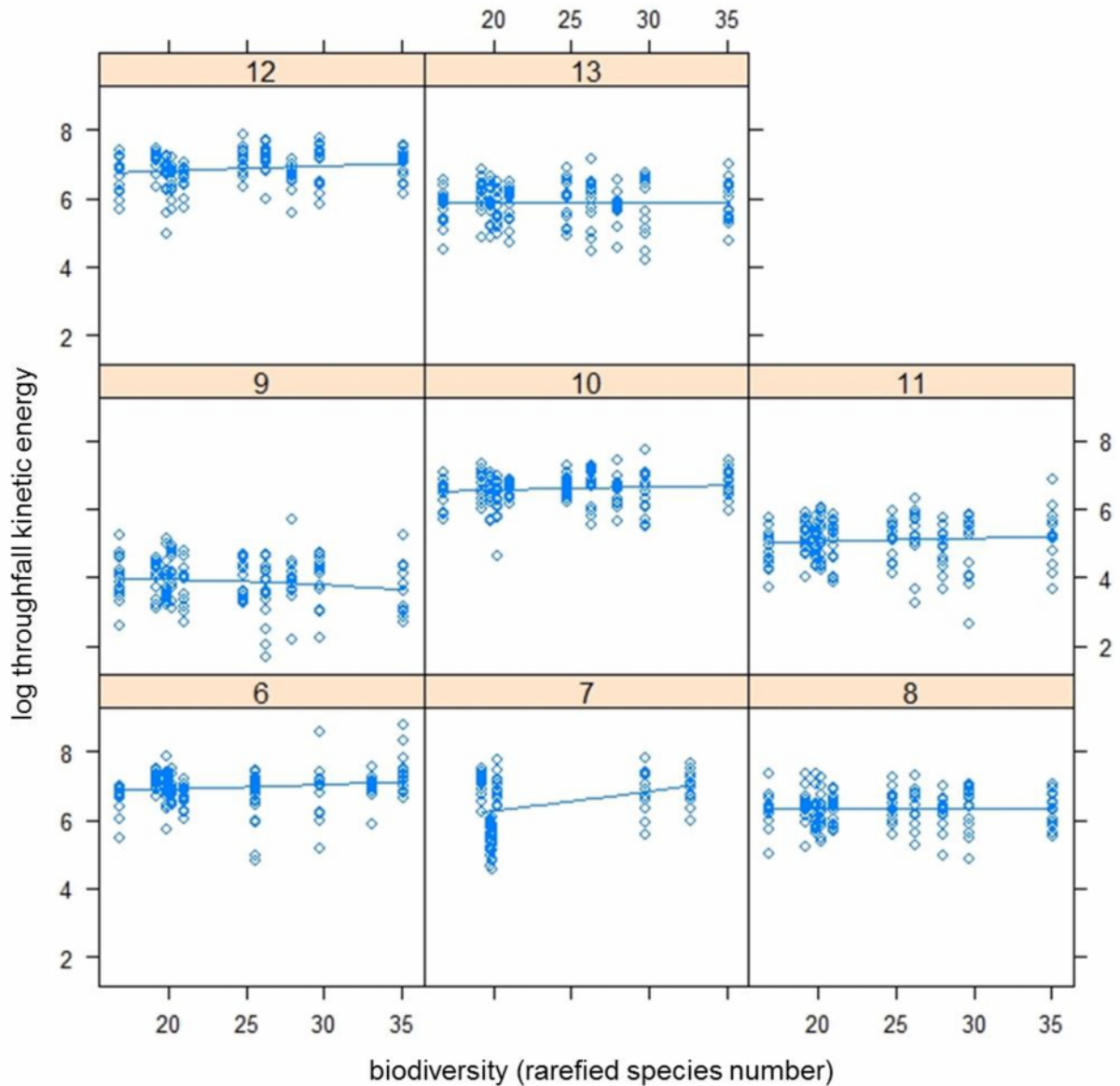


Fig. 14: Relation between log throughfall kinetic energy and biodiversity for rainfall events 6-13.

Concerning the variability of throughfall KE only variables from block 1 (event characteristics) and from block 3 (diversity measures) showed significant trends. During model selection rainfall intensity appeared to describe variability of throughfall KE better than rainfall amount and rainfall KE. According to our data, increasing rainfall intensity seems to lead to a decreasing variability of throughfall KE. As described above KE under forest is closely connected to rainfall amount and many related variables (e.g. LAI, crown openness, weighted mean height) are responsible for redistributing rainfall by temporary canopy storage. Nevertheless, concerning higher rainfall intensities storage on leaves is reduced because of two reasons resulting in canopy vibration:

- (i) permanent impact of large drops and
- (ii) high wind speeds often associated with high rainfall intensities (e.g. Nanko et al. 2006).

Therefore, for higher rainfall intensities it is less likely for a given position within the forest being in a rain shadow and thereby enhancing spatial variability of throughfall KE.

The significant positive relationship between variability of throughfall KE and biodiversity is reasonable as both the variability of throughfall KE and biodiversity are measures of heterogeneity. With increasing biodiversity of a forest stand also the variability of throughfall increases substantially (Fig. 15).

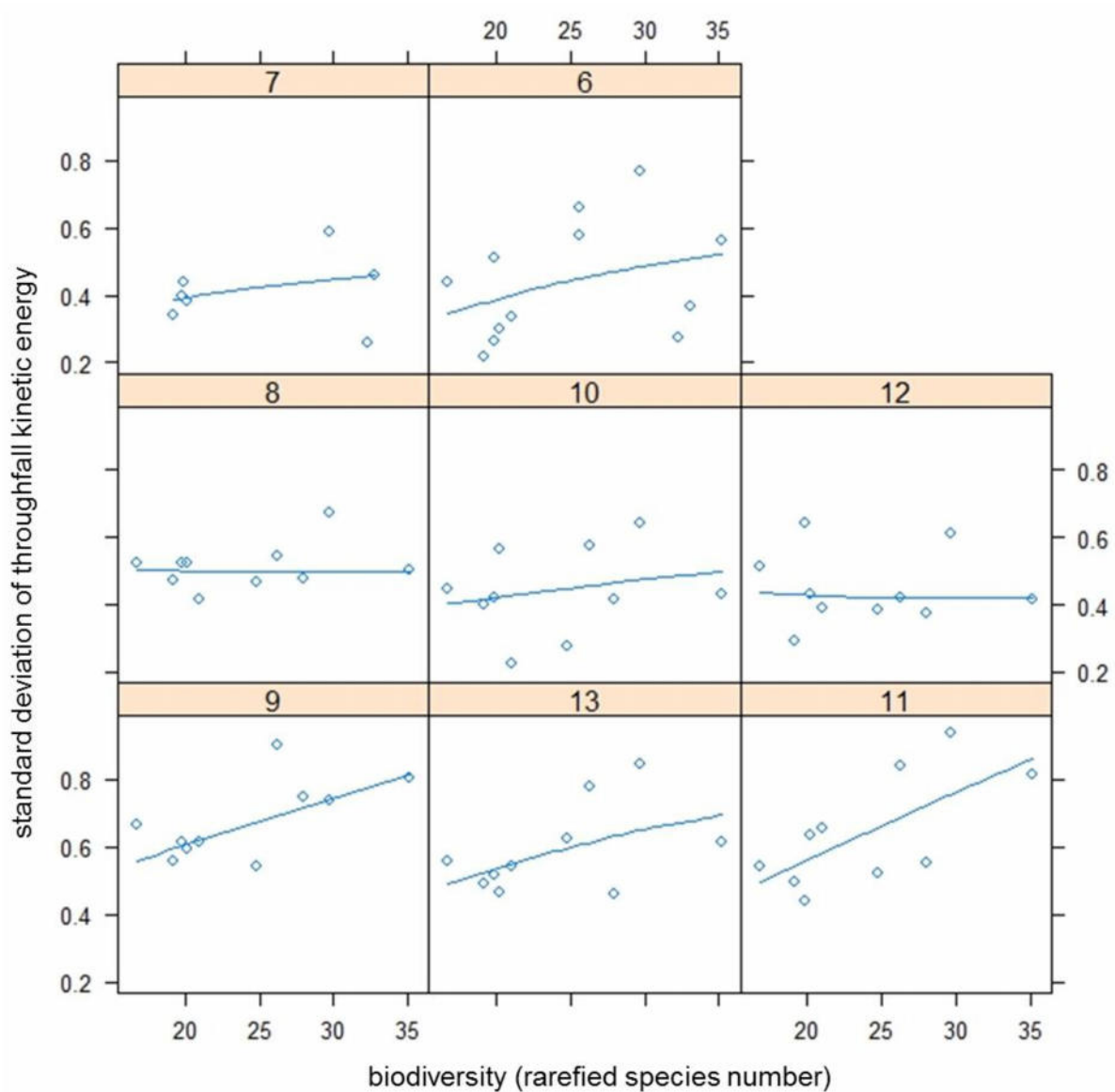


Fig. 15: Relation between standard deviation of throughfall kinetic energy and biodiversity for rainfall events 6-13.

As mentioned above, biodiversity in the GNNR is closely related to the successional stage of a specific forest stand (Bruelheide et al., 2011) and one might argue the variability of throughfall just being a function of forest age. Nevertheless, through backward model selection none of the parameters describing the age or height of a specific forest stand (block 2: successional stage, basal diameter, weighted mean height) showed to have any significant influence on the variability of throughfall.

Moreover, as it is supposed that both throughfall volume and KE are species specific (Hall and Calder, 1993; Levia and Frost, 2006; Nanko et al., 2006; Geißler et al., 2010a). Hence, a higher number of species in a given plot should result in a more heterogeneous pattern of throughfall amount and KE. In more diverse plots a high number of species is occupying several ecological niches (Hutchinson, 1957) thereby increasing total plant cover in different heights. Consequently, in a highly diverse forest plot, throughfall is very likely to be intercepted in e.g. different heights or to a different extent resulting in a more heterogeneous pattern of throughfall amount and KE.

It could be shown that a variety of variables describes the alteration of rainfall into throughfall in a highly diverse forest ecosystem. Basically, the differences between rainfall KE and throughfall KE are supposed to be controlled by the redistribution of rain water within the canopy as every species or individual has its own capacity to store water in the canopy. Basic measures describing this redistribution and alteration are biodiversity, LAI, weighted mean height of the vegetation and the proportion of coniferous species within a plot. Through varying rainfall amount and intensity this process system of redistribution is controlled and influenced externally.

3 Conclusions

This thesis is the first to relate aspects of soil erosion to species richness in a forest ecosystem. It is part of BEF-China, a multidisciplinary project on biodiversity and ecosystem functioning in subtropical China. By using calibrated splash cups, a high number of replications could be accomplished and a large dataset could be compiled and analyzed. In general, the main results of the thesis contribute substantially to the understanding of mechanisms of soil erosion under forest in relation to biodiversity, specific species and forest structure.

T splash cups as a valuable tool for measuring rainfall and throughfall kinetic energy

By refining the splash cups, calibrating them and optimizing the measuring procedure a highly precise and reliable device could be developed and applied in large numbers. Through different calibration measures using standard rainfall characterizing values and a laser disdrometer it could be shown that the splash cups yield precise and reproducible results. The feasibility of the approach – despite steep slopes, remote sites and harsh meteorological conditions – was shown by using temporarily more than 450 splash cups at once with a team of three people. The Tübingen splash cups are a high precision device measuring KE of rainfall and throughfall.

Throughfall mechanisms during the earliest phase of succession

In the earliest phase of succession mechanisms controlling throughfall KE become activated gradually. During growth the relation of throughfall components (esp. free throughfall, drip) to each other changes substantially affecting the total amount and variability of throughfall. The velocity of canopy closure then determines the degree of the lowering of throughfall KE before – due to ongoing growth – throughfall KE increases and then – after passing a certain threshold – exceeds rainfall KE.

A species specific throughfall kinetic energy

A species specific effect on throughfall KE is still under discussion in literature. Yet, it could only be shown for species with strongly contrasting leaf morphologies. In our studies measurements in an experimental forest plantation with tree saplings and in a secondary forest have shown a distinct effect of the type of species on throughfall KE. Especially leaf size, number of branches, inclination of the first branch and branch count influence throughfall KE. A detailed measurement of architectural traits of trees and saplings leads to a better understanding of the process of throughfall generation. Besides canopy architecture, canopy storage is the second controlling factor for throughfall KE.

Increase of throughfall kinetic energy during forest succession

It could be shown that forest succession largely influences throughfall KE and is best described by an asymptotic relationship. Substantial increases during succession do exist especially for younger successional stages where increasing tree height affects throughfall KE directly. For later successional stages, the effect of tree height on throughfall KE diminishes more and more.

A highly variable relation between rainfall and throughfall kinetic energy

External influences on throughfall KE like rainfall amount and intensity affect the relation between rainfall and throughfall KE substantially. Basically, higher amounts of rainfall and higher rainfall intensities lead to a narrower ratio between rainfall KE and throughfall KE. These external factors further influence canopy storage which is supposed to be the main controlling factor for throughfall KE in the spatial scale of forest stands and the temporal scale of rainfall events. The range of the rainfall KE/ throughfall KE ratio reached from 1.37 to 7.61. This suggests a stronger dependency of throughfall KE on event characteristics as it has been previously discussed in the literature.

Main forest stand characteristics influencing throughfall kinetic energy

Especially variables describing or depending on forest structure substantially influence throughfall KE, namely the balance point of height and coverage of the tree and shrub layer(s) in a specific forest stand (weighted mean height), LAI and the proportion of coniferous species. Again, the basic mechanisms of KE under forests (drop falling height and the amount of stored and redistributed water within the canopy) can be described by these values. It is proposed that dependency of throughfall KE on the proportion of coniferous species is not solely a result of the redistribution of water within the canopy but rather an effect of different drip mechanisms between coniferous and evergreen resp. deciduous species resulting in smaller throughfall drops in forest stands with a considerable proportion of coniferous species.

Biodiversity influences on throughfall kinetic energy

The influence of biodiversity or species richness in this case is rather complex. Biodiversity is the only variable describing parts of the variance of both throughfall KE and its variability. In the forests studied species richness increases with successional stage resp. age of the specific forest stand. Nevertheless, a clear consequent increase of throughfall KE with increasing species richness could not be detected. The data show throughfall KE rather remaining constant than increasing. The species rich forests in SE China achieve to keep throughfall KE constant despite a potential increase in drop falling height. Due to strong relationships between biodiversity, plant biomass and total plant cover throughfall drops in species rich forests are much more likely to be intercepted by the various vegetation layers. This feature has strong effects on the total amount of water reaching the ground and on spatial variability of throughfall. This appears to be one of the basic mechanisms of the ecosystem service of erosion control in species rich forest ecosystems.

In this thesis basic mechanisms and dependencies of throughfall KE in subtropical forests have been described and analyzed. A wide range of factors is responsible for the alteration of throughfall KE including biotic and abiotic variables. This could be shown for subtropical forests from earliest succession to old growth forests. At the single species level, crown architectural traits and interplant distances largely control throughfall KE. At the forest stand level however, LAI, height of the tree layer(s), the proportion of needle leaved species and

biodiversity are the main drivers supporting the ecosystem service of soil erosion. Through variations in throughfall amount, this process system is strongly influenced externally. Highly diverse forest ecosystems can be seen as an effective measure against soil erosion.

4 Outlook

The main experiment of BEF-China, an experimental afforestation of about 50 ha focusing on research on ecosystem services and biodiversity, bears a vast amount of possibilities for future research regarding soil erosion and its relation to biodiversity. Here, a combination of both basic parts of the process system of soil erosion under forest (see section 1.2) is possible. Refining the results of part 1 (throughfall generation) and gathering results from part 2 (forest floor processes) would lead to a comprehensive understanding of the processes of soil erosion under forest in relation to biodiversity. Nevertheless, it is still suggested to study these parts separately like in the present thesis to be able to control as much factors as possible for the sake of clearer results.

5 References

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Summary

This thesis is part of the BEF (Biodiversity and Ecosystem Functioning) China research unit (DFG FOR 891) “The role of tree and shrub diversity for production, erosion control, element cycling, and species conservation in Chinese subtropical forest ecosystems” founded by the German Research Foundation (DFG) and the National Science Foundation of China (NSFC). The overall aim of the project is to analyze the influence of tree and shrub species diversity on ecosystem functioning and ecosystem services. The research approach consists of the combination of research in an experimental forest stand with studies in existing forests. The study area of the present thesis is the Gutianshan National Nature Reserve (GNNR) in Zhejiang Province, P.R. China.

To combat soil erosion is a prominent and most important ecosystem service of forests. Yet, little is known about the mechanistic relation of this ecosystem service to biodiversity. We hypothesize that the underlying processes can be explained by mechanisms that alter rainfall properties and those that change forest floor properties. This thesis concentrates on the alteration of rainfall properties and seeks to relate forest succession, specific species, forest stand variables and species richness as measures of biodiversity to throughfall kinetic energy (KE).

For measuring throughfall KE, splash cups have been developed (T splash cups) to facilitate reliable and precise measurements with a large number of replications. By using partly more than 450 splash cups at once it was possible to show an asymptotic increase of the highly variable and spatially inhomogeneous throughfall KE with succession. The youngest trees were less than two years old, the oldest representing late successional forest stands are more than 80 years of age. Tree saplings reduce KE of throughfall down to 40 % of that of open field rainfall. In mature forests KE is amplified. Throughfall KE can count up to 7.61 times the KE of open field rainfall. The experiments and observations show that this effect is highly heterogeneous in space and time.

Part of this heterogeneity can be attributed to plant physiology. Differences between specific species refer to their canopy architecture as well as their ability of storing and intercepting water on vegetative surfaces like leafs and branches.

Furthermore, forest stand variables related to forest structure affect the amount and spatial variability of throughfall. These are primarily (i) height and coverage of the different

tree layers, (ii) leaf area index (LAI), and (iii) the proportion of coniferous species within a specific forest stand. These variables control (i) the potential falling height of a given drop, (ii) the potential of the canopy cover to store and detain water, (iii) and the drop size distribution (DSD) of throughfall related to different drip mechanisms.

Biodiversity expressed as species richness influences both the total amount and the spatial variability of throughfall KE. In the GNNR, species richness increases with succession and keeps throughfall KE low compared to younger and less diverse forests. The species rich forests are complex structured and layered. Plant biomass and total plant cover reach high values. The remaining throughfall KE is kept at relatively low values although the potential falling height of single drops increases with tree height.

Summarizing, biodiversity and the ecosystem service of a forest canopy to prevent soils from being eroded are positively related. Increasing diversity compensates the effect of increasing falling height in older stands to a large extent and widens the drop size spectra of throughfall intensity and throughfall KE. It can be concluded that diverse forest ecosystems are an important and very effective measure to combat soil erosion.

Zusammenfassung

Die vorliegende Arbeit ist Teil der BEF (Biodiversity and Ecosystem Functioning) China-Forschergruppe (DFG FOR 891) „The role of tree and shrub diversity for production, erosion control, element cycling, and species conservation in Chinese subtropical forest ecosystems“, gefördert von der Deutschen Forschungsgemeinschaft (DFG) und der National Science Foundation of China (NSFC). Ziel der Forschergruppe ist es, den Einfluss von Baum- und Strauchdiversität auf Ökosystemfunktionen und -dienstleistungen zu erforschen. Der Forschungsansatz beinhaltet die Kombination einer experimentellen Aufforstung mit Studien in bestehenden, etablierten Wäldern. Das Arbeitsgebiet der vorliegenden Arbeit ist das Gutianshan National Nature Reserve (GNNR) in der Provinz Zhejiang, Volksrepublik China.

Die Verhinderung von Bodenerosion ist einer der zentralen und wichtigsten Ökosystemdienstleistungen von Wäldern. Bisher ist noch wenig über den mechanistischen Zusammenhang dieser Ökosystemdienstleistung mit der Artenvielfalt bekannt. Dieser Arbeit liegt die Annahme zugrunde, dass die unter Wald stattfindenden Prozesse erklärt werden können durch (i) Mechanismen, die die Niederschlagseigenschaften verändern und (ii) Mechanismen, die die Eigenschaften der Bodenoberfläche verändern. Der Fokus der vorliegenden Arbeit liegt auf der Veränderung von Niederschlagseigenschaften und versucht einen Zusammenhang zwischen Waldsukzession, einzelnen Arten, Waldstruktur und Walddiversität auf der einen Seite und der kinetischen Energie (KE) des Bestandsniederschlags auf der anderen Seite herzustellen.

Um die KE des Bestandsniederschlags zu erfassen, wurden sog. splash cups (T splash cups) entwickelt, um verlässliche und präzise Messungen mit einer großen Anzahl an Messwiederholungen durchzuführen. Das gleichzeitige Benutzen von teilweise mehr als 450 splash cups ermöglichte es, einen asymptotischen Anstieg des hochvariablen und inhomogenen Bestandsniederschlags mit fortschreitender Waldsukzession zu zeigen. Die jüngsten Bäume waren jünger als zwei Jahre, die ältesten mehr als 80 Jahre. Junge Bäume reduzieren die KE des Bestandsniederschlags auf ca. 40 % des Freilandniederschlags. In älteren Wäldern ist die KE des Bestandsniederschlags deutlich erhöht, und kann die KE des Freilandniederschlags um das bis zu 7-fache übersteigen. Die Experimente und Beobachtungen zeigen, dass dieser Effekt räumlich und zeitlich hochvariabel ist.

Ein Teil dieser Heterogenität kann der Physiologie der Bäume zugeschrieben werden. Unterschiede zwischen bestimmten Arten beziehen sich meist auf die Kronenarchitektur sowie ihrem Vermögen, Wasser auf Blättern oder Ästen abzufangen oder zu speichern.

Weiterhin beeinflussen Variablen, die die Waldstruktur beschreiben, Menge und räumliche Variabilität des Bestandsniederschlags. Diese sind primär (i) Höhe und Bedeckungsgrad der verschiedenen Baumschichten, (ii) Blattflächenindex (LAI) und (iii) der Anteil an Nadelbaumarten innerhalb eines bestimmten Waldbestandes. Diese Variablen kontrollieren die (i) potentielle Fallhöhe eines Tropfens, (ii) das Potential des Kronendachs, Regenwasser zu speichern und zurückzuhalten, und (iii) die Tropfengrößenverteilung (DSD), die durch unterschiedliche Abtropfmechanismen beeinflusst wird.

Biodiversität beeinflusst die Gesamtmenge und die räumliche Variabilität der KE des Bestandsniederschlags. Im GNNR steigt die Artenanzahl mit fortschreitender Sukzession. Dennoch bleiben die Werte für die KE des Bestandsniederschlags, verglichen mit jüngeren oder weniger artenreichen Wäldern, vergleichsweise niedrig. Artenreiche Wälder sind sehr komplex strukturiert und geschichtet, Biomasse sowie Pflanzenbedeckung erreichen hier Spitzenwerte. Die KE des Bestandsniederschlags wird dadurch gering gehalten, obwohl die potentielle Fallhöhe eines Tropfens mit zunehmender Baumhöhe ansteigt.

Zusammenfassend kann gesagt werden, dass Biodiversität und die Ökosystemdienstleistung, Bodenerosion zu verhindern, positiv zusammenhängen. Eine hohe Anzahl an Arten kompensiert den Effekt zunehmender Fallhöhen in älteren Waldbeständen deutlich und erweitert das Tropfengrößenspektrum des Bestandsniederschlags. Es kann gefolgert werden, dass hoch diverse Wälder sehr effektive Ökosysteme in Bezug auf Verhinderung von Bodenerosion darstellen.

Manuscript 1

Community assembly during secondary forest succession in a Chinese subtropical forest

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Abstract

Subtropical broad-leaved forests in south-eastern China support a high diversity of woody plants. Using a comparative study design with 30 x 30 m plots ($n = 27$) from five successional stages (< 20 , < 40 , < 60 , < 80 and ≥ 80 yrs) we investigated how the gradient in species composition reflects underlying processes of community assembly. In particular, we tested whether species richness of adult trees and shrubs decreased or increased and assessed to which degree this pattern was caused by negative density dependence or continuous immigration over time. Furthermore, we tested whether rare species were increasingly enriched and the species composition of adult trees and shrubs became more similar to species composition of seedlings during the course of succession. We counted the individuals of all adult species and shrubs > 1 m in height in each plot and counted all woody recruits (bank of all seedlings ≤ 1 m in height) in each central 10 x 10 m quadrant of each plot. In addition, we measured a number of environmental variables (elevation, slope, aspect, soil moisture, pH, C, N and C/N ratio) and biotic structural variables (height and cover of layers). Adult species richness varied from 25 to 69 species per plot and in total 148 woody species from 46 families were recorded. There was a clear successional gradient in species composition as revealed by non-metric multidimensional scaling (NMDS) but only a poor differentiation of different successional stages with respect to particular species. Adult richness per 100 individuals (rarefaction method) increased with successional stage. None of the measured abiotic variables were significantly correlated with adult species richness. We found no evidence that rare species were responsible for the increasing adult species richness, as richness of rare species amongst both adults and recruits was independent of the successional stage. Furthermore, the similarity between established adults and recruits did not increase with successional stage. There was a constant number of recruit species and also of exclusive recruit species, i.e. those that had not been present as adult individuals, across all successional stages, suggesting a continuous random immigration over time.

Keywords: BEF-China; chronosequence; detrended correspondence analysis (DCA); Gutianshan National Nature Reserve; immigration; negative density dependence; nonmetric multidimensional scaling (NMDS); permanent forest dynamic plots; random assembly; secondary forest succession; Zhejiang Province, China.

Nomenclature: Flora of China (<http://flora.huh.harvard.edu/china>)

Introduction

The last decades have much improved our understanding of the forces that affect tree species richness in forests. Local or community species richness, i.e. α -diversity, is increased by immigration and reduced by extinction and both processes may be stochastic or deterministic (MacArthur and Wilson 1967, Hubbell 2001). While stochastic immigration mainly depends on the difference between regional species richness, i.e. γ -diversity, and α -diversity, and on the degree of dispersal limitation (Hubbell et al. 2008), deterministic immigration additionally depends on the characteristics of the immigrating species, of the receiving community and interactions between the two (Rejmanek 1996, Crawley et al. 1999, Mwangi et al. 2007). Stochastic extinction usually affects species with small population size (Simberloff 1988, Fischer and Stöcklin 1997, Matthies et al. 2004), whereas deterministic extinction may be due to environmental filtering (Lavorel and Garnier 2002) or exclusion of a plant species by competitors, pathogens or herbivores (Schmid and Matthies 1994). An important mechanism acting against extinction is negative density or frequency dependence, which either occurs when negative interactions are less detrimental or positive interactions are more favorable among different species than among individuals of the same species (Wright 2002, Wills et al. 2006).

Interestingly, not much attention has been paid to the question of how stochastic and deterministic processes affect community assembly during secondary forest succession, although for a number of reasons such succession series are highly suitable systems for studying community assembly and diversity maintenance. First, some processes are directly observable, such as recruitment and mortality (Chazdon 2008). However, other processes such

as the development of positive interactions are much less obvious, although it is generally assumed that they increase with time, as the ecosystems get more structured and more complex (Odum 1971, Margalef 1963). There is ample evidence for a temporal development of complementarity from biodiversity–ecosystem functioning (BEF) experiments (Tilman et al. 2001, Cardinale et al. 2007, Duffy 2009, Marquard et al. in press), but not much is known from secondary forest succession series. Second, the general development of species richness along successional series is well known for many forest types (Howard and Lee 2003, Chazdon 2008). According to Howard and Lee (2003), four main patterns can be distinguished: species richness can monotonously decrease or increase with ongoing succession, peak at middle successional stages or may not show any temporal trend. The absence of any trend might occur if changes in successional stages involve changes in environmental conditions to which only a limited but unpredictable number of species are adapted (Denslow 1980). While these patterns describe the net changes in species richness during succession, they do not discuss the underlying community assembly processes, i.e. immigration and extinction dynamics. So far, it has not been analyzed to which extent the above mentioned negative and positive forces act on net species richness during the course of secondary forest succession.

A continuous decrease in diversity during succession, caused by prevalence of extinction processes, is consistent with the hypothesis of initial floristic composition (Egler 1954): At the beginning of succession a large number of species immigrate but more and more species go extinct as competition for increasingly depleted resources, mainly light, increases over time. In addition, stochastic extinction increases when individuals increase in size and the overall density of individuals declines. This sampling effect (Denslow 1995, Hubbell et al. 1999) also contributes to decreasing richness. In contrast, two major processes might promote an increase in tree species richness with successional age, either resulting in a monotonous increase or in a mid-successional peak:

First, effects of negative density and frequency dependence, for example Janzen/Connell-effects (Janzen 1970, Connell 1971, Condit et al. 1992, Freckleton and Lewis 2006), might accumulate with time, and thus be more prominent in mature stands. Studying the diversity in subtropical and tropical forests in Queensland, Australia, Connell et al. (1984) called this effect compensatory recruitment, as it would compensate for the tendency of competitively stronger species to increase at the expense of weaker ones. Based on the observation that more

common species had fewer seedling recruits per adult than rarer species, Connell et al. (1984) suggested that rare species were favored over common ones in terms of a per capita recruitment rate. Recently, Wills et al. (2006) compared the diversity of cohorts of different age and size in repeated census intervals of seven tropical forest plots. They found preferential establishment and survival of less abundant compared to more abundant species, which resulted in an increased enrichment of rare species with successional stage. As a consequence, rare species would be prevented from local extinction and diversity would increase from the group of seedlings to the one of young and old trees.

Second, young successional stages might experience continuous immigration from late successional stages because those contain a considerable part of the regional species pool. Thus, young successional stages might start with a low number of tree species and then become enriched with time. Given a constant stream of immigrants from a random set of species, newly established cohorts would be expected to have a low floristic similarity to already established ones when the number of residents is low, such as in young stands. With progressing succession composition of new cohorts would become increasingly similar to the established species, because more and more of the newly arriving species would be already present in the community (Anderson 2007). However, similarity between recruits and the established trees might also reach local minima if there are clear successional stages that fundamentally differ in species composition (Chao et al. 2005).

In this paper, we ask whether tree species richness increases or decreases with increasing age of successional stages in a warm-temperate laurophyllous forest (in the following called subtropical forest) in Zhejiang Province, China (see below), and how stochastic or deterministic immigration and extinction may contribute to the net changes in species richness. These subtropical mixed forests are of particular interest for diversity research since they are similarly rich in woody species as tropical forests (Wills et al. 2006, Condit 1995, Legendre et al. 2009). In addition, they represent a formerly widespread ecosystem in South and East China (Wu 1980), which currently is under high pressure from intensive land use (Wang et al. 2007). Our motivation to address the impact of successional age on diversity originates from a recently initiated experiment that uses a large set of subtropical tree and shrub species in Jiangxi, China, close to the forest plots studied here, to explore the relationships between biodiversity and ecosystem functioning (www.bef-china.de). In the experiment, artificial stands of defined tree species diversity levels are established by planting

seedlings, and in consequence, during the first years will only reflect the conditions of young successional stages with respect to microclimate, food web structure and nutrient fluxes and pools. Thus, we were interested to learn to which extent young forest stands differ from old ones in all types of ecosystem functioning variables. This paper is the first contribution to this topic, asking how much tree and shrub richness and variables related to richness vary along a gradient of different stand ages. Our specific hypotheses were:

(1) Richness of tree and shrub species recorded on a fixed plot size is highest in young successional stages and decreases in the course of succession, mainly because of declining density of individuals. If the sampling effect is taken into account, i.e. if richness is corrected for a decreasing density of individuals in the course of succession, richness is expected to increase. In addition, we tested whether successional stage is a better predictor for species richness than other variables related to structure and site characteristics.

(2) Rare species increasingly contribute to the potential effect of increasing richness with successional age. A preferential survival of rare species provided, an increase in proportions of rare species should be less conspicuous in seedlings as compared to adult trees and shrubs. Consequently, a higher contribution of rare species should also be visible in a higher per capita recruitment success of rare species as compared to common ones as well as higher average per capita recruitment rates of plots containing a higher proportion of rare species.

(3) In contrast to the former hypotheses, which are based on the assumption of a differential recruitment of common and rare species, we further hypothesized that establishment from a common recruitment pool could be a random process. Assuming continuous but random immigration, the richness of recruits should be constant over the different successional stages. However, given a limited regional species pool and increasing richness with successional time, the probability that species new to a plot would be among the recruits, i.e. those that are not yet present as adult individuals, should decrease in the course of succession. Likewise, the similarity in species composition between established adults and recruits is expected to decrease.

Materials and Methods

Study site

The Gutianshan National Nature Reserve (NNR) is located in the western part of Zhejiang Province (29°8'18"–29°17'29" N, 118°2'14"–118°11'12" E, Fig. 1). The forest is representative of Chinese mixed broad-leaved forests (Wu 1980, Hu and Yu 2008, Legendre et al. 2009), with evergreen species dominating the forest in number of individuals (Yu et al. 2001) but with approximately similar proportions of deciduous species in terms of species number (Lou and Jin 2000). A total of 1426 seed-plant species of 648 genera and 149 families has been recorded as occurring naturally in the NNR. About 258 of the species are woody (Lou and Jin 2000). The Gutianshan NNR has an area of approximately 81 km², was initially established as a National Forest Reserve in 1975 and became a National Nature Reserve in 2001. The NNR comprises a large portion of broad-leaved forests of advanced successional stages (Hu & Yu 2008), which have not been managed since the beginning of the 1990s, as well as young successional stages and conifer plantations, mainly of the economically important timber species *Cunninghamia lanceolata* and *Pinus massoniana* (for author names of species see Appendix 1).

Most of the stands are secondary forests, evidenced by maximum tree ages of only 180 years, by the presence of relicts of agricultural terraces in almost all plots and by the presence of charcoal in almost all soil profiles. Within and adjacent to the Gutianshan NNR extensive deforestation has occurred during the Great Leap Forward in the 1950s, as in most parts of Southeast China. However, owing to very steep slopes with some of them exceeding 30°, the Gutianshan area was only marginally usable for agricultural activities, and thus an exceptionally intact forest cover has been preserved.

The climate at Gutianshan NNR is warm-temperate with a short dry season in November and December and with warm summers. The climate conditions are characteristic of the subtropics with an annual average temperature of 15.1 °C, January minimum temperatures of –6.8 °C, July maximum temperatures of 38.1 °C and an accumulated temperature sum (≥ 5 °C) of 5221.5 degree days per year.

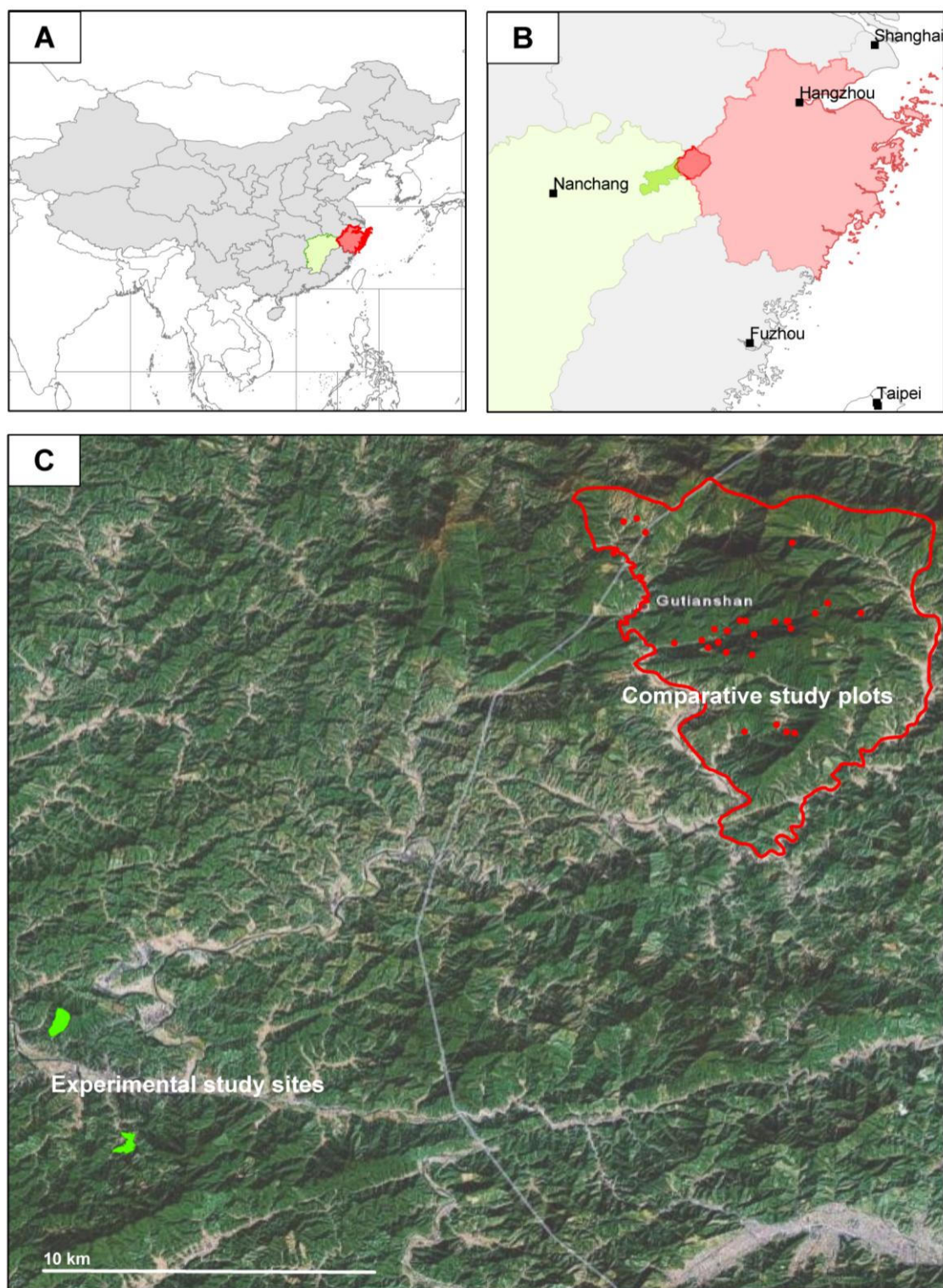


Fig. 1: Study area: (A) Zhejiang (red), and Jiangxi (green) Provinces; (B) Kaihua county in Zhejiang Province (red, area of Comparative Study Plots [CSPs] used for the study reported in this paper), Dexing county in Jiangxi Province (green, area where an associated forest biodiversity–ecosystem functioning experiment has been set up). (C) Gutianshan NNR (red line) with CSPs (red dots) in Kaihua county (Zhejiang Province) and the two associated experimental sites (green areas) in Dexing county, Jiangxi Province.

Study design

Plots were randomly selected, stratified by successional age. In the following the plots are called Comparative Study Plots (CSPs). Different successional ages are the result of differences in elapsed time since the last forest harvesting, carried out manually by the local population for timber and fire-wood. Five successional stages were distinguished according to the age of the oldest tree individuals in a plot, supported by additional knowledge of the last logging event in this part of the forest and local status as ‘feng shui’ forest (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: \geq 80 yrs). The plot assignment in the field was later confirmed by additional measurements of diameter at breast height (dbh) of all trees with > 10 cm dbh in a plot, and of tree age, determined on 159 stem cores taken at breast height from 64 different tree species across all CSPs. CSP locations within strata were selected randomly; however, due to inaccessibility and extremely steep slopes (> 50°), parts of the NNR had to be excluded from sampling, thus resulting in an uneven spatial distribution of some of the plots (Fig. 1C). In total, 27 CSPs were established between May and July 2008. The number of plots per successional stage were 5 (< 20 yrs), 4 (< 40 yrs), 5 (< 60 yrs), 6 (< 80 yrs) and 7 (\geq 80 yrs).

Species recording was performed between May and October 2008 with several visits per plot. Each CSP has a size of 30 x 30 m on the ground. In horizontal projection this corresponded to an average area of 0.074 ha, close to the Chinese areal measure of 1 mu (=0.067 ha) and thus to the plot size used in the associated biodiversity–ecosystem functioning experiment at Xingangshan (Jiangxi Province, Fig. 1C). Soil moisture was assessed gravimetrically on soil samples taken from five depth increments (0-10, 10-20, 20-30, 30-40, 40-50 cm) in June/July 2008, November 2008 and March 2009. Here, we used mean values per plot by averaging the soil water contents over all depths and all dates. Soil samples for determination of pH, C and N were taken in summer 2009 from nine locations in each plot at 0-5, 5-10, 10-20, 20-30, and 30-50 cm. The samples were pooled to form one bulk sample per CSP and depth interval, sieved (< 2mm) and air-dried. Soil pH was measured potentiometrically in a 1:2.5 soil-H₂O suspension. Total C and N were determined on milled samples after heat combustion (1150 °C) using Vario ELIII elemental analyzer. Since all soil samples are non-calcareous, the measured total C content equals organic carbon (C_{org}). In this paper only the topsoil (0–5 cm) data have been used, because these showed the highest variation among plots. A complete inventory of woody species (> 1 m height) was carried out

in the entire plot. All herbaceous species and woody seedlings ≤ 1 m height (i.e. the seedling bank, in the following called recruits) were recorded in a central subplot of 10 x 10 m on the ground. All individuals were identified to the species level, making use of herbarium samples and comparisons with correctly identified individuals, and counted per species. The proportion of unidentifiable individuals (> 1 m height) in a CSP ranged between 0–2.3 %. These individuals were not included in the subsequent data analysis. All measures in this paper are expressed per area on the ground (i.e. not converted to horizontal projection area).

Data analysis

We calculated the concentration of all species in one of the five successional stages, using the Phi value as measure of fidelity, calculated with the Juice software (Chytrý et al. 2002). The Phi values were tested for significance by Fisher's exact test, using a significance level of $p=0.01$. At this level a species would be identified as being significantly characteristic of a successional stage if, for example, it occurred at least in 3 plots of this stage (assuming that the stage comprised 4 to 7 plots), but not in the other successional stages. The presence and absence of species in the different successional stages was used to calculate community turnover rates between successional stages according to Anderson (2007), defined as number of species that were either new to a successional stage or had disappeared, divided by the total sum of species in the preceding and subsequent successional stage. To analyze the floristic composition of all woody species we employed non-metric multidimensional scaling (NMDS) using counts of individuals per CSP and Bray-Curtis dissimilarity. The statistics were computed with R (R Development Core Team 2008), using the vegan package (Oksanen et al. 2006). All 148 species of trees and shrubs with at least one individual > 1 m in height were used in the analysis. Wisconsin double standardization, where species are first standardized by species maxima and then sites are standardized by site totals, was applied to square root transformed abundance data. Default options were used for scaling, so that one unit means halving of community similarity from replicate similarity. Species scores were added as weighted averages. In a subsequent multiple regression, the NMDS plot scores on axes 1 and 2 were related to (i) variables describing plot characteristics (elevation, aspect, slope, geographical coordinates, height and cover of the different layers, coverage of bare ground, soil moisture, pH, C, N and C/N ratio) and successional stage and (ii) to variables related to

species richness (number of woody species and woody lianas [height > 1 m] in the 30 x 30 m plot as well as number of herb species, woody recruit species [seedlings], woody climber species and herb climber species in the 10 x 10 m subplot [only recorded if height \leq 1 m]). The significance of the correlations was assessed using permutation tests (n=999). In addition, a detrended correspondence analysis (DCA) was performed to determine the gradient lengths and to yield an estimate of β -diversity (Jongman et al. 1995).

All ordinary linear regressions with single predictors were calculated with R. A multiple regression was used to test the dependence of species richness of adult trees and shrubs (individuals > 1 m height) on all variables describing plot characteristics and structure (for a list of variables see Table 1A). The input variables were standardized (i.e. z transformed) prior to analysis, resulting in a model with intercept = 0. Model fitting started with a full set of independent variables and was simplified using backward selection. Multiple regression analyses were performed with the SAS 9.1 package (proc reg, SAS Institute 2002, Cary, North Carolina, USA).

To obtain estimates of species richness that are unaffected by individual density, rarefaction analysis was based on Hurlbert's (1971) formula, as implemented in the vegan package in R, using a fixed number of 100 individuals per plot. Rarity was assessed by ranking all species both in the group of adult trees and shrubs as well as in the group of seedlings in the order of their abundance across all plots. Species were considered "rare" or "common" when they occurred in the lower or upper half of all ranks, respectively (rarity threshold 50%). We also tested whether the definition of rarity had an impact on the results by considering species to be "rare" when they occurred in the lower quartile (rarity threshold of 25%).

To relate the number of recruits to the number of adults, the census from the central 10 x 10 m subplot was extrapolated to the whole plot area by multiplying all counts of recruits by 9. As Wright (2002) pointed out, the species' per capita recruitment rate should not be plotted against the species' abundance, as this takes the form of y/x versus x . Thus, we directly regressed the number of recruits on the number of adult plants and tested for a log-log relationship after transforming both the count data of adults and recruits by $\log_{10}(x+1)$. We then compared the observed and expected slope and identified outliers from this prediction by plotting confidence intervals using a tolerance of \pm two standard deviations. To test whether

the recruits of a species were concentrated in the same successional stage that was preferred by conspecific adults, we calculated the ratios of number of individuals ($x+1$) in late successional stages (4 and 5) to their number in early successional stages (1 and 2) for each species. We then compared this ratio (expressed as log ratio) between recruits and adults. Again, we plotted confidence intervals using a tolerance of ± 2 standard deviations to identify outliers (e.g. long-lived pioneer species that might occur in old successional stages as adults but have recruits only in young successional stages).

Table 1: Correlation coefficients of (A) variables describing plot characteristics and structure and (B) variables describing species diversity of the different strata and life-forms with the first and second axis of the NMDS ordination.

A. Plot characteristics	Abbreviation in Fig. 3	NMDS1	NMDS2	r^2	P
Successional stage	Successional_stage	0.997	0.079	0.616	0.001
Age of the 5 th but largest tree [years]	Tree_age_max5	0.968	0.252	0.405	0.007
Elevation [m a.s.l.]	Elevation	0.135	0.991	0.780	0.001
Location in the NNR [Degrees N °]	Coordinates_N	-0.143	0.990	0.319	0.012
Location in the NNR [Degrees E °]	Coordinates_E	0.947	0.320	0.395	0.003
Eastness = sin(aspect [°])	Aspect_E	-0.880	-0.475	0.185	0.095
Northness = cos(aspect [°])	Aspect_N	-0.572	0.820	0.075	0.413
Slope [°]	Slope	0.790	-0.613	0.047	0.555
Height of upper tree layer [%]	T1_height	0.985	-0.170	0.650	0.002
Cover of upper tree layer [%]	T1_cover	0.945	0.326	0.333	0.008
Height of lower tree layer [%]	T2_height	0.995	-0.098	0.557	0.001
Cover of lower tree layer [%]	T2_cover	-0.839	-0.544	0.130	0.170
Height of shrub layer [%]	SL_height	0.995	0.103	0.310	0.008
Cover of shrub layer [%]	SL_cover	-0.888	0.459	0.545	0.001
Cover of herb layer [%]	HL_cover	-0.428	-0.904	0.161	0.121
Percentage of bare ground [%]	Open_soil	-0.803	0.596	0.110	0.226
Soil moisture [g H ₂ O/g dry soil]	Soil_moisture	0.561	0.828	0.456	0.002
pH (0-5 cm) measured in H ₂ O	pH	-0.718	-0.696	0.201	0.070
Total carbon content (0-5 cm) [%]	C	0.691	0.723	0.332	0.007
Total nitrogen content (0-5 cm) [%]	N	0.724	0.690	0.390	0.003
Carbon/nitrogen ratio (0-5 cm) [%/ %]	C_N	-0.553	-0.833	0.039	0.633

B. Richness variables	Abbreviation in Fig. 3	NMDS1	NMDS2	r ²	P
Number of individuals of adult trees and shrubs (> 1 m height)	N_individuals	-0.817	0.576	0.498	0.001
Number of adult tree and shrub species (> 1 m height)	N_adult_species	1.000	0.011	0.183	0.091
Number of adult tree and shrub species (> 1 m height) based on rarefaction with n = 100 individuals	N_adults_100	0.926	-0.378	0.421	0.004
Proportion of rare adult species	Prop_rare_adults	0.001	1.000	0.073	0.381
Proportion of deciduous adult species	Prop_decid_adults	-0.737	0.676	0.656	0.001
Number of adult climber species	N_adult_climber	0.363	0.932	0.015	0.839
Number of woody seedlings (≤ 1 m height)	N_recruit_species	0.166	-0.986	0.085	0.337
Number of woody and herbaceous climber species in the herb layer	N_HL_climber	-0.869	-0.495	0.024	0.743
Number of herbaceous species	N_herb_species	-0.867	0.498	0.409	0.01
Number of herb layer species (= N_recruit_species + N_HL_climber + N_herb_species)	N_HL_species	-0.978	-0.208	0.107	0.243
Proportion of rare recruit species	Prop_rare_recruits	0.060	0.998	0.113	0.235
Bray-Curtis similarity between adults and recruits	BrayCurtis_adult_recruits	-0.939	-0.344	0.028	0.725
Sørensen similarity between adults and recruits	Sorensen_adult_recruits	-0.870	-0.494	0.029	0.705
Per capita recruitment rate per plot	Per_capita_recruitment	-0.999	0.052	0.165	0.112
Prop of recruit species new to a plot	Prop_exclusive_recruits	-0.740	-0.673	0.073	0.404

For each species, per capita recruitment rates were calculated by relating the number of recruits (multiplied with 9 as explained above) to the number of adult trees and shrubs. This was done at three levels, at the level of each plot, across all plots of one successional stage and for all 27 plots of the whole study. Plot-wise per capita recruitment rates were obtained by averaging the per capita recruitment rate of all species present in a plot. Using a mixed model with successional stage as fixed factor and species identity as random factor, we tested for the impact of successional stage on species-specific per capita recruitment rate (proc mixed, SAS 9.2).

Species similarity between adults and recruits was calculated for each plot, both based on counts of individuals using Bray-Curtis similarity and on presence/absence using the Sørensen index (Sørensen 1948). In addition, we counted those species among the recruits that were not yet present in a plot among the adults (i.e. species in a plot exclusively found in the group of

recruits, not among the adults).

Results

The assignment of CSPs to the five different successional stages was well reflected in the age of the largest trees in the plot. Age determination of the stem cores taken from 64 tree species was possible except for three species (*Castanopsis eyrei*, *Cyclobalanopsis myrsinaefolia*, *Cyclobalanopsis stewardiana*). Across all species and across all plots diameter at breast height (dbh) was well related to tree age (Fig. 2A). Few old trees, which were retained during harvesting, occurred even in the youngest plots. This means that in every plot 1, 2 or 3 trees might be older than the time of the harvesting event. Therefore, the fifth largest tree in a plot was chosen as being representative for the stand age. Fig. 2B shows that the age of the fifth but largest tree closely matched the assignment to successional stages, with a mean age (\pm standard deviation) for the successional stages 1, 2, 3, 4 and 5 of 34.7 (\pm 11.9), 43.2 (\pm 6.3), 66.3 (\pm 10.9), 79.4 (\pm 16.2) and 94.8 (\pm 15.0) years, respectively. The comparably high age of the successional stage 1 resulted from the fact that in some plots 5 or more old trees had been retained during harvesting (e.g. CSP 16, with 11 trees $>$ 20 cm dbh).

In total, 148 woody species from 46 families were recorded with at least one individual $>$ 1 m. A full list of species is given in Appendix 1. Maximum richness was 69 woody species per 30 x 30 m plot. A total of 21 species occurred only with one individual in one of the CSPs and further 14 species occurred only in one CSP. However, these rare species were quite evenly distributed across the successional age classes. The fidelity analysis showed that only two species were significantly concentrated in the youngest plots (*Glochidion puberum*, *Platycarya strobilacea*) and only one species significantly concentrated in the oldest plots (*Photinia glabra*) (Appendix 1). Percent community turnover rates between stages 1 and 2, 2 and 3, 3 and 4, 4 and 5 were 22%, 22%, 16%, and 11%, respectively.

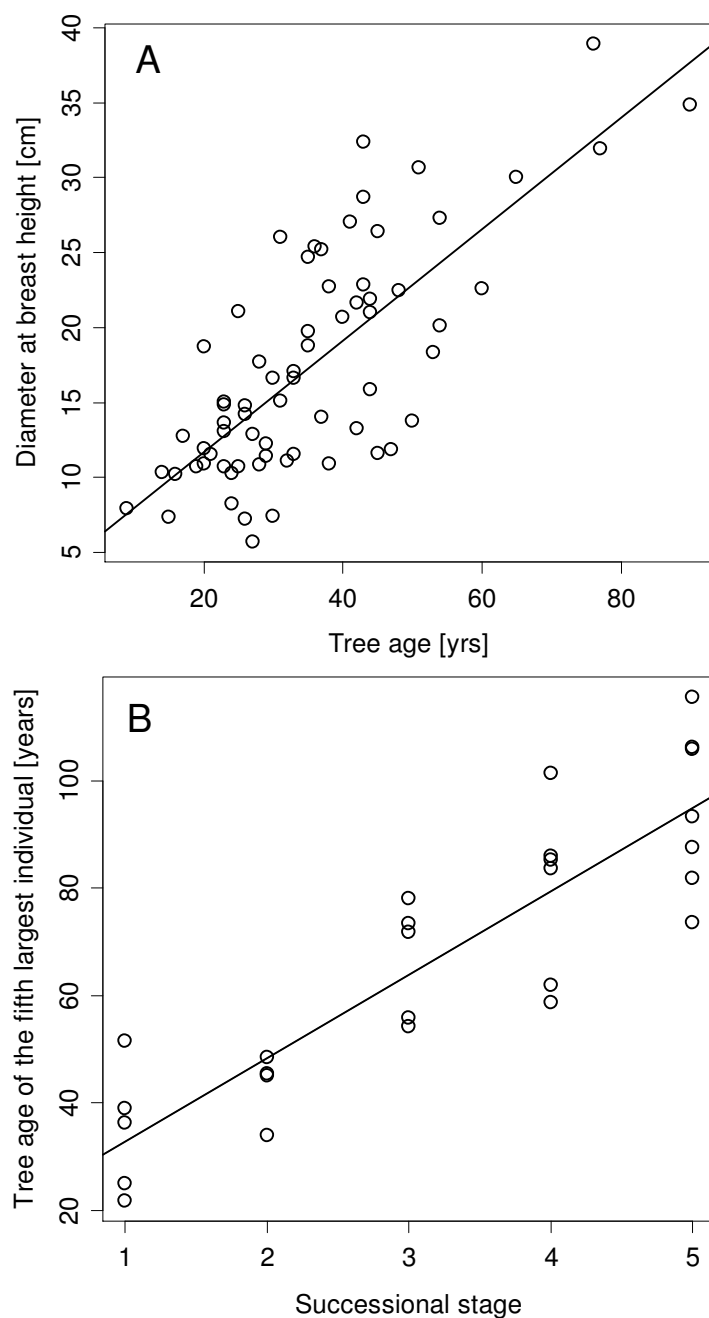


Fig. 2: Definition of plot age classes. (A) Diameter at breast height (dbh) as a function of tree age, across all comparative study plots (CSPs) and all species. The solid line shows the significant linear regression: $dbh = 4.252 + 0.371 * age$; $r = 0.753$, $P < 0.001$. (B) Age of the fifth-largest individual tree in the plot as a function of successional stage (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, ≥ 80 yr). The solid line shows the significant linear regression: $age = 17.39 - 15.52 * successional\ stage$, $r = 0.880$, $P < 0.001$.

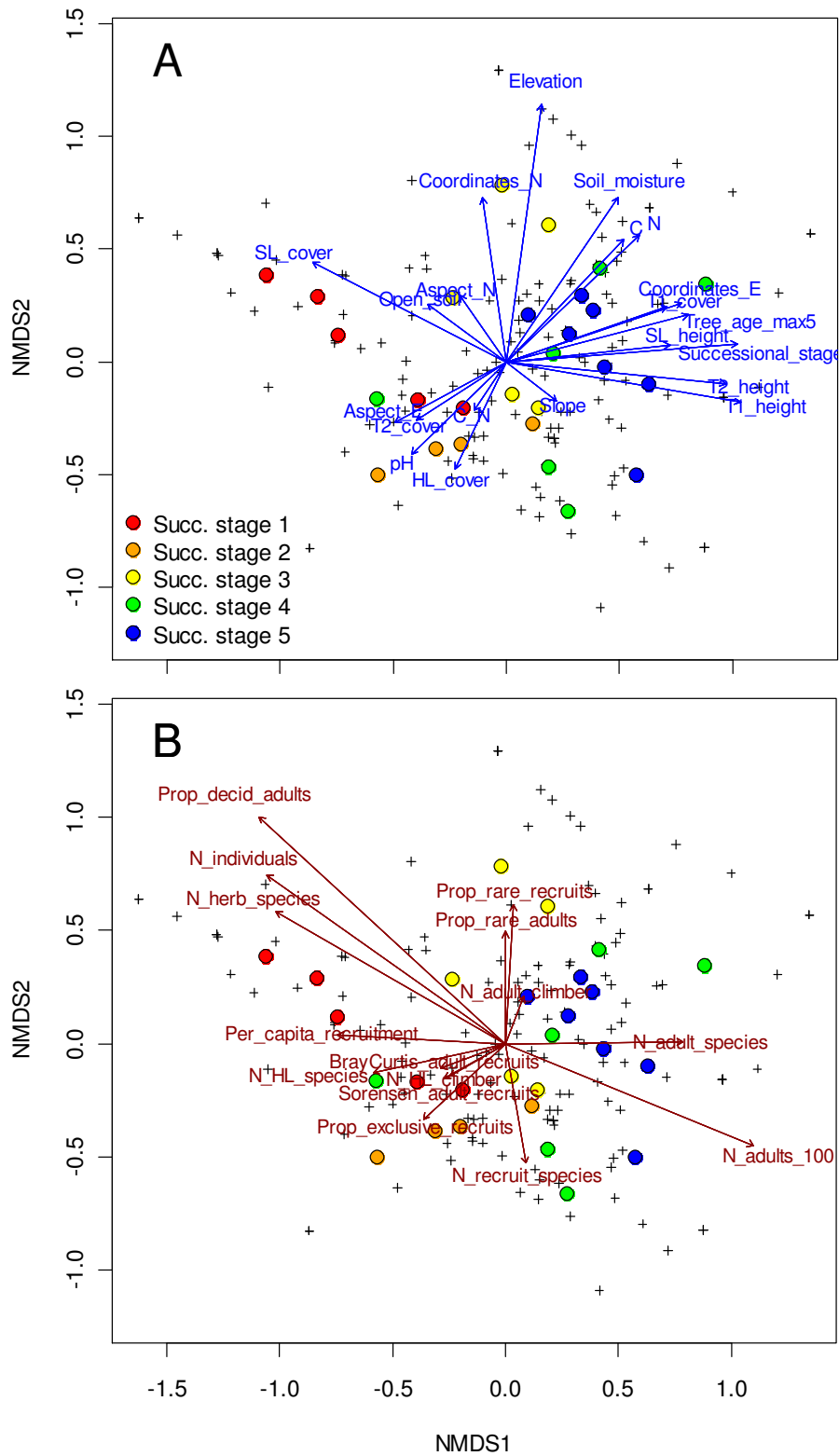


Fig. 3: Nonmetric multidimensional scaling (NMDS) ordination of abundance of all adult tree and shrub species with at least one individual > 1 m in height ($n = 148$, black “plus” [+] symbols) in the Comparative Study Plots (CSP, $n = 27$); colored circles indicate the different successional stages. In various runs, a stable solution was found, on average, after four random starts (stress= 15.86). (A) Post hoc correlation of variables describing plot characteristics and structure. (B) Post hoc correlation of variables describing species diversity of the different strata and life forms. See the Methods section; see also Table 1 for abbreviations and significance of correlations.

The CSPs were evenly scattered and without obvious outliers in the NMDS ordination (Fig. 3). The same applied to the species. The DCA revealed a length of 3.56 standard deviation units for axis 1, showing a significant turnover of species, and thus a comparably high α diversity among CSPs. The NMDS centroids of the successional stages 1, 2, 3, 4 and 5 on axis 1 were -0.65 , -0.24 , 0.02 , 0.23 and 0.39 , respectively, thus showing decreasing differences between successive stages with increasing stand age.

Post-hoc correlation of NMDS scores with variables describing abiotic plot characteristics and stand structure (Fig. 3A) and with diversity variables of the different strata and life forms (Fig. 3B) allowed an interpretation of the encountered gradients (Table 1). NMDS axis 1 was significantly positively correlated with successional stage: plots of early successional stages are located on the left hand and plots of late successional age on the right hand in Fig. 3A. Along with increasing successional age, structural variables such as height of the tree and shrub layers increased from the left to the right in Fig. 3A, while shrub layer cover, number of herbaceous species and number of individuals of adult trees and shrubs (> 1 m height) decreased (Fig. 3B). The structural variables also showed significant univariate correlations with successional stage (Table 2). For example, density of individuals decreased with successional stage ($r = -0.772$), with a maximum and minimum density of 1233 and 207 individuals per 30 x 30 m plot, respectively. Using the age of the fifth largest tree in the plot gave essentially the same significant or non-significant relationships for all tested variables (Table 2).

The proportion of deciduous species in the group of adult shrubs and trees decreased significantly with successional stage, both in the multivariate permutation test (Table 1) and in the univariate regression (Table 2). On average, youngest stands (< 20 yrs) had a degree of deciduousness of 44 % and 39 % in terms of number of species and individuals, respectively, while the proportion for oldest stands (≥ 80 yrs) were 26 % and 8 %, respectively.

The NMDS ordination in Fig. 2 shows that adult species richness increased with successional stage, although this relationship was not significant according to the permutation test (Table 1) and in the univariate regression (Table 2). Adult species richness became significant once corrected for the different number of individuals per 30 x 30 m plot by rarefaction to 100 individuals per plot (Fig. 4, Table 1, 2).

The explanatory variable “successional stage”, according to which the plots had been chosen, was also among those four predictor variables that were finally retained in the optimized multiple regression model to explain species richness of adult shrubs and trees in the CSPs (Table 3). The results of this model were the same, irrespective of whether adult species richness per 30 x 30 m plot area (Table 3) or per 100 individuals (data not shown) was used as dependent variable. The three other predictor variables were height, cover of the lower tree layer (T2) and amount of bare ground. Further environmental variables had little influence on adult species richness. For example, neither aspect (eastness and northness) nor slope had significant effects on tree and shrub species composition (Table 1). Elevation was significantly positively correlated with NMDS axis 2 (Fig. 3A, Table 1), but was neither related to adult species richness ($r = 0.024$, $p = 0.906$) nor to successional stage (Table 2).

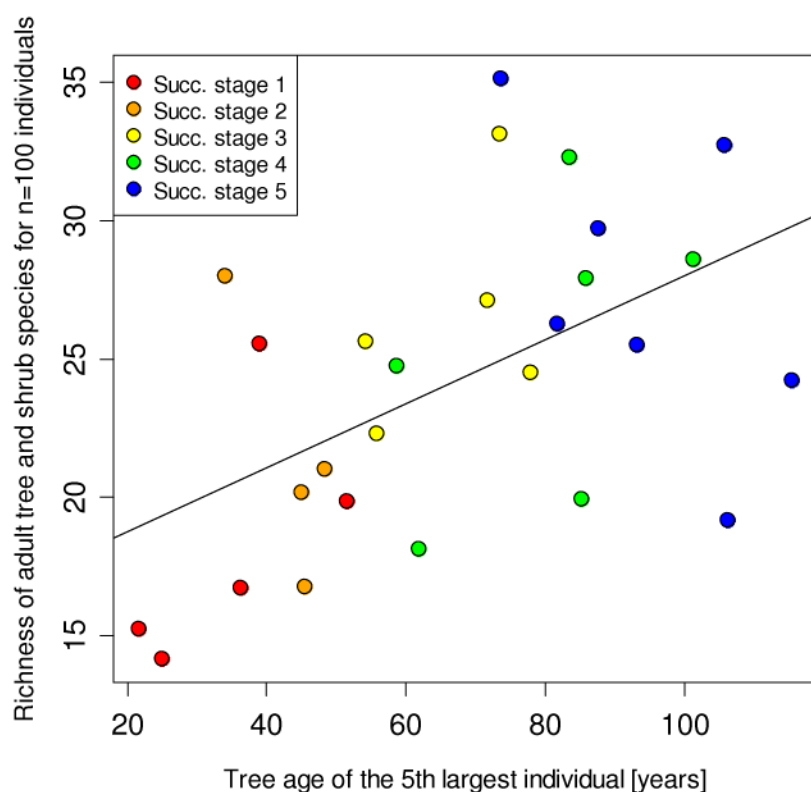


Fig. 4: Species richness based on 100 individuals (rarefaction) of adult trees and shrubs (> 1 m height) as a function of successional stage (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: □ 80 yrs). . The solid line shows the significant linear regression: $r = 0.558$, $p = 0.003$.

Table 2: Results of univariate relationships of different response variables to successional stage (columns on the left) or to the age of the fifth largest tree in a plot (columns on the right). Adult trees and shrubs refer to individuals of > 1 m height, woody recruits to seedlings ≤ 1 m height.

Response variables	Successional stage (stage 1 to 5)			Age of the 5th but largest tree [yrs]		
	Slope	Correlation coefficient r	P	Slope	Correlation coefficient r	P
Density of adult trees and shrubs (number per 30 x 30 m)	-151.770	-0.772	<0.001	-7.705	-0.692	<0.001
Proportion of deciduous species in the group of adult shrubs and trees	-0.044	-0.514	0.006	-0.002	-0.506	0.007
Proportion of deciduous individuals in the group of adult shrubs and trees	-0.077	-0.556	0.003	-0.004	-0.552	0.003
Species richness of adult trees and shrubs per 30 x 30 m	1.978	0.282	0.154	0.097	0.311	0.222
Species richness of adult trees and shrubs per 100 individuals	2.167	0.558	0.003	0.116	0.524	0.005
Elevation [m]	33.150	0.085	0.140	1.502	0.233	0.242
Proportion of rare species among adult trees and shrubs, rarity threshold 50%	-0.005	-0.078	0.698	0.001	-0.234	0.239
Proportion of rare species among woody recruits, rarity threshold 50%	0.007	0.138	0.492	0.000	0.081	0.688
Proportion of rare species among adult trees and shrubs, rarity threshold 25%	0.000	-0.004	0.984	0.000	-0.110	0.586
Proportion of rare species among woody recruits, rarity threshold 25%	0.004	0.143	0.477	0.000	-0.053	0.794
Species richness of woody recruits	-0.143	-0.035	0.860	0.007	0.030	0.883
Similarity between species composition of adults and recruits based on counts of individuals and the Bray-Curtis index	-0.006	-0.078	0.701	0.000	-0.018	0.930
Similarity between species composition of adults and recruits based on presence/absence and the Sørensen index	-0.011	-0.219	0.272	0.000	-0.042	0.834
Number of recruit species new to a plot	-0.231	-0.080	0.692	-0.018	-0.112	0.578
Proportion of recruit species new to a plot	-0.007	-0.085	0.675	-0.001	-0.129	0.522

Table 3: Results of multiple regressions of species richness of adult trees and shrubs (> 1 m height, not corrected for density of individuals) on predictor variables describing plot characteristics and structure in the comparative study plots (CSPs). For the full list of variables and abbreviations see Table 1A. All variables were z transformed prior to analysis. Model selection was performed with backward selection eliminating independent variables according to their F statistics, until P was < 0.05 for all variables. P gives the probability values for the parameter estimates. Partial r^2 is the partial variance explained using Type II sums of squares. The whole model had $df = 4$ with $df = 23$ for the error term, $F = 5.27$, $P = 0.0037$, $r^2 = 0.478$, adjusted $r^2 = 0.388$.

Variable	df	Parameter estimate	SE	t	P	Partial r^2
Successional_stage	1	0.701	0.334	2.10	0.047	0.161
T2_height	1	0.520	0.205	2.54	0.018	0.219
T2_cover	1	0.979	0.328	2.98	0.007	0.279
Open_soil	1	0.739	0.257	2.88	0.009	0.265

The proportion of rare species both among adults (Fig. 5A) and among recruits (Fig. 5B) was not related to the successional stage. The pattern was essentially the same when other thresholds of rarity were chosen (e.g. 25% of the least abundant species, Table 2). The regression line of the relationship between number of adult species and number of recruit species closely matched the 1:1 line, indicating a constant recruitment rate across all levels of abundance of adults (Fig. 6A). With the exception of twelve species, all were included in the confidence intervals of \pm two standard deviations. Among these twelve species, eight were not found among the adults but occurred as seedlings in high amounts (*Evodia fargesii*, *Lithocarpus harlandii*, *Choerospondias axillaris*, *Ardisia punctata*, *Pertusadina hainanensis*, *Cyclocarya paliurus*, *Manglietia yuyuanensis* and *Sapindus mukorossi*), only two species occurred each with two (*Lespedeza formosa* and *Tarenna molissima*), one species with three (*Wikstroemia monnula*) and one species with four (*Glochidion puberum*) adult individuals. With a few exceptions, all species showed the tendency to have recruits in the same successional stages in which the adults were more abundant (Fig. 6B). Species with a preferential occurrence of adults in early successional plots (marked in red in Fig. 6B) also had a higher proportion of recruits in these plots. Conversely, late successional adult species (marked in blue in Fig. 6B) also had a higher proportion of recruits in these late successional stages. There were only nine outliers, i.e. species of which the preferred occurrence of recruits according to successional stage diverged from that of adults. This allows, for example, to identify long-lived pioneers, i.e. species with a preferred recruitment in the early successional stages but a preferential occurrence of adults in late successional stages (*Toxicodendron sylvestri*, *Litsea elongata*).

The plot averages of per capita recruitment rates of all adult species in a plot were not correlated with the proportion of rare species in a plot (Fig. 7). Per capita recruitment rates were also not related to successional stage, which was revealed by a mixed model based on the species-specific per capita recruitment rates in each plot and using species as random factor ($y = -0.131x + 10.492$, $t = -0.17$, $df = 294$, $p = 0.864$). Averaged over all plots for each successional stage, the per capita recruitment rates were 7.5, 15.4, 4.2, 8.1 and 8.5 recruits per adult for the successional stages 1, 2, 3, 4 and 5, respectively. The arithmetic mean per capita recruitment rate over all plots was 22.9 recruits per adult. In accordance with per capita recruitment rates, species richness of recruits was also not related to successional stage (Table 2).

Similarity between species composition of adults and recruits was low, with on average 0.382 and 0.556 for the Bray-Curtis and Sørensen index, respectively. In total, the 148 adult tree and shrub species (at least one individual > 1 m) and the 136 recruit species (≤ 1 m) only had 109 species in common. In contrast to expectations, neither similarity based on counts of individuals (Fig. 8), nor on presence/absence (Table 2) showed a significant relationship to successional stage. However, the proportion of recruit species new to a plot (i.e. woody species with no individual > 1 m in the corresponding plot) decreased with adult species richness per 30 x 30 m (Fig. 9), but showed no relationship to successional stage (Table 2).

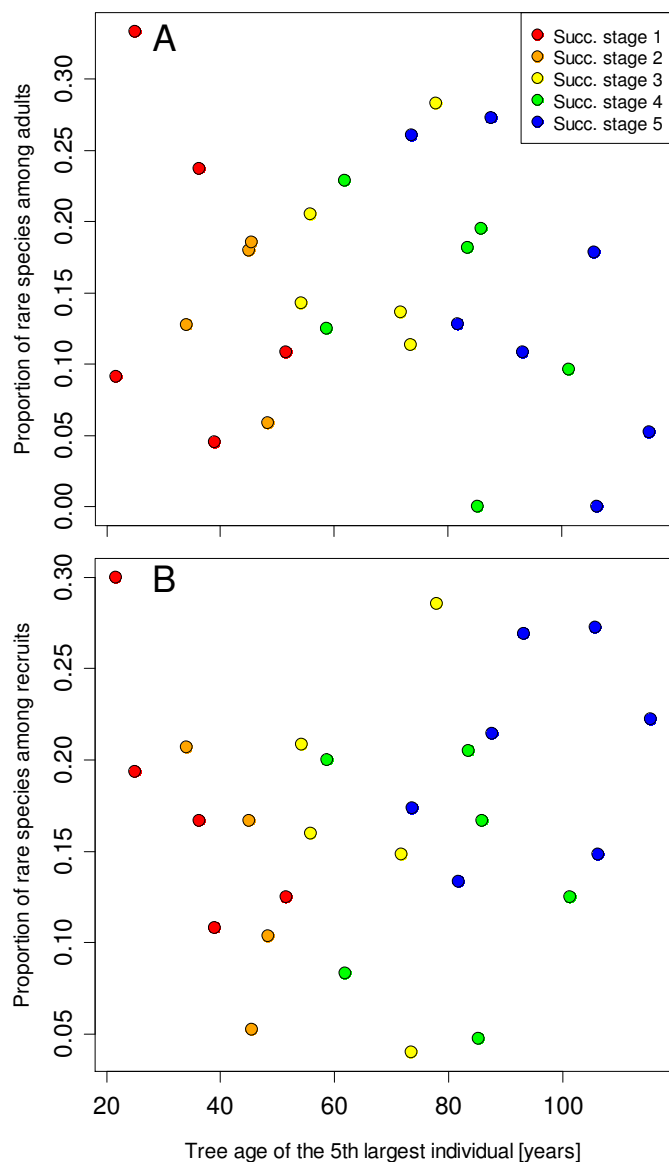


Fig. 5: Proportion of rare species calculated as the ratio of the number of rare species to the number of all species per plot as a function of the age of the fifth-largest tree in the plot. The different colors show the successional stages (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, \geq 80 yr). (A) Proportion of rare species among adult trees and shrubs (> 1 m in height): $r = -0.078$, $P = 0.689$. (B) Proportion of rare species among recruits (seedlings \leq 1 m in height): $r = 0.158$, $P = 0.430$.

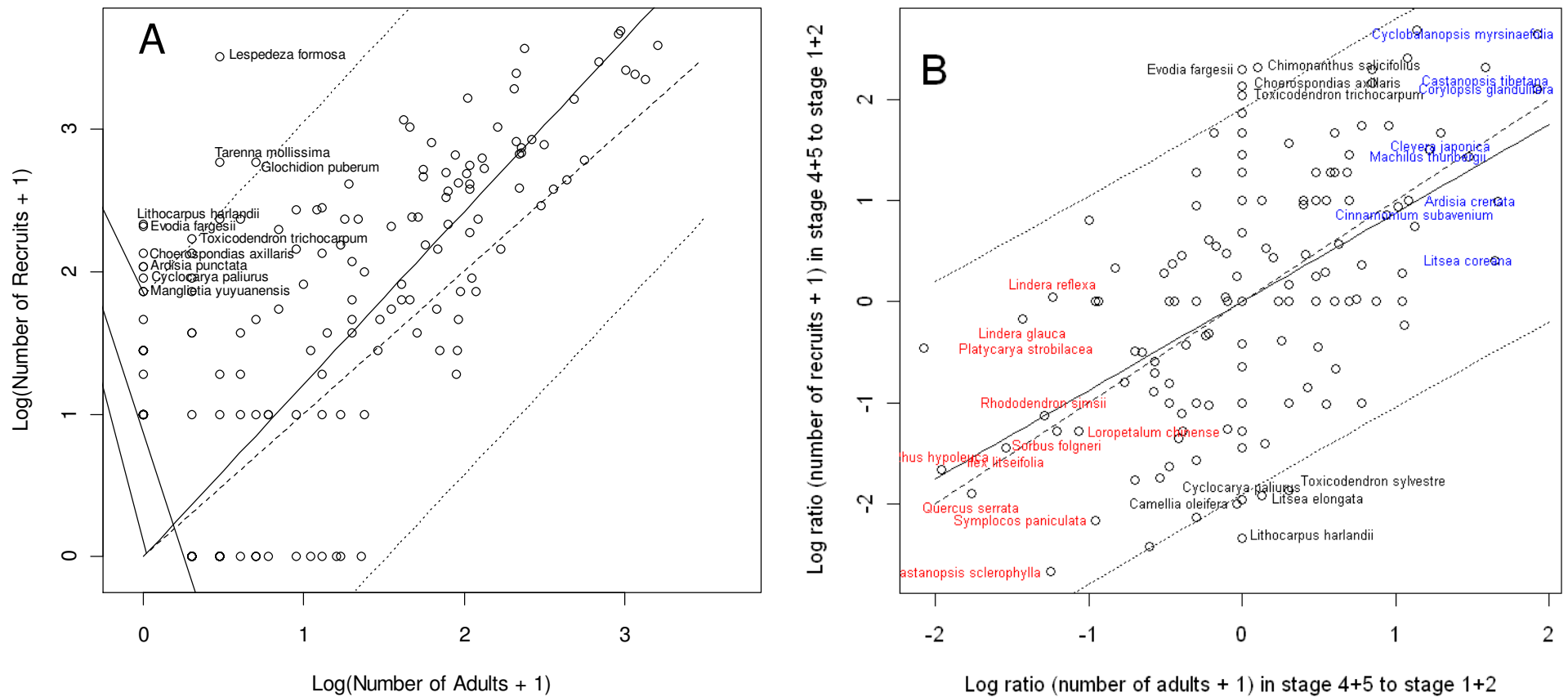


Fig. 6: (A) Number of recruits as a function of number of adults for the 175 species that occur in any of the plots as adult or recruit. Both variables were $\log_{10}(x + 1)$ -transformed. The solid regression line gives the linear regression through the origin: $y = 1.211x$, $r^2 = 0.776$, $df = 174$, $P < 0.0001$. The dashed line shows a line with slope = 1 for comparison, assuming that the per capita recruitment rate = 1 for all species. Confidence intervals are shown as dotted lines and were plotted based on a tolerance of ± 2 SD. (B) Log ratios of number of individuals in late-successional stages (4 and 5) to their number in early-successional stages (1 and 2), with log ratio of recruits regressed against log ratio of adults. Confidence intervals are shown as dotted lines and were plotted based on a tolerance of ± 2 SD. Species in the bottom left corner (some of them marked in red) are those where both adults and recruits prefer young successional stages. Species in the top right corner (some of them marked in blue) are those in which both adults and recruits prefer old successional stages. Species names in black type are outliers, with recruits concentrated in other successional stages than adult individuals (see Results).

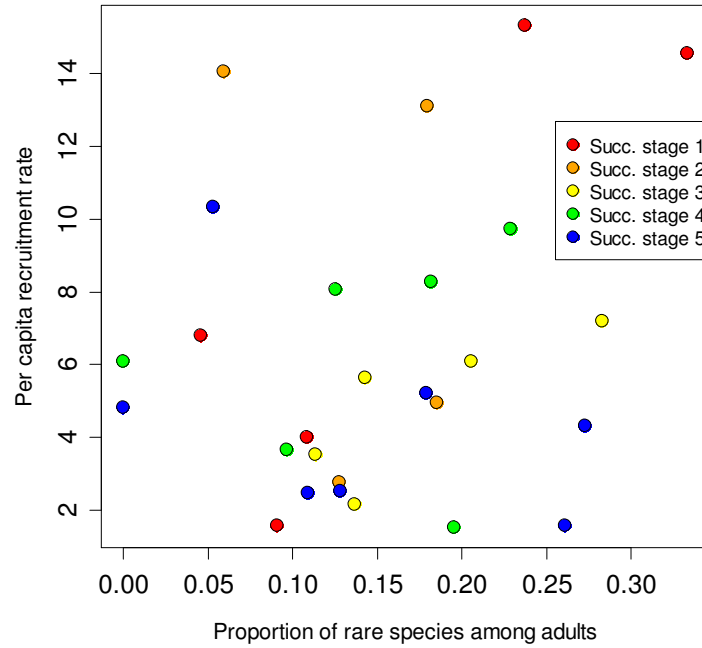


Fig. 7: Per capita recruitment rate per plot (calculated as the average of the per capita recruitment rates of each species present as adults in a plot), as a function of the proportion of rare species in a plot (calculated as the ratio of number of rare species to number of all species per plot): $r = 0.211$, $P = 0.291$. The different colors show the successional stages (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, ≥ 80 yr).

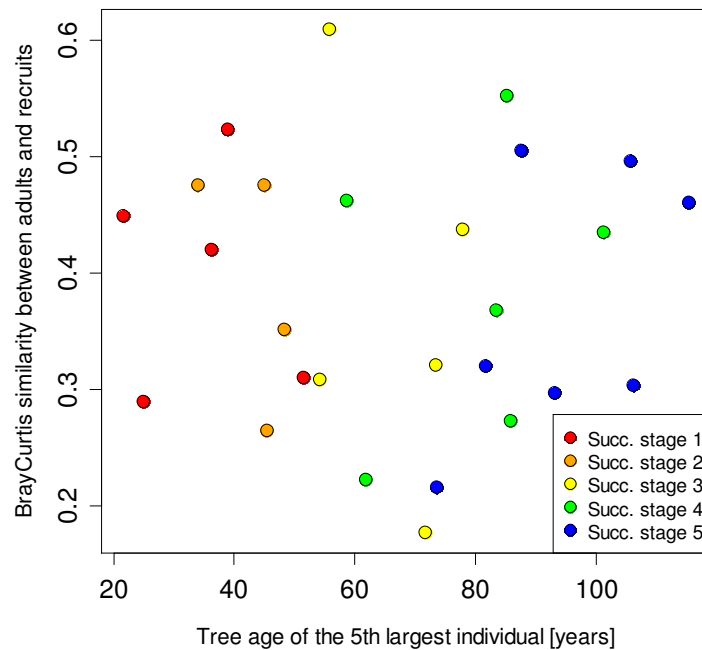


Fig. 8: Similarity between species composition of adults and recruits based on counts of individuals and the Bray-Curtis index as a function of the age of the fifth-largest tree in the plot. The different colors show the successional stages (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, ≥ 80 yr): $r = -0.078$, $P = 0.701$.

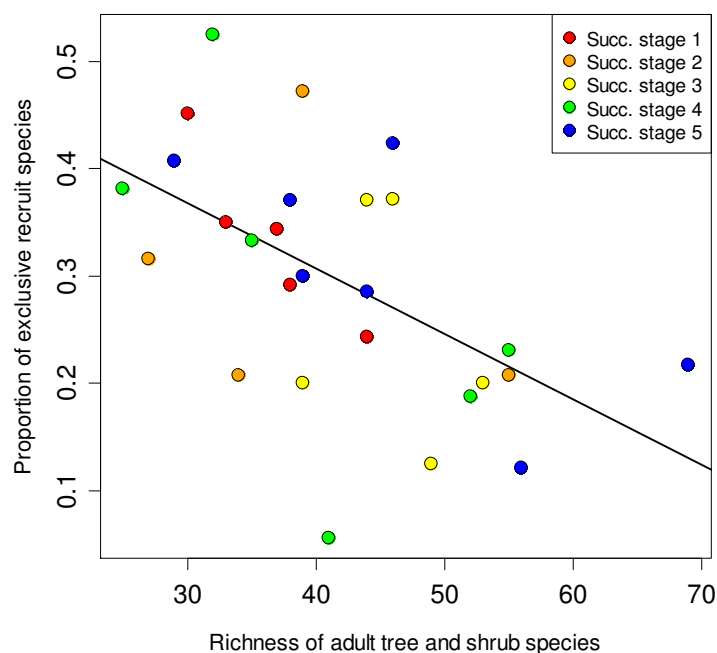


Fig. 9: Proportion of recruit species new to a plot (no individual > 1 m height, i.e., exclusive recruit species) as a function of species richness of adults of trees and shrubs (> 1 m height): $r = -0.549$, $P = 0.003$. The different colors show the successional stages (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, ≥ 80 yr).

Discussion

Species richness increases along the successional gradient

The vegetation analysis revealed a clear successional gradient and, if corrected for a decreasing density of individuals, an increase in species richness with time as postulated in the first hypothesis. The species turnover along the successional gradient was lower than reported in previous succession studies from temperate or tropical forests with a reported β -diversity along the first DCA axis of about 5.0 (Hermý 1988, Terborgh et al. 1996). In their study of comparable forests in Zhejiang Province, Li et al. (1999) hypothesized that species composition in subtropical forests in China is primarily driven by ‘initial floristic composition’ (Egler 1954). Our results support the view that many woody species arrived early in succession. Similarly, the finding that there were only very few species specific to any particular successional stage lends support to the prevalence of ‘initial floristic composition’. This is in contrast to the general pattern of secondary succession in the wet tropics and subtropics, which is often perceived as following the concept of ‘relay floristics’

(sensu Egler 1954; Finegan 1996, Guariguata and Ostertag 2001, Wang et al. 2006, Chazdon 2008). According to this concept, a first stage is usually dominated by herbs, shrubs and climbers, a second stage by short-lived pioneer trees; these are replaced in a third stage by long-lived pioneers. Owing to a simultaneous continuous enrichment of shade-tolerant late-successional species, sometimes a fourth stage occurs. There are several potential reasons why the successional stages in Gutianshan were only poorly differentiated in terms of presence or absence of particular tree and shrub species. On the one hand, we might have missed the full gradient as we deliberately excluded the early herbaceous stages directly after a clear cut. The forests may also grow much older than the oldest ones we observed at Gutianshan. On the other hand, resprouting from cut trees and shrubs might have contributed to the presence of some woody species right from the beginning of the succession (Li et al. 1999), thus rendering the initial stages similar to the older ones.

However, despite the lack of floristically distinct successional stages, the tree and shrub species in Gutianshan have not become established at once at the beginning of the succession, thus precluding a strict interpretation of the initial floristics hypothesis (Anderson 2007). In contrast to our first hypothesis, the number of species per plot did not decrease with successional stage. Rather, adult tree and shrub species richness, when expressed as number of species per 100 individuals, increased with successional stage as species accumulated with time, corresponding to the succession schemes described from the wet tropics (Finegan 1996, Kammesheidt 1998). Similar trends have been reported by Wang et al. (2007) for broad-leaved evergreen forests in Zhejiang varying in stand age from > 20 yrs, >43 yrs, > 63 yrs to \geq 63 years. With proceeding stand age, they found an increase in richness of woody species in the shrub layer from 20 species to 38 species per 400 m² (not corrected for density of individuals). The net accumulation of species over the first 80 years of secondary succession in Gutianshan is very similar to values described from Colombia and Venezuela (Saldarriaga et al. 1996). Species number recorded on the same plot size as in our study (900 m²) increased from on average 45 tree species (> 1 cm dbh) after 12 years since start of succession to 71 species after 80 years. Similar values have also been reported from neotropical secondary forests (Guariguata and Ostertag 2001) or from Japan (Aiba et al. 2001). The absence of a peak in species richness at mid-successional stages, as reported from the Western Great Lakes area (Auclair and Goff 1971) may be due to the shorter time span of the successional gradient (the oldest stands at Gutianshan were not older than 180 yrs), which is a typical feature of

Chinese subtropical forests (e.g. Wang et al. 2006).

The increase of species richness with successional age could not be explained by the measured site characteristics. Neither soil pH nor topographical variables such as aspect and slope were related to species richness or composition of adult woody species. On the one hand, this confirms the validity of our chronosequence approach because differences in site conditions were not covarying with successional stage. On the other hand, the low level of site heterogeneity encountered for all measured variables except for elevation suggests that the sampled forests have not been predominantly shaped by abiotic conditions but by biotic processes. This finding is in contrast to single-species habitat models developed for a subtropical permanent forest plot in Dinghushan (Guangdong Province, China), where the majority of species showed a significant dependence on slope, aspect, elevation and convexity (Wang et al. 2009). However, data from a single plot may possibly show such effects due to spatial auto-correlation. Using data from a single 24 ha plot in Gutianshan and accounting for auto-correlation, Legendre et al. (2009) found the contribution of spatially-independent habitat effects to be less than 5% both for explaining species richness and β -diversity. They identified only eight species out of a total of 159 species with a statistically significant indicator value for one of five distinguished habitat types (valley, mid-altitude ridges, highly convex plots, and less convex mid- and high-altitude plots). In the present study, we could neither predict species occurrences from site characteristics, nor was there a strong association between species and successional stages as revealed by our fidelity analysis where only three out of 148 species were significantly concentrated in a particular successional stage. All these results indicate that species assembly processes at the plot level were largely random. This view is also supported by other studies from Asian subtropical broad-leaved forests, which revealed a similar “habitat generality” of most species (Aiba et al. 2001, Wang et al. 2007).

Rare species do not accumulate

Our second hypothesis of increasing proportion of rare species with successional stage was not supported. Richness of rare species amongst both adults and recruits was independent of the successional stage. Thus, the increasing species richness with successional stage could

not have been caused by preferential survival of rare species, thus contradicting findings from some tropical forests (Wills et al. 2006). The ratio between the density of adults and those of recruits remained remarkably constant with the exception of only nine species, of which adult trees were either absent from our plots or had a very low stem density. However, rareness defined as abundance of stems in plots only captures one aspect of rarity. In Rabinowitz's (1981) system of classifying rare plants, the size of the geographical range and habitat-specificity are alternative ways in which a plant can be rare. It is conceivable that the majority of woody species in our plots might be locally rare but not according to geographical range and habitat-specificity, as was shown by Pitman et al. (1999) for a network of 21 forest plots in the Manu National Park (Peru). They found that most of the Amazonian forest tree species are habitat generalists, have a wide range in the South American lowlands and attain large (i.e. > 1.5 individuals ha^{-1}) population sizes at least in some localities, although their average density over the whole study area might be very low (i.e. < 1 individuals ha^{-1}). Although such an analysis is still missing for Chinese subtropical forests, it seems that only a few tree species are local endemics, such as *Lithocarpus glaber* and *Machilus thunbergii* (Song 1988).

Random immigration leads to increasing species richness

Our third hypothesis that the increasing species richness in the course of succession was caused by continuous immigration was supported by the results. There was a constant number of recruit species and also of exclusive recruit species, i.e. those that had not been present as adult individuals in a plot, across all successional stages. This pattern of constant arrival of new recruit species in the plot does not support the view that a large portion of species in the early successional stages (i.e. < 40 yrs) originates from resprouting (Li et al. 1999, Wang et al. 2007). The constant immigration of recruit species into the plots in the course of succession and the concomitant maintenance of dissimilarity in species composition between established adults and recruits suggest effective seed dispersal into the plot from the neighborhood. The recruits did not predominantly originate from individuals growing inside the plot but to a considerable degree arrived from the outside. This implies that recruitment limitation, defined as the failure of a species to regenerate in all sites favorable for its growth and survival (Hubbell et al. 1999), occurred in both young and old successional stages, but decreased in the course of succession. The negative relationship between richness of adult

woody species and the proportion of exclusive recruits indicates that the regional species pool, i.e. γ diversity of tree and shrub species is more and more approached with increasing α diversity. This points to the importance of the regional species pool for preserving such species-rich subtropical forests. With a given species pool, local richness will continuously increase, even when parts of the forest are affected by occasional disturbance. Such a gradual approximation of species richness to saturation is a pattern often observed in secondary succession (Tilman 2004). Accordingly, the percent community turnover rate decreased with successional time, both visible in percent community turnover rates based on presence/absence as well as in decreasing centroid differences between successional stages along the first NMDS axis based on species abundances. This result extends the general tendency of decelerating rates of community change with time, as described by Anderson (2007) based on presence/absence data, to datasets based on abundance. Our findings are also consistent with Hubbell's (2001) neutral theory. The virtual absence of specialist species for certain successional stages would provide some support to the community drift model (Hubbell et al. 1986), although our floristic gradient in the course of succession precludes a fully random walk in community composition across all taxa of trees and shrubs. An exclusive random drift would also contradict the observed dominance patterns of tree species, which seem to be remarkably similar across different regions in Southeast China. Thus, there might be yet unknown species-specific differences in immigration and establishment rates, which would contradict a fully neutral model. Irrespective of absence or presence of species-specific differences we would assume that local species richness would ultimately converge towards the regional species richness, or more precisely, towards the number of species drawn randomly from the regional species pool according to the density of individuals. However, in Chinese subtropical forests high degrees of convergence between local and regional species richness may rarely occur before a new disturbance event restarts the secondary succession at a local site.



Plate 1: Chinese mixed broad-leaved forest in the Gutianshan Nature Reserve, near Hong Yuan, Zhejiang Province (CSP21). This stand is a “feng shui” forest with an estimated age of the fifth-largest tree of 106 yr (age class 5). Photo credit: H. Bruelheide.

Conclusions

Local species richness and species composition in this Chinese subtropical forest appears to be mainly caused by unspecific immigration, with fairly constant immigration rates in the course of succession. This is consistent with results obtained from tropical permanent plots (Hubbell et al. 1999). In contrast, our current data neither support the concept of species being characteristic of certain successional stages or environmental conditions, nor the idea of differential survival of rare species. These results have important implications for the design of experimental communities, as those that have been recently established in the biodiversity–ecosystem functioning experiment nearby (see Fig. 1C). An important lesson learned from our comparative study is the awareness that stands of young demographic age are not entirely different from old ones with respect to species composition, richness and other features. This means that young experimentally established stands might yield results that can be transferred to the conditions found along natural successional gradients. Furthermore, our results suggest

that it is not important to select tree species for the design of experimental communities based on rarity or environmental requirements. One of the criticisms of past biodiversity experiments focused on the use of randomly drawn species combinations out of a constant species pool to establish a gradient of species richness (Leps 2004). Instead, it was advocated to use extinction scenarios based on rarity of species (Grime 2002). However, with our current knowledge, at least for subtropical forest ecosystems as the ones studied here, it seems to be the best strategy to assemble communities randomly from the regional species pool.

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Manuscript 2

A new splash cup to measure the kinetic energy of rainfall

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Abstract

Splash cups have long been successfully used for both the quantification of kinetic energy of rainfall and the detachability of soil particles by rainfall impact, the so-called “splash erosion”. Measurements of kinetic energy, however, have been difficult to operate in the field especially in remote areas, on steep slopes and in forests since boundary conditions need to be controlled precisely. This paper introduces a new splash cup based on Ellison’s archetype that reliably and accurately measures kinetic energy as a function of sand loss under a large variety of conditions. The Tübingen splash cup is relatively easy to operate under

harsh field conditions and it can be used in experimental designs with a large number of plots and replications at reasonably low costs. The cup is constructed from PE laboratory flasks and plastic pipes from water supply equipments. The unit sand is held by a removable carrier system that can easily be replaced in the field. The splash cups have been calibrated in combination with a laser disdrometer using a linear regression function with $r^2 = 0.98$. They measure kinetic energy over a wide range of rainfall intensities from 0.6 to 40 $\text{l}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. Kinetic energy per area varies between 10 and 250 $\text{J}\cdot\text{m}^{-2}$. Two years of field test measurements in a subtropical forest ecosystem in China proved the reliability, durability and usability of our new splash cups and allowed detecting differences in kinetic energy between different tree species and biodiversity levels.

Keywords: Splash cups; kinetic energy; soil erosion; subtropical forests; China; biodiversity.

Introduction

In soil erosion studies, most measuring systems like rainfall simulators or sediment traps collect and measure the eroded soil material. This implies that (a) all and (b) only eroded particles reach the measuring device, which is often a challenging task and leads to significant errors (e.g. Stroosnijder, 2005). The splash cup technique measures the soil or unit sand lost by comparison of a given amount of material prior to the erosive event and the remaining material thereafter. Splash cups have successfully been used throughout the last decades since Ellison (1947) presented the first prototype to conduct research on the detachment of soil particles by raindrops. Since then modifications have been presented following two lines of research: (a) measurements on the detachment of soil particles from a given cup and (b) measurements on soil particles collected in a given cup that have been detached from natural ground. Ellison originally used soils with different textures to assess the detachability of soil material in relation to standard sand. Since then, most splash cups were designed to measure the amount of soil splashed from the soil surface to a target (Morgan, 1978; Salles and Poesen, 2000; van Dijk et al., 2003; Legout et al., 2005). However, these methods are not

appropriate for estimating differences in kinetic energy of rainfall or throughfall as the results are confounded by the erodibility of the soil. Further, measurements of particle detachment with splash cups face some technical requirements that are similar to rainfall simulation, especially concerning the steadiness of boundary conditions and the need to guarantee that all detached particles leave the measuring unit. Three main aspects of measuring errors can be named, (a) the rim-effect, (b) the size effect and (c) the wash-off effect.

(a) When the sand surface is lowered it becomes harder for the remaining sand to be splashed out. This results in a non-linear decrease of sand loss with increasing rainfall amount. This rim effect was first mentioned by Bisal (1950). He tried to establish a correction function for a lowering of the sand surface when using Ellison splash cups being 8.89 cm in diameter. If splash cups are used to collect soil material from the surroundings, larger sized cups > 10 cm in diameter minimize the impact of the rim-effect (Poesen and Torri, 1988).

(b) The size effect is based on the relation of velocity, frequency and angle of raindrop impact to particle size and other particle characteristics like aggregation (Erpul et al. 2005, Leguédouis et al., 2005). For single grain sand at given moisture content the average splash length is a function of particle size. Especially when using small-sized cups the rim effect should be taken into account and bigger sized cups are supposed to better reflect the mean erosivity per unit area (Poesen and Torri, 1988; van Dijk et al., 2003).

(c) The wash-off effect describes ponding of water on the surface of a splash cup followed by loss of material due to surface runoff. This was investigated by Kinnell (1974, 1982) who used modified splash cups (K-cups) for relating rainfall properties to the loss of sand from splash cups. The main objectives were to measure the amount of sand which is supposed to be washed off the cup during the initial stage of the rainfall event and to relate the loss of sand to the properties of the raindrops. In order to collect the material supposed to be washed off, a second circular rim was added to the splash cup. Kinnell (1974) concluded that, when using Ellison Cups, the wash-off effect affects the results by causing greater inaccuracy.

Further applications of splash cups concentrate on the role of vegetation cover to prevent soil erosion. Mosley (1982) placed Ellison type splash cups filled with standard sand (1000-2000 μm) in a New Zealand beech forest. He found a notably higher mean amount of sand loss from splash cups (factor 3.1) under forest compared to the open field. For studying the effects of different vegetation layers on surface erosion Wiersum (1983) used splash cups with a diameter of 8.5 cm filled with standard sand (250-500 μm). Measurements in the open

field showed very good relations to total rainfall amount and kinetic energy. Kinetic energy under a plantation of *Acacia auriculiformis* exceeds that of open rainfall by 57 percent. In a similar study in a Colombian rainforest, Vis (1986) obtained comparable results using calibrated splash cups. Unlike Mosley (1982) and Wiersum (1983), Vis measured the standard sand (300-850 μm) splashed out of the cups and demonstrated that the kinetic energy per area under forest is between 20 and 70 % higher than in the open field. These findings were supported by Geißler et al. (2010a) for subtropical forest ecosystems in Central China. Moreover, Geißler et al. (2010b) reported significant differences in sand loss from splash cups between deciduous and evergreen tree species.

Morgan (1978) used splash cups as receiving devices for studying the effect of slope on splash erosion from soil. Contrary to Kinnell (1974), his 10 cm wide field splash cups have catching trays which are separated in upslope and downslope compartments. Nevertheless, an effect of slope could not be detected.

Beside water erosion studies, splash cups have been calibrated and used successfully to study wind erosion (Cornelis et al., 2004; Erpul et al. 2005) where constant erodibility is necessary. It could be shown that strong wind may have a considerable effect on erosion rates and that splash cups are an appropriate tool for measuring these interrelationships.

To ensure that our Tübingen splash cups meet the requirements to minimize the rim, size and wash-off effects and to be applicable to ecosystem research worldwide, the objective was to develop a splash cup that (a) measures sand loss as a function of kinetic energy and, thus, can be calibrated, (b) has a constant soil moisture over a reasonable period of time, (c) keeps soil moisture actively constant under natural rainfall and under evaporation conditions, (d) is sensitive to very low rainfall intensities, and (e) has acceptable uniformity over a wide range of rainfall intensities and durations. Furthermore, the splash cups must be easy to transport and to install under any kind of frost-free field conditions, maintenance-free during measurements, durable under harsh climatic conditions, as well as inexpensive and fast to install and collect in order to allow for a large number of measurements at a time.

Material and Methods

Design and construction

The Tübingen splash cups were developed based on the archetype of Ellison (1947). In contrast to previous studies with splash cups (Vis 1986) or other types of splash cups (Kinnell 1974; Morgan 1981) we measured the unit sand remaining inside the cup after single natural rainfall events. The new splash cups consist of a PE flask to which a carrier system has been attached (Fig. 1). In this carrier system a cup filled with a unit sand of 125-200 μm particle size is inserted. At the bottom of the cup a silk cover prevents loss of sand and guarantees free drainage of water from the cup to the carrier and vice versa. Cup and PE flask are hydraulically connected by a cotton wick (Fig. 2, upper left) to ensure constant moisture content throughout the time of measuring. If the sand-filled cup is inserted, the bottom stays in contact with the cotton wool and the wick for the whole time of measuring. Cotton wool and wick are separated from the rest of the system by an upper and a lower wire mesh (Fig. 2, upper left). The wick allows the saturation of both the cotton wool and the sand-filled cup. Additionally, vents in the carrier system ensure that the pressure arising from the insertion of the cup does not lead to loss of sand. The vent in the PE flask guarantees free drainage of excess water which may accumulate during high intensity rainfall events. All components of the Tübingen splash cup are easy to obtain and assembling is not challenging for the user.

Calibration

The splash cups were calibrated under natural rainfall with five replications per event. A laser precipitation monitor (Thies Laser Disdrometer) was used for calibration. The disdrometer measures the velocity (20 classes) and the diameter (22 classes) of every raindrop down to 0.16 mm diameter passing a laser beam of 46 cm^2 measuring area. The sum of drops per event in every class was then used to calculate total kinetic energy by multiplying mass and velocity ($\frac{1}{2}m \cdot v^2$). The splash cups were placed around the laser disdrometer in a semi-circle during 8 distinguishable natural rainfall events (Fig. 2, lower left). For further calculation the median of five replications per event was taken.

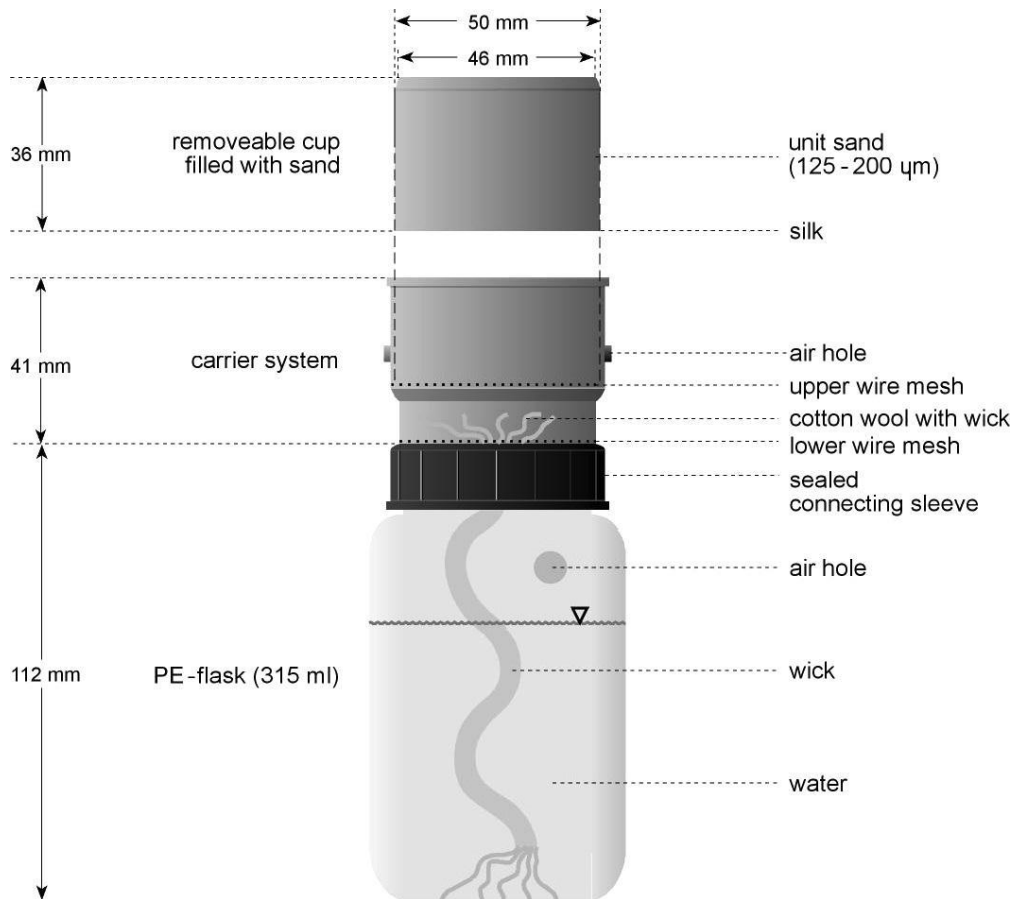


Fig. 1: Three main components of the Tübingen splash cup: (i) a removable cup at the top, (ii) a carrier system that ensures a perfect hydraulic contact between the cup itself and (III) a water reservoir at the bottom of the splash cup.

Portability

The measuring procedure starts by installing the PE flask/carrier system under the target vegetation (single tree or shrub, Fig. 2, lower right) or, for example for comparative measurements, under open field conditions (Fig. 2, lower left). Then, the PE flask is filled with water and the wick/cotton wool system starts saturating. The empty cup is weighted, filled completely with sand and weighted again. The difference is used as “initial weight”. Before field use, the sand-filled cups are placed in shallow water until the sand becomes saturated and then sealed using laboratory film to ensure that no sand is lost. The prepared cups are now placed into styrofoam carriers with a top cover (Fig. 2, upper right). One person is able to safely carry about 40 sand-filled cups even in remote areas.

At the measuring sites, the field-ready cups are put into the carrier system where a close contact to the wick/cotton wool system is assured. Then, depending on the amount and intensity of rain, the whole system is exposed to natural rainfall. After measuring, the cups are

removed from the tray system and can be replaced simultaneously. In the lab the cups are emptied and all residual sand is oven-dried at 105°C for at least 6h and weighed. The difference to the initial weight is recorded as loss of sand. For the measurements under forest vegetation the splash cups are attached to wooden sticks in a height of 1 m (Fig. 2, lower right) to prevent disturbance by animals and lower shrubs. In this case, in addition to the splash cup one rainfall collector is attached to each stick to measure the amount of throughfall at the position of the splash cup.



Fig. 2: Disassembled splash cups (upper left), styrofoam cup carrier for the field (upper right), setup for the calibration measurements with splash cups and laser disdrometer (lower left), and setup of splash cups and throughfall collectors under forest vegetation (lower right).

Results

Kinetic energy and loss of sand from splash cups

The results of the calibration (Fig. 3, upper left) show a very close relationship between kinetic energy as measured by the laser disdrometer (KE-LD) and the loss of sand (LOS) as measured by the splash cups ($R^2 = 0.98$). The kinetic energy per area ranges between 20 J*m⁻² and 250 J*m⁻² while the loss of sand ranges between 1.14 g*m⁻² and 16.49 g*m⁻².

Rainfall intensity, rainfall amount and kinetic energy

In general, the results obtained from the tests in Tübingen and the validation in Central China showed a clear relationship between the amount and intensity of rainfall and the kinetic energy as measured by the splash cups (KE-SC, Figs. 3, upper right and lower left). Rainfall amount and KE-SC correlate with a coefficient of determination (R^2) of 0.92, rainfall intensity and KE-SC with R^2 of 0.96. Rainfall amounts up to 51 mm and rainfall intensities up to 35 mm*h⁻¹ are covered. The average standard deviation of the five single measurements for KE-SC for all measurements in the open field is 17.06, while the mean kinetic energy per area as measured by the splash cups is 139.27 J*m⁻².

Vegetation and kinetic energy

The splash cups were exposed to different tree species and in the open field. A total number of 3,000 partly simultaneous (max. 300 at once) measurements covering 10 different natural rainfall events have been carried out during the initial stage of the project. The first results show that for given amounts of throughfall tree species show a significant different behavior (Fig. 3, lower right). Kinetic energy under *Castanopsis eyrei* is generally lower than kinetic energy under *Schima superba* trees. The variability of kinetic energy under *Schima superba* is more or less stable for different throughfall amounts, whereas the kinetic energy seems to be of higher variability for higher throughfall amounts under *Castanopsis eyrei* trees.

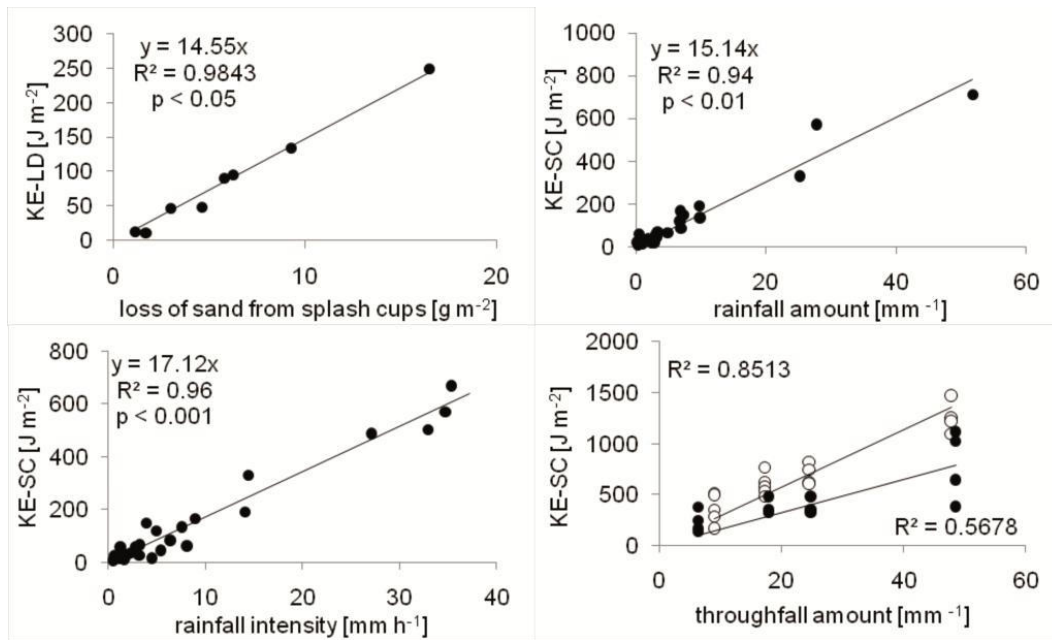


Fig. 3: Loss of sand from splash cups versus kinetic energy (KE-LD, upper left), rainfall amount versus kinetic energy based on splash cup measurements (KE-SC, upper right), rainfall intensity versus KE-SC (lower left), and throughfall amount versus KE-SC under a *Schima superba* tree and a *Castanopsis eyrei* tree respectively (lower right). Every dot represents the median of five replications.

Discussion and Conclusions

In this study we present the Tübingen splash cups as a valuable tool for measuring kinetic energy of rainfall and throughfall. Kinetic energy is widely accepted as the main variable controlling splash erosion (e.g. Lal, 1976; Salles and Poesen, 2000; Salles et al., 2002; Legout et al., 2005). This relation is most pronounced when erodibility is kept constant (Poesen and Savat, 1981; Leguédois et al., 2005). Thus, we used unit sand instead of soil to fill our splash cups. The objective of the construction was to build a reliable measuring device for remote areas and to ensure a high number of replications at reasonable costs. This was achieved by a very light-weighted and modular construction with splash cups that can be loaded and weighted in the laboratory prior to in-field installation. In the field a setup of 400 splash cups measuring simultaneously appeared to be feasible with at least 3 persons. Depending on the remoteness of the area, more people may be necessary to measure a rainfall event with this setup.

Like in other studies (e.g. Vis, 1986; Cornelis et al., 2004) our splash cups were successfully calibrated and the relation between loss of sand and kinetic energy of rainfall is

very close. Accordingly, the loss of sand converted to kinetic energy shows good correlations with the standard variables characterizing rainfall events (amount, average of the highest intensities per event) over a range of values. This is consistent with the results of other researchers (e.g. Wiersum, 1983) and shows the reproducibility and reliability of the measurements with the Tübingen splash cup. This is further supported by the low standard deviation of the measurements in the open field (cf. Fig. 3).

During the measurements the sand surface was not lowered substantially. Therefore, the relationship between loss of sand and kinetic energy of rainfall is best described with a simple linear correlation. However, for higher kinetic energy the slope of the calibration function is supposed to be different due to a higher and more pronounced rim effect (Bisal, 1950). Due to the small size of the cups we suppose that the rim effect has only substantial influence on the results with Tübingen splash cups for far higher kinetic energies than those observed in Tübingen and in subtropical China or for longer measuring intervals at both high rainfall amounts and intensities.

Since the initial water content is a crucial point in splash erosion studies (Poesen and Savat, 1981), much effort was spent on the construction of a hydraulic contact that reacts fast on difference between the actual water content and the saturated water content of the unit sand over a reasonably long period of time. Due to the good drainage performance of our splash cups and the hydraulic contact of unit sand in the carrier system and water in the reservoir (cf. Fig. 1), the wash-off effect (Kinnell, 1974) could not be observed in the field. The same is true concerning the relationship between soil moisture and size. The holes in both carrier and PE flask provide sufficient drainage of excess water during higher rainfall intensities. During phases of evaporation, water deficit in the carrier system is balanced immediately ensuring constant moisture conditions up to one week time without rain.

The size effect was further minimized by the dimension of the cup and by the equivalent diameter of the unit sand. According to the investigations of Leguédois et al. (2005), we chose unit sand of 125-200 μm particle size because the splash length are greatest in this fraction ranging from 5 to 23 cm. This determines the diameter of the cup as well, in our case set to 4.6 cm.

Concluding, we can state that the Tuebingen splash cup is a high-precision device to measure the loss of sand due to the impact of raindrops (splash effect). It suits perfectly the specific needs for biodiversity experiments under natural conditions in forest ecosystems were

a large number of replications under very diverse vegetation are needed. Referring to the very durable and easy to handle construction we would like to point out that our splash cups are designed to work unattended under to rough field conditions like steep slopes and remote areas that can be accessed by feet only. Another advantage is that the splash cup measurements with the Tuebingen splash cup can easily be calibrated using laser precipitation monitors (disdrometers). Thus, they record the kinetic energy of rainfall per area and can be used to calibrate soil erosion models. Further, our splash cup can cope with high-intensity rainfall which is typical for subtropical regions. This allows a wide range of applications in the future not only under natural conditions but also in rainfall simulation studies.

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Manuscript 3

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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Abstract

For estimating 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 by means of calibrated splash cups. Two experiments were carried out: one focusing on density effects and the second testing for species-specific effects and effects of species mixtures. The morphology of the saplings was characterized by measuring important architectural traits. For statistical analysis we used mixed effects models. 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. The main cause for this circumstance is the relation between free throughfall and release throughfall. As free throughfall possesses a far higher KE than release throughfall originating from saplings, a lower density results in a

higher total throughfall KE. Moreover we could show that the influence of density on throughfall KE decreases with increasing sapling height due to lateral growth and canopy closure of the saplings.

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

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

1. Introduction

Soil erosion is an important issue 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 and a central topic for a long time (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, 2002; Shi et al., 1998, 2000; Yu et al., 2006).

It is commonly accepted that vegetation is a key control 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). Known since 1948, key mechanisms of plant cover in reducing or enhancing erosion are 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 some will coagulate on leaves before falling to the ground as large drops. The kinetic energy (KE) of throughfall in subtropical forests is up to 2.7 times higher than under open field conditions (Brandt, 1988; Geißler et al., 2010b; 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 due to clogging soil pores at the soil surface (Le Bissonnais and Singer, 1992; Salles and Poesen, 2000; Singer and Shainberg, 2005).

Brandt (1989) has shown that large drops from leaves may be significant sources of splash detachment in forests, indicating that drop size may overplay drop velocity (see also Massman, 1983; Salles and Poesen, 2000; Styczen and Høgh-Schmidt, 1988).

It can be assumed that mechanisms that control soil erosion under forest are very 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 et al., 1979), beech forest in New Zealand (Mosley, 1982) or tropical rain forest in Colombia (Vis, 1986).

One of the central issues regarding KE of throughfall in forests is its relation to forest stand variables, to specific species and to canopy architecture. Forest stand variables like tree density (Bochet et al., 2002; Pressland, 1976; Stogsdill et al., 1989) and tree morphological factors like tree height (Geißler et al., 2010b; Wainwright, 1999; Wakiyama et al., 2010), height of the first branch (Nanko et al., 2008b), canopy thickness (Levia and Frost, 2006;), 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 supposed 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. It is important to improve our knowledge on the impact and extend of these factors as it is one of the major questions in soil erosion science and ecology, when focusing on the atmosphere-plant-soil relationship. Further, design and management of forests for soil erosion control is largely depending on knowledge of the role of stand density, tree architecture and species identity.

The aim of this study was to analyze the KE of throughfall 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 measurements were done by means of 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 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 reaches 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 (Bruehlheide et al., 2010).

2.2 Experimental Design

In March 2009, the experiment has been established on a former agricultural field with a total area of 5400 m². 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), respectively. 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). Species were planted in either monoculture or four-species mixture. 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 at an age of 2 yrs 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 at the 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 at the remaining positions (1A, 1C, 3A, 3B). In cases where the number of dead individuals was that high 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 KE of throughfall measured below the canopy (Nanko et al., 2008b).

The density experiment (A) was conducted before the full development of leaves from the deciduous species (22nd of March - 10th of April 2010) and thus includes only the two evergreen species. Hypothesizing that release throughfall (which has a greater proportion in less dense plantings) is more related to specific species than free throughfall, we concentrated only on low density plots in the species identity experiment (B). It was conducted after the full development of the leaves of the deciduous species (15th of May - 21st of June 2010) including both evergreen and deciduous species.

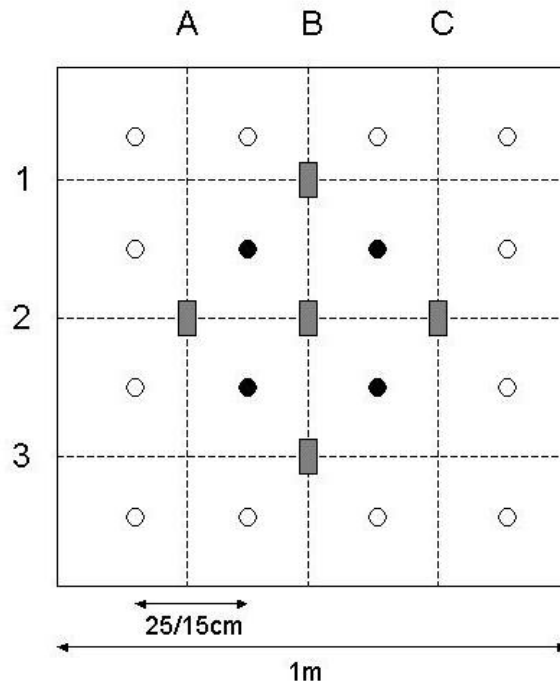


Fig. 1: Schematic design of an experimental plot (1 m² in size). Saplings are represented by circles, splash cups by grey boxes. The optimal positioning of splash cups is shown. Filled circles symbolize the four individuals in the centre of the plot for which additional measurements of crown architecture were carried out.

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 in 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*. Additionally, we 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).

2.3 Measurement of KE of throughfall

The methods applied for measuring erosive power of throughfall under vegetation were originally designed for studying properties of open field rainfall. These include the paper stain method (Wiesner, 1895), the flour pellet technique (Bentley, 1904) and laser disdrometers (Hall and Calder, 1993; Joss and Waldvogel, 1967; Nanko et al., 2008a). Except for laser 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 to measure rainfall events without interrupts. However, the number of replications is limited because of high technical and financial demands. Taking into account these limitations, Mosley (1982) in New Zealand and Vis (1986) in Colombia used splash cups for estimating throughfall erosivity successfully. The major advantage of splash cups is their easy handling and the high number of replications that can be obtained at reasonable costs. Moreover they are able to measure the whole event rather than a short time span.

For measuring KE of throughfall “T Splash cups” were used in this experiment (Scholten et al., 2011). These splash cups 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).

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 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 off a trunk). The LAI was measured with a LAI-2000 Plant Canopy Analyser (PCA) (“One-Sensor-Mode”; Li-Cor, Lincoln Inc.,

NE, USA). At each splash cup position, a LAI-2000 measurement was conducted at dawn under diffuse radiation conditions.

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 (considering only first-order branches with a length > 1 cm) 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: $0-30^\circ$ from horizontal, class 2: $30-60^\circ$, class 3: $60-90^\circ$).

2.5 Statistical analysis

Statistical analyses were performed using R 2.12 (R Development Core Team, 2010) together with the packages “nlme” (Pinheiro et al., 2010) and “multcomp” (Hothorn et al., 2008). For the analysis of the splash cup measurements mean values of throughfall KE per area as well as mean values of LAI for each plot were used.

We tested the effect of density and species identity on the mean KE of throughfall 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 characteristic of the rainfall event, LAI, 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).

3.2 Effect of tree density on throughfall KE

In the density experiment (A) KE of rainfall together with the factor “density” and the interaction between both were the most important effects on throughfall KE ($p < 0.0001$, Tab. 1). The higher the KE of rainfall, the higher was the throughfall KE (effect size: 0.31 ± 0.02 , obtained from R summary). Throughfall KE was significantly higher in the plots with the saplings planted in low density than in those planted in high density (Tab. 1). However, this was also affected by the magnitude of the rainfall event, since the 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 ($p = 0.0006$). Throughfall KE was differently influenced by sapling height in the density treatments: Height was negatively related to throughfall KE in the low density plots, whereas height 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), which was indicated by the significant threefold interaction ($p = 0.0055$). Neither species identity of the two evergreen species nor LAI entered the final model.

Table 1: Effects influencing throughfall KE. Results of simplified mixed effects models, including block as random intercept for both experiments.

Fixed effects	F-value	p-value	
Kinetic energy of rainfall	499.35	<.0001	***
Density	50.28	<.0001	***
Mean sapling height	5.17	0.0266	*
Density * Mean sapling height	13.1	0.0006	***
Kinetic energy of rainfall* Density	33.24	<.0001	***
Kinetic energy of rainfall* Mean sapling height	2.15	0.1475	
KE of rainfall* Density* Mean sapling height	8.32	0.0055	**

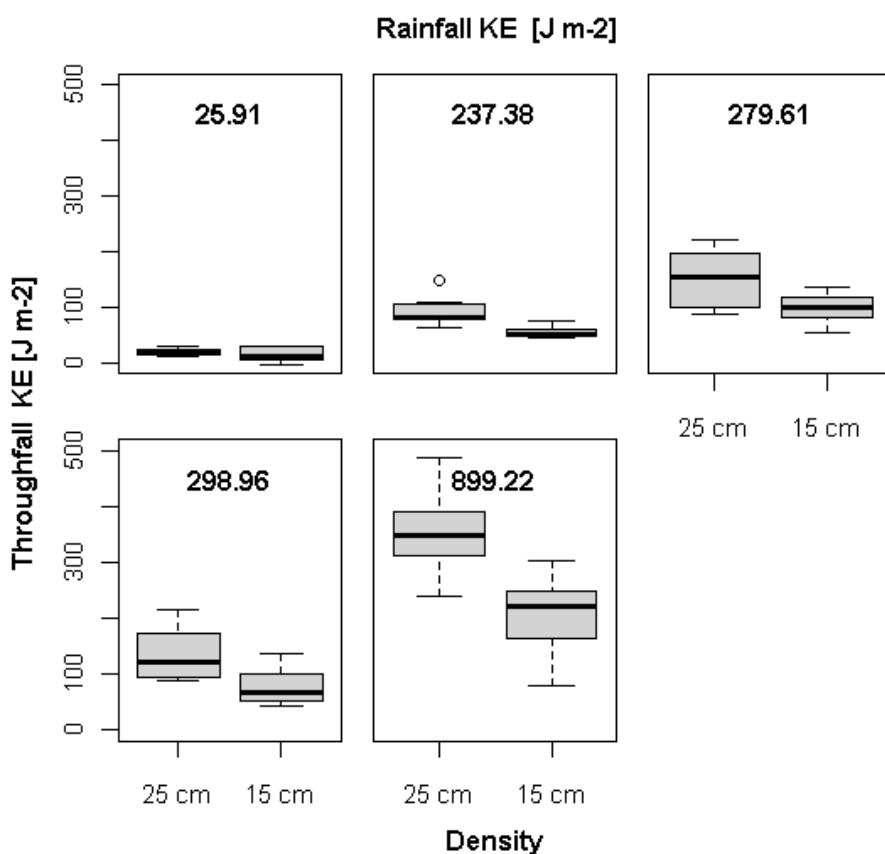


Fig. 2: Effect of tree density on throughfall KE in five different rainfall events. Rainfall events are classified by their rainfall KE.

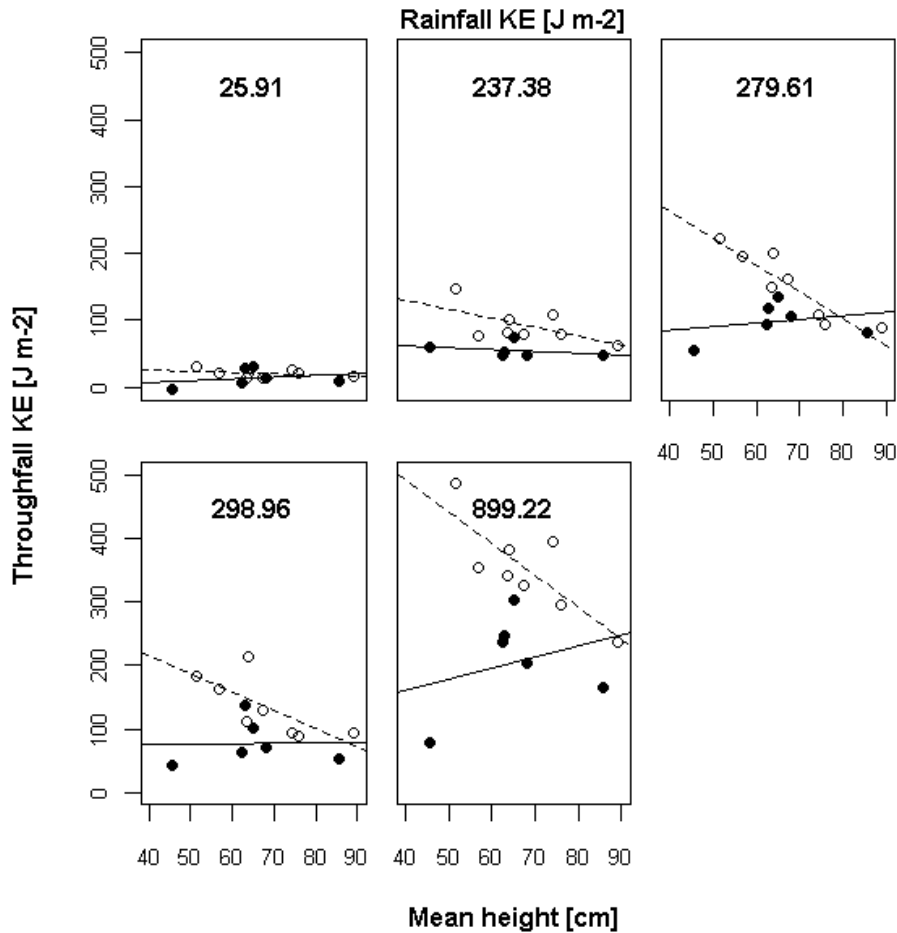


Fig. 3: Effect of sapling height on throughfall KE in five different rainfall events. Open circles represent the low density plots (dashed regression line), black dots the high density plots (black regression line).

3.3 Effect of species identity on throughfall KE

In the species identity experiment (B), the KE of rainfall also had a significant effect on throughfall KE (Tab. 2). 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 mediated 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. LAI did not enter the final model.

Table 2: Effects influencing throughfall KE. Results of simplified mixed effects models, including block as random intercept for both experiments.

Fixed effects	F-value	p-value	
Kinetic energy of rainfall	326.54	<.0001	***
Mean sapling height	14.59	0.0001	***
Species identity	9.84	<.0001	***
Kinetic energy of rainfall* Mean sapling height	6.2	0.0246	*
Kinetic energy of rainfall* Species composition of plot	4.16	0.0048	**

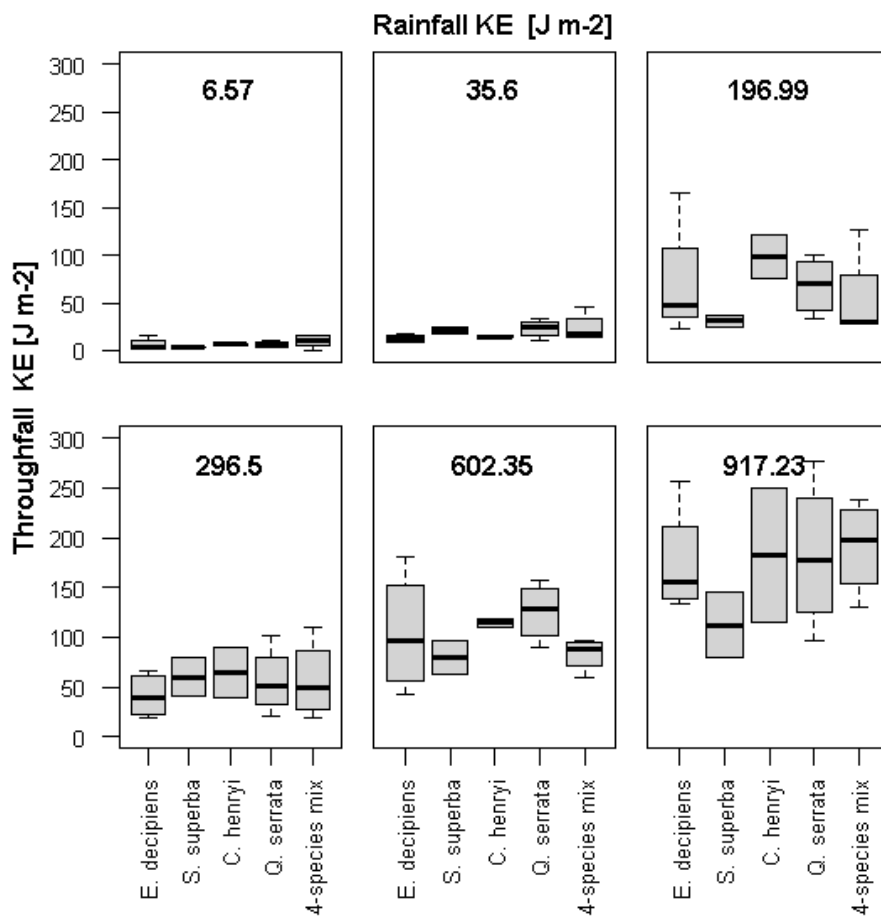


Fig. 4: Effect of species identity on throughfall KE for six different rainfall events.

3.4 Architecture of species in the experiment

Total height of *Q. serrata* saplings (mean: 54.9 cm ± 13.5) was significantly lower than the total heights of the other species (Tab. 3). Height of the first branch, crown length and length of the first branch did not differ significantly between species. However, considerable differences in the number of branches and in the angle of the first branch were found between

Table 3: 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).

Response variable	Fixed effect: Species			Mean values									
	F-value	p-value		E. decipiens		S. superba		C. henryi		Q. serrata		4-species mix	
Height	13.18	0.0015	**	82.5 cm	b	78.6 cm	b	74.3 cm	b	54.9 cm	a	77.7 cm	b
Crown length	3.7	0.0546		76.0 cm		61.0 cm		65.1 cm		45.5 cm		58.5 cm	
Height of 1 st branch	1.7	0.2421		6.5 cm		17.6 cm		9.1 cm		9.5 cm		19.3 cm	
Number of branches	8.34	0.0059	**	18.8	a	6.6	bc	5.3	c	11.8	bc	13.8	a
Length of 1 st branch	1.14	0.4041		22.0 cm		36.4 cm		42.4 cm		23.7 cm		25.7 cm	
Angle of 1 st branch	5.65	0.0185	*	57°	bc	45°	a	72°	c	48°	ab	54°	abc

species. 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 according to the measured mean values. The mixture of the four species was generally characterized by intermediate mean values of the morphological characteristics (Tab. 3).

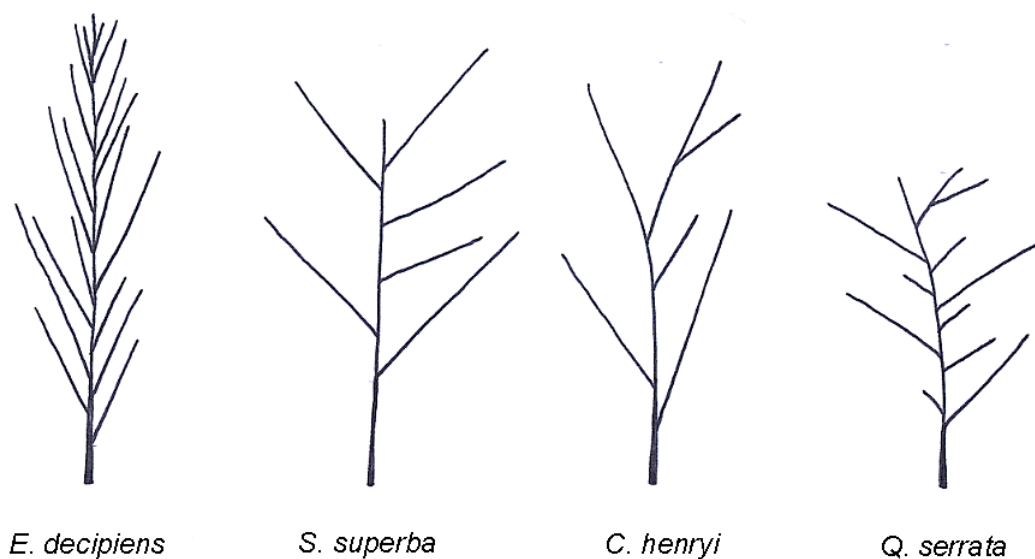


Fig. 5: Schematic drawing of species-specific sapling architecture. Mean values of total height, height of the first branch, number of branches, length and angle of the first branch are derived from the data (Tab. 2). Branching pattern was adapted according to field observation.

4. Discussion and Conclusion

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. This is clearly 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 are balanced. This is consistent

with the results of other studies dealing 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, 1999).

4.2 Planting distance of tree saplings affects throughfall KE

In experiment A we could show the effect of sapling density. The higher density of the saplings resulted in a 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 is supposed to be a result of a shift in the proportion of throughfall components.

For the high density planting, the main component of total throughfall is “released throughfall”, and “free throughfall” is supposed to play a minor role. Consequently, the gain in sapling height results only in a slight increase of throughfall KE which is mainly caused by drip from leaves and branches. For the low density planting, the effect of height is more obvious. It was, however, contrary to the pattern which is often found, i.e. that throughfall KE increases with increasing tree height. This is supposed to 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 is 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 the low density planting than for the high density planting (cf. Raat et al., 2002).

In our experiment LAI had no effect on throughfall KE. This is in contradiction to the literature, where LAI is thought to have a strong influence on KE or amount of throughfall (e.g. Aston, 1979; Gómez et al., 2001). A reason for that may be that we determined LAI indirectly by means of the LAI-2000 PCA. It has been shown, however, that this method may overestimate actual LAI in low LAI stands as well as in very young stands because of the effects of branch and stem area index on the estimation of LAI (Dovey and du Toit, 2006). A direct determination of the LAI may have, therefore, yielded different results. Species

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

We state that any effects revealed in this experiment are supposed to be caused by shifts in the proportion of throughfall components. This shift causes differences in the amount and therefore also KE of throughfall.

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 species-specific influential crown traits. Differential crown architectural traits may influence KE of throughfall contrarily and interact with each other.

S. superba generally had the lowest throughfall KE among the observed species and events. However, the morphological characteristics of this species regarding 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 the lateral extension and result in an increased crown width. Wider crowns of *S. superba* in turn yield a higher canopy cover as compared to the other species. This may lead to less free throughfall reaching the soil surface or, in other words, a substantially reduced total throughfall KE.

E. decipiens, the second evergreen species, also showed a relatively low throughfall KE. Individuals of *E. decipiens* were higher than the ones 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 very likely re-interception of release throughfall under *E. decipiens* lead therefore to a reduced KE of throughfall. The

effects tending to decrease throughfall KE superimposed effects that increased throughfall KE in this case.

For most rainfall events the deciduous tree species *Q. serrata* had a 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, *Q. serrata* tended to have a low length of the crown and the first branch. Both parameters resulted in a quite 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 a very low number of branches and a wide angle of the first branch from the horizontal, which induces a low canopy storage (Herwitz, 1985) capacity. In addition, steeply inclined branches lead to a higher amount of stemflow (van Elewijck, 1989), strongly reducing the amount of water being able to fall from leaves and branches as drops.

It has been shown that the crown architecture of individual trees is influenced by the species identity of 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 hardly or not 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 could, thus, not identify any specific mixture effects on throughfall KE.

Summarizing we can say that planting density and specific species have a substantial effect on throughfall KE. The first can be explained by the proportion of throughfall components to each other and the latter by taking the detailed sapling architecture into account.

We state that already after two years after planting canopy closure was achieved (especially for the evergreen species) even for the low density plots and rainfall KE was reduced substantially. Fast canopy closure showed to be the crucial point when considering soil erosion potential under tree saplings.

We could show that the effect of density decreases very fast as sapling height (and therefore crown width) increases. Again this shows the importance of canopy closure on the extent of throughfall KE under 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 to be taken into account when focussing on the soil erosion potential below these.

Besides canopy closure, which prevents highly erosive raindrops to hit the soil, canopy storage appears to be important as it controls the amount of water (and therefore influencing KE directly) being 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 KE of throughfall even at this spatial scale.

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Manuscript 4

Splash erosion potential under tree canopies in subtropical SE China

CATENA, Article in Press, Corrected Proof

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Abstract

Sand-filled splash cups were used to study the erosivity of rainfall and throughfall in the humid subtropics of southeast China. Our results showed that the splash cup measurements yielded precise and reproducible results both under open field conditions and under forest vegetation. The splash cups were exposed to forest stands of different age and to selected species (*Schima superba*, *Castanopsis eyrei*) in the Gutianshan National Nature Reserve (GNNR). The measurements in the open field revealed a close relationship between unit sand loss (g m^{-2}), rainfall amount (mm) ($R^2=0.94$) and maximum rainfall intensity (mm h^{-1}) ($R^2=0.90$). The highest correlation was obtained between unit sand loss (g m^{-2}) and the

average of the five highest five minute interval rainfall intensities (mm h^{-1}) ($R^2=0.96$). This underlines the reliability of the splash cups used.

The best results on the relationship between variables related to precipitation and sand loss were obtained with the Vaisala sensor compared to a standard tipping-bucket rain gauge. This is mainly due to the fact that the drop impact-based Vaisala sensor (0.8-5.0 mm drops are recorded assuming their terminal velocity) does not measure drops with low kinetic energy, whereas drop size distribution plays no role for the measurements with the tipping-bucket rain gauge.

The results obtained under forest vegetation show that the erosive power of throughfall drops is 2.59 times higher compared to the open field, which accentuates the importance of shrub, herb and litter layers in forest ecosystems to protect the soil against erosion. Coalescing drops from leaves and branches (drips) are responsible for this enormous gain in erosive power. Moreover, the results show that the erosion potential under forest is related to the forest structure, especially height and canopy cover. The erosion potential of medium and old grown forests is 1.53 times higher than of young forests.

Further, differences in sand loss between *Schima superba* and *Castanopsis eyrei* indicate that the erosion potential and the spatial heterogeneity of throughfall is species-specific, highlighting the importance of selecting species for afforestation projects considering soil erosion potential.

Keywords: BEF-China; Gutianshan National Nature Reserve; forest vegetation; rainfall erosivity; soil erosion; soil erosion experiment; splash cups; throughfall erosivity.

1. Introduction

Forest vegetation controls on erosion

In soil erosion research it is widely accepted that vegetation is a key control for the type and intensity of erosion (e.g. Hudson, 1971; Wiersum, 1985; Thornes, 1990; Morgan, 2005).

The controls of vegetation on erosion processes do not only tackle soil erosion on a single agricultural field but also link to landscape evolution and landforms on a regional scale (Kirkby, 1995; Bork and Lang, 2003). The current paradigm is that natural or quasi-natural vegetation protects the soil against erosion while agricultural land use generally enhances erosion. Most of the work during the past decades focused on the latter and less attention was paid to natural systems, which are difficult to study (Collins et al., 2004; Istanbuluoglu and Bras, 2005). Nevertheless, afforestation is widely used as a measure of soil protection against soil erosion.

Contrary to these findings, Zhou et al. (1999) and Cao (2008) could not confirm the positive effect of afforestation on erosion control. Runoff shows significant seasonal variations and tends to increase very fast if the canopy cover is thinning out due to leaf fall or low stand density. Recent findings from forest experiments in Japan underpin the latter. Forest stand density and management control soil loss largely, especially in forest plantations on slopes (Miura et al., 2002; Razafindrabe et al., 2010). Further, leaf exudates and low sunlight in dense forest plantation often result in bare ground and lack of a shrub or herb layer (Tsukamoto 1991; Zhao, 2006; Nanko et al., 2008). In such places, the infiltration rate decreases and runoff occurs quite easily (Tsujimura et al., 2006).

Splash erosion measurement techniques

In literature several methods for measuring splash erosion in the field are reported. Most of the methods are designed to measure the amount of soil splashed from the soil surface to a target. These include splash boards (Ellison, 1944), field splash cups (Morgan, 1978) and splash boxes (van Dijk, 2003). The objective of these methods is to draw conclusions about the current soil loss under controlled conditions, which has been shown by several studies (e.g. Morgan, 1978; Salles and Poesen, 2001; Legout et al., 2005). However, these methods are not appropriate for estimating differences in kinetic energy of rainfall or throughfall as the results are confounded by the erodibility of the soil. This means that the soil properties at the soil surface would have to be controlled for, if using such a type of measurement for estimating kinetic energy of precipitation.

Other methods are designed to measure the erodibility of different soil material or standardized sediment by placing it into a unit cup and determine a difference in weight

before and after a rainfall event. In most studies the sediment splashed out of a cup is measured. Splash cups were first introduced by Ellison (1947). Several researchers applied this method with few modifications of e.g. the diameter of the cup or of the material used (Poesen and Torri, 1988; Salles and Poesen, 2000; Cornelis et al., 2004; Erpul et al., 2005).

When using small sized cups the rim-effect (Bisal, 1950; Hudson, 1965) should be taken into account and bigger sized cups are supposed to better reflect the mean erosivity per unit area (Poesen and Torri, 1988; van Dijk et al., 2003). The rim-effect is a result of a lowering of the sand surface in relation to the solid rim of the cup. The lower the sand surface inside the cup, the less sand will be detached from the cup. Moreover, Kinnell (1974) states that excess water on the sand surface could lead to an initial “wash-off” of sand out of the cup.

Drop formation by forest canopies and its measurement

Based on Chapman (1948), throughfall in forests shows higher erosivity compared to open field rainfall. Measurements were made in several regions of the world with different methods confirming Chapman's findings. For example Ovington (1954) in Great Britain, Tsukamoto (1966) in Japan, Mosley (1982) in New Zealand, Vis (1986) in Colombia, Brandt (1987, 1988) in Brazil, Hall and Calder (1993) in India, Brooks (1995) in Malaysia and more recently Nanko (2004, 2008) in Japan. Key mechanisms of a forest vegetation cover in reducing or enhancing erosion are the modification of drop size distribution, retention of raindrop impact on the soil and changes in amount and spatial distribution of rainfall at the ground surface. Controlling determinants are rainfall intensity, drop size distribution, drop fall velocity, height and density of the canopy, crown and leaf traits, leaf area index and litter cover of the soil (Chapman, 1948; Mosley, 1982; Wiersum, 1985; Vis, 1986; Brandt, 1989; Hall and Calder, 1993; Park and Cameron, 2008). However, the mechanisms reducing or enhancing splash detachment under different types of vegetation, especially secondary shrub land and forest, are not well understood. Some studies indicate that raindrop impact is species specific (Calder, 2001; Nanko et al., 2006; Roldan and Fernandez, 2006) and some neglect the effects of species specific impacts (Brandt, 1989; Foot and Morgan, 2005). The methods applied for measuring erosive power of throughfall under vegetation were originally designed for studying properties of open field rainfall comprising the paper stain method (Wiesner, 1895), the flour pellet technique (Bentley, 1904) and laser disdrometers (Hall & Calder,

1993; Nanko et al., 2008). Except laser disdrometers these techniques were not able to determine species specific change in throughfall characteristics. They lack temporal continuity as they only represent a very short time span of a rainfall event (Nanko, 2008). The advantage of disdrometers is to measure rainfall events without interrupts. However, the number of replications is limited because of high technical and financial demands. Taking into account these limitations, Mosley (1982) in New Zealand and Vis (1986) in Colombia used splash cups for estimating throughfall erosivity successfully. The major advantage of splash cups is their easy handling and the high number of replications that can be obtained at reasonable costs.

Objectives

This paper focuses on the application of sand-filled splash cups to study rainfall and throughfall erosivity in natural systems. In contrast to highly sophisticated and expensive techniques like laser disdrometers, splash cups allow a high number of replications and are easy to handle in mountainous and remote areas. The main objective of this study is to show that splash cups are an appropriate method for comparing erosivity of both rainfall and throughfall. Further objectives are:

- (a) to show the performance of the splash cups by open field measurements
- (b) to compare rainfall and throughfall erosivity in a natural forest ecosystem (regardless of the actual soil properties)
- (c) to study the differences in throughfall erosivity between successional stages
- (d) to test for a tree species specific effect on throughfall erosivity

2. Materials and Methods

2.1. Study site

This study was conducted in the Gutianshan National Nature Reserve (GNNR), Zhejiang Province, P.R. China. The centre of the GNNR is located at N 29°14.657' and E 118°06.805' and covers an area of 81 km². The elevation ranges between 320 m and 910 m above sea

level. The soils are predominantly Cambisols (cf. IUSS Working Group WRB, 2007) developed on granite or on saprolite. The climate at the GNNR is typical of subtropical monsoon regions with an annual average temperature of 15.1°C and a mean annual rainfall of 1963.7 mm (Hu and Yu, 2008) (Fig. 1). The forest in the GNNR is extraordinary rich in species (Hu and Yu, 2008, Bruelheide et al., 2010) and *Schima superba* and *Castanopsis eyrei* are the most common trees (Legendre et al., 2009). The frequency of *Schima superba* counts 388 species per ha, while for *Castanopsis eyrei* 375 species occur per ha on average.

In the framework of the BEF-China research group, a multidisciplinary research unit focusing the relationship between biodiversity and ecosystem services, 27 Comparative Study Plots (CSP) were established stratified by successional stages (Tab.1). From these 27 CSPs nine were equipped with splash cups. All measured plots are in a circumference of some hundred meters around the center of the GNNR and the climate station respectively.

Generally, the height of the different tree and shrub layers increases with increasing age of the forest stand (Tab. 1). The cover of the first tree layer is at maximum in the intermediate successional stage, followed by the old successional stage. The cover of the second tree layer is at maximum in the young successional stage and is much lower in older stages. The shrub layer only plays a major role in the youngest stage. The summed up cover across all layers underpins this difference between the successional stages. The combined coverage was calculated using the following formula:

$$x = \text{proportion TL1} = \text{TL1\%} * 100$$

$$y = \text{proportion TL2} = \text{TL2\%} * 100$$

$$\text{Proportion combined} = x + (1-x) y = x + y - x y$$

This formula allows for the fact that one layer might overlay another and makes sure that cover values cannot transgress 100%.

Table 1: The observed forest successional stages with average tree heights and cover rates.

Successional stage	Age (years)	Height TL 1* (m)	Cover TL 1* (%)	Height TL 2* (m)	Cover TL 2* (%)	Height SL* (m)	Cover SL* (%)	Cover sum* (%)	Plots
Young forests	10-30	15	9	8	65	4	50	74	2
Intermediate forests	30-80	24	30	12	18	4	10	56	3
Old forests	80+	25	28	14	14	5	14	50	4

* = average values from selected CSPs

TL = tree layer

SL = shrub layer

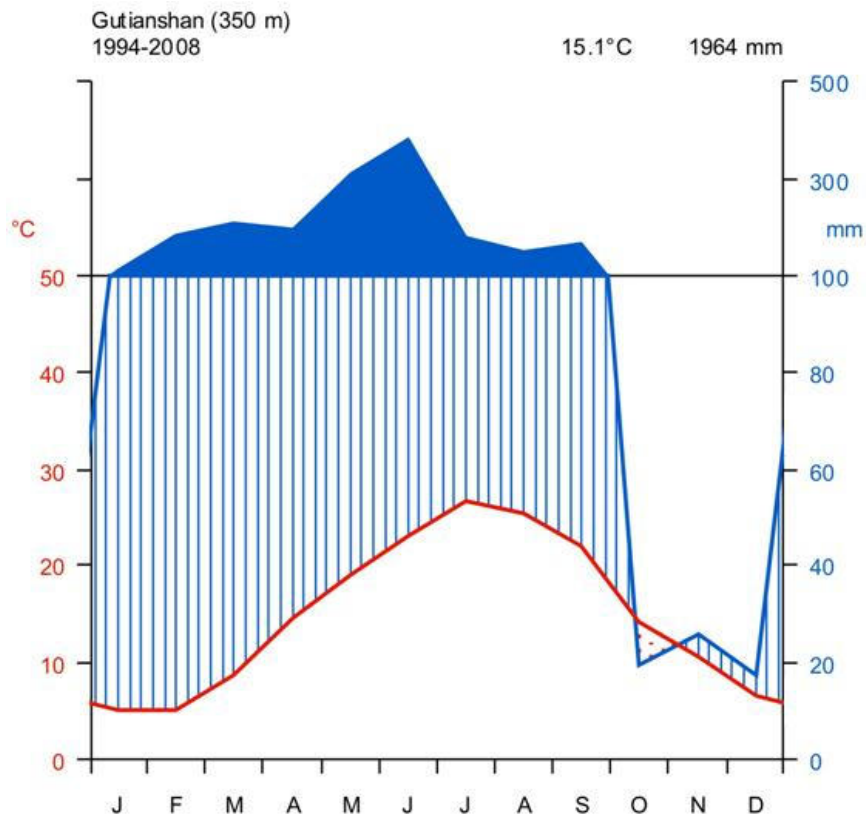


Fig. 1: Walter and Lieth climate diagram of monthly average temperature (red solid line) and precipitation (blue solid line) at Gutianshan National Nature Reserve (GNNR). Vertical area indicates moist season, dotted area indicates dry season.

2.2. Precipitation measurement

In the centre of the GNNR a climate station was installed. Rainfall was measured using:

- (i) a standard tipping-bucket rain gauge of 0.1 mm accuracy and a collecting area of 200 cm².
- (ii) a piezo-electric sensor (Vaisala Raincap ® built in the Vaisala WXT510 multi-sensor) measuring single drop impacts with an accuracy of 0.01 mm and a collecting area of 63.6 cm². The sensor converts the drop impact into an electrical signal proportional to the volume of the specific drop. Drops between 0.8 and 5.0 mm in diameter are recognized (Salmi and Ikonen, 2005). Regarding the speed of the specific drops terminal velocity is assumed. By conversion of this information, the rainfall amount is calculated automatically.
- (iii) a bottle rain gauge in the centre of the open field splash cups (see 2.4 Experimental design).

The measurement interval of the climate station is 5 minutes. Rainfall intensities (mm h⁻¹) are derived from those intervals. The measurement interval significantly affects the calculated intensities, as the calculated intensities increase as the measurement interval decreases (Agnese et al., 2006). Since the measurement interval remained the same during all measurements, this circumstance does not affect our results.

2.3. Splash cups

The splash cups have a diameter of 4.6 cm and a surface of 16.619 cm² and were developed based on the archetype of Ellison (1947). In contrast to previous studies with Ellison splash cups (Vis, 1986) or other types of splash cups (e.g. Kinnell, 1974; Morgan, 1981; Poesen and Torri, 1988) we measure the unit sand remaining inside the cup after single natural rainfall events.

The objective of the modification was to construct a splash cup with cheap and easily available components to ensure high replication rates. Requirements were a facile handling in steep mountainous remote areas and the possibility to exchange the splash cup in field without removing the whole system from its position. The general functionality is as follows: to a standard PE-flask a carrier system is attached (lower part). In this carrier system the

sand-filled cup is inserted (upper part). At the bottom of the cup a silk cover is attached to avoid the loss of material and to guarantee free drainage of water from the cup to the carrier and vice versa. If the cup is inserted, its bottom stays for the whole time of measuring in contact to the cotton and the wick which are separated from the rest of the system by an upper and a lower wire mesh. The wick itself assures the saturation of the cotton and the cup filled with soil or sand respectively. The vents in the carrier system ensure that pressure arising from the insertion of the cup doesn't lead to a loss of material. The vent in the PE-flask guarantees the free drainage of excess water which could arise from high precipitation.

In accordance with the objectives of the study (e.g. detecting differences in throughfall erosivity between successional stages and specific species) a grain size highly susceptible to erosion was chosen (Poesen and Savat, 1981; Poesen, 1986). We used unit quartz sand being 125-200 μ m in size as filling for the splash cups.

Measurement procedure

The cups were filled and the sand filling of each cup was weighed. The splash cups were exposed to different natural rainfall events in the open field and under vegetation cover. After a single rainfall event the cups were removed from the carrier system and subsequently brought back to the field laboratory, the sand filling was removed and dried for 12 hours at 105 °C in a drying oven. After cooling, the sand was weighed again. The weighing difference was used for calculating the sand loss per unit area.

2.4. Experimental design

The experimental design of the splash cup and rainfall / throughfall measurements covers measurements in the open field and under vegetation. At each measuring point five splash cups and one rain gauge were installed. In a CSP, three tree individuals (target trees) were selected resulting in three times five splash cups and three rain gauges per CSP (Fig. 2a). The splash cup measurements were event-based. After each rainfall event, all splash cups were replaced.

To get reference measurements under open field conditions a set of five splash cups was positioned in a pentagon in a distance of 3 m from the climate station. In the center of the pentagon a rainfall collecting bottle was placed (Fig. 2b). The minimum distance between the single splash cups is 60 cm to avoid interference between single splash cups (Poesen and Savat, 1981; Legout et al., 2005).

The target tree represents a typical individual of *Schima superba* and *Castanopsis eyrei* (Tab.2), which are core species in the BEF-China Project that are used for detailed allometric, botanical and physiological studies. Depending on tree age, the target trees are part of different successional stages represented by different CSPs. To reveal the effects of different successional stages on the erosivity of throughfall the average of all measurements in one successional stage per rainfall event was taken.

The splash cups were established 1 m above ground to avoid disturbance by animals, forest floor vegetation and differing inclination of slopes. The sand loss (g m^{-2}) per pentagon was calculated as the median of the five single measurements. Thus, every n (cf. Tab. 3) represents the median of one pentagon. By taking the median of five replications (surface: 83.095 cm^2) the effect of cup size (Poesen and Torri, 1988, see above) is supposed to be diminished.

An outlier test was applied both to the rainfall data and the splash cup measurements with standard deviation * 2 + mean as a criterion for exclusion. For correlating rainfall characteristics to sand loss a simple linear regression and the “coefficient of determination” (R^2) was used to explain the differences.

Table 2: Average height and leaf sizes of *Schima superba* and *Castanopsis eyrei*.

Species	Average height (m)	Average leaf size (cm^2)	Trees measured
<i>Schima superba</i>	17.15	38.09	4
<i>Castanopsis eyrei</i>	16.86	12.92	8

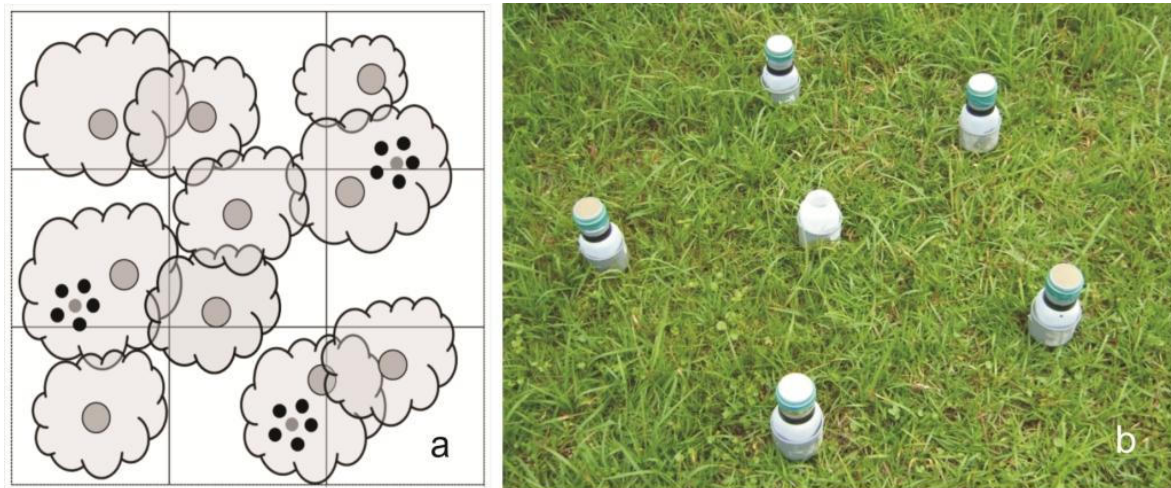


Fig. 2: (a) Experimental design for the measurements under vegetation (grey circles = stems, black dots = splash cups, dark grey dots = rainfall collector) and (b) splash cup arrangement in the open field at GNNR, southeast China.

3. Results

3.1. Sand loss from splash cups under open field conditions

Sand losses under open field conditions were compared to the recordings of the standard tipping-bucket rain gauge and the Vaisala sensor (Fig. 3a-h). Those results correlate well with standard rainfall characteristics: rainfall amount (mm), average rainfall intensity (mm h⁻¹), maximum rainfall intensity (mm h⁻¹), average of the five highest five minute interval rainfall intensities (mm h⁻¹). The correlation sand loss with rainfall amount (Vaisala sensor) was notably higher ($R^2=0.94$) than the correlation found with the standard tipping-bucket rain gauge ($R^2=0.74$). The rainfall data recorded by the Vaisala sensor (average rainfall intensity, maximum rainfall intensity and the average of the five highest rainfall intensities during the measuring period) correlated better with the splash cup data than the records of the tipping-bucket rain gauge. Regarding the rainfall amount the results showed that there is a close relationship between rainfall amount and intensity and sand loss per unit area.

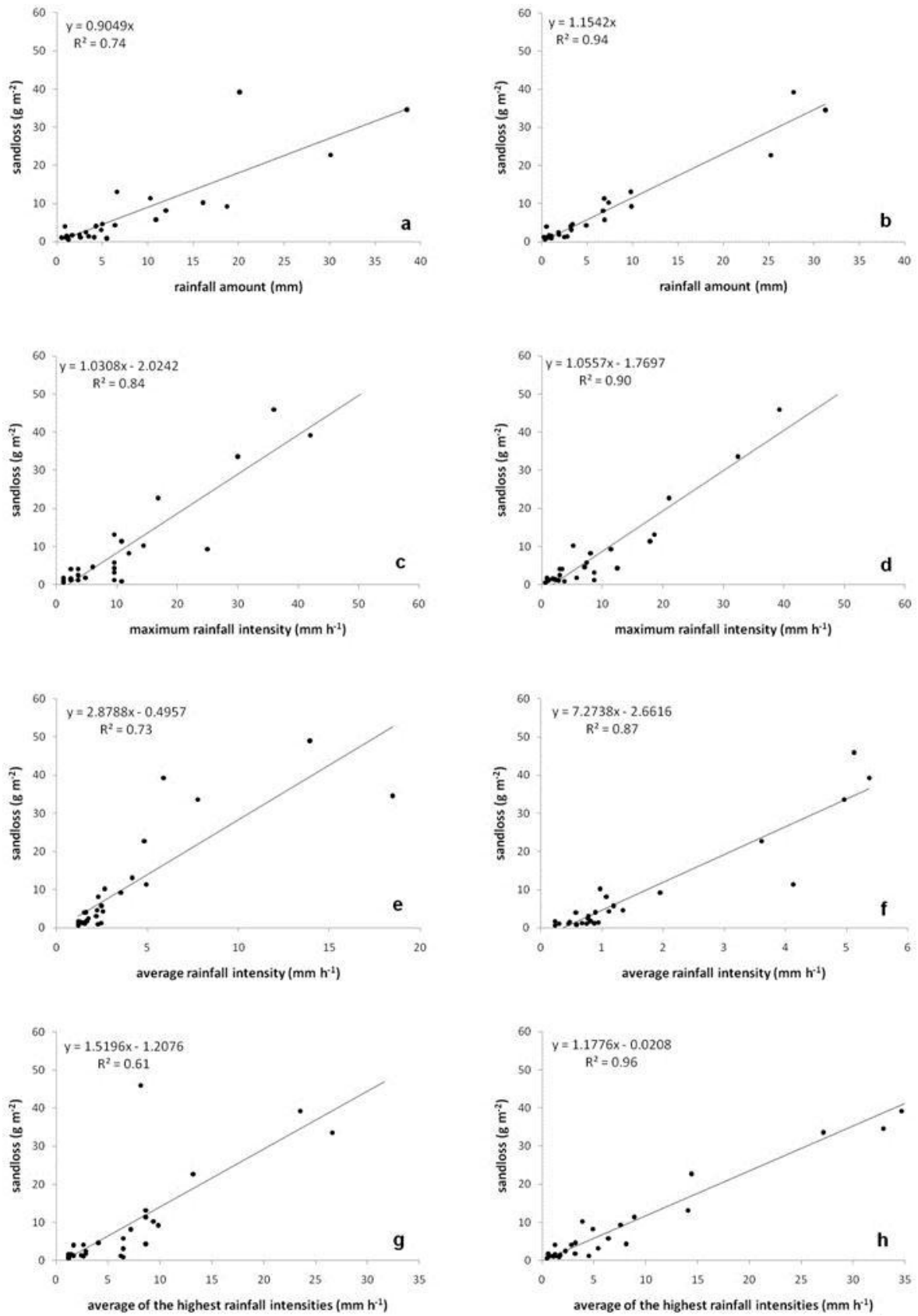


Fig. 3: Sand loss from splash cups for the tipping-bucket rain gauge (left) and the Vaisala sensor (right) in relation to rainfall amount (a, b), maximum rainfall intensity (c, d), average rainfall intensity (e, f) and the average of the five highest five minute interval rainfall intensities (g, h). The significance of correlation coefficients is $p < 0.01$.

3.2. Sand loss from splash cups under vegetation

Simultaneous measurements under open field conditions and in CSPs of the three successional stages showed a remarkable difference in splash potential (Tab. 3). Throughfall varied between 57% and 70% of total precipitation. The average sand loss under vegetation (44.69 g m⁻²) was 2.59 times higher than under open field conditions (17.24 g m⁻²). This remarkable difference was already obvious in the field (Fig. 4). The difference between the young successional stage and the intermediate successional stage (16.71 g m⁻², factor 1.51) is much higher than between the intermediate successional stage and the old successional stage (1.45 g m⁻², factor 1.03). The results from the different rainfall events show that the ratio sand loss open field vs. sand loss under vegetation is variable, ranging from 2.37 to 3.38.

The resulting standard deviations between the measurement replicates can be considered in two ways: (i) For open field conditions the standard deviation is much lower than for all successional stages and (ii) the difference in standard deviation between the young successional stage (average 13.78) and the intermediate successional stage (average 21.72) was much higher than between the intermediate and the old successional stage (average 22.99). The standard deviation found under two common species (*Schima superba*, *Castanopsis eyrei*) was much higher (average 10.27 and 19.12 respectively) than under open field conditions (average 1.16). Nevertheless, there were distinct differences in splash potential represented by sand loss between *Schima superba* (55.05 g m⁻²) and *Castanopsis eyrei* (42.52 g m⁻²), although the average amount of throughfall was quite similar (24.8 mm for *Schima superba* and 23.2 mm for *Castanopsis eyrei*).



Fig. 4: Sand detachment from splash cups under open field (a) and under forest vegetation (b) (black line = 1 cm).

Table 3: Amounts of sand loss and precipitation (measured with Vaisala sensor) for open field, two species and different successional stages for four rainfall events.

		Single species			Successional stages			Average (succ. stages)	Ratio vegetation / open field
		Open field	Castanopsis eyrei	Schima superba	Young forests	Intermediate forests	Old forests		
Event 1	Precipitation [mm]	39.7	23.9	23.6	22.0	25.3	29.3	25.5	0.64
	Std Precipitation	-	9.61	6.62	4.12	7.07	11.89	7.69	
	Sand loss [g m ⁻²]	19.39	41.23	55.16	40.75	47.77	52.39	46.97	2.42
	Std sand loss	1.50	18.71	9.39	17.93	21.36	16.73	18.67	12.41
	n	1	6	3	6	6	6	18	
Event 2	Precipitation [mm]	42.1	28.2	37.0	19.4	37.3	31.5	29.4	0.70
	Std Precipitation	-	14.01	11.24	7.66	12.56	12.60	10.94	
	Sand loss [g m ⁻²]	21.76	60.50	77.42	34.51	66.17	66.56	55.75	2.56
	Std sand loss	0.96	29.36	13.96	16.67	24.37	35.86	25.63	26.63
	n	1	6	3	6	6	9	21	
Event 3	Precipitation [mm]	21.0	11.3	12.5	15.6	11.5	12.4	13.2	0.63
	Std Precipitation	-	4.20	3.65	3.83	4.21	5.50	4.51	
	Sand loss [g m ⁻²]	9.93	25.15	34.03	30.73	34.63	35.30	33.55	3.38
	Std sand loss	1.32	13.60	11.61	8.18	19.92	11.91	13.34	10.08
	n	1	6	3	6	6	12	24	
Event 4	Precipitation [mm]	40.5	29.5	25.9	18.7	23.2	27.2	23.0	0.57
	Std Precipitation	-	6.58	2.28	5.87	4.41	11.55	7.28	
	Sand loss [g m ⁻²]	17.91	43.21	53.60	26.29	50.53	50.65	42.49	2.37
	Std sand loss	0.84	14.80	6.14	12.34	21.24	27.44	20.34	24.14
	n	1	6	4	6	9	12	27	
Total ϕ	Precipitation [mm]	35.8	23.2	24.8	18.9	24.3	25.1	22.8	0.64
	Std Precipitation	-	8.60	5.95	5.37	7.06	10.39	7.61	
	Sand loss [g m ⁻²]	17.24	42.52	55.05	33.07	49.78	51.23	44.69	2.59
	Std sand loss	1.16	19.12	10.27	13.78	21.72	22.99	19.50	16.83
	n	4	24	13	24	27	39	90	

4. Discussion

4.1. Applicability of our splash cups for measuring splash erosion potential

The reproducibility of the results of the splash cups has been confirmed in this study by the low average standard deviation of only 1.16 (five replications per measurement; cf. Vis, 1986) and the high values for R^2 ($p < 0.01$) for the correlation between sand loss and the rainfall characteristics derived from the Vaisala sensor. The considerably better correlation of rainfall characteristics measured by the Vaisala sensor with sand loss of splash cups under open field conditions compared to those measured by the tipping-bucket rain gauge is clearly a result of a difference in the method of precipitation measurement. Since the Vaisala sensor records only drop impacts between 0.8 and 5.0 mm in size, less erosive drops below 0.8 mm are not considered in the calculation of rainfall amount per time. Consequently, the tipping-bucket rain gauge is recording more rainfall including smaller and less erosive drops from drizzle which hardly cause sand loss from splash cups. The higher precision of the Vaisala sensor by one order of magnitude has also to be taken into account, especially regarding events of low rainfall amount and intensity. Moreover, the relationship between rainfall intensity and sand loss per unit area indicates a threshold value for incipient sand loss being greater than zero. Nevertheless, the scatter around the origin inhibits a definite quantitative statement. Since the modified construction of the splash cups provides a sufficient drainage even at high rainfall intensities, a wash-off effect (Kinnell, 1974) has not been observed. During the rainfall events the sand surface was not substantially lowered and no rim-effect (Bisal, 1950; Hudson, 1965; Poesen and Torri, 1988) occurred.

4.2. Erosive potential of throughfall under forest vegetation as measured by splash cups

The measurements under forest vegetation showed splash erosion potential being on the average 2.59 times higher than under open field conditions. This corresponds well to the results of Nanko et al. (2004) who measured a 2.7 times higher kinetic energy under *Chamaecyparis obtusa* than under open field conditions. Concerning the difference between rainfall and throughfall erosivity, Vis (1986) measured a 1.4 times higher kinetic energy in a Colombian forest compared to open field conditions. This difference in magnitude compared

to our study might have been caused by a bigger size of the cups used by Vis (1986). In bigger sized cups, the central part is more distant from the edge making it more difficult for this sand to detach from the cup (Poesen and Torri, 1988). Moreover, much coarser and therefore less erodible sand was used for the filling of the cups. Both facts result in an underestimation of erosion potential compared to our study where much finer sand and smaller sized cups have been used. Mosley (1982) found slightly higher differences (factor 3.1) of sand loss in splash cups between open field conditions and a beech forest although using bigger sized cups and coarser unit sand. However, Mosley (1982) measured one extreme rainfall event (51 mm in 36 h) which might have resulted in an extraordinary erosion potential. Our results show that the differences in erosion potential between open field rainfall and throughfall are variable between rainfall events. This supports the findings of Nanko et al. (2004, 2006) who could show that wind speed and rainfall intensity affect the properties of throughfall as both factors influence for example the amount of canopy storage.

Due to the lowering of the sand surface of more than 3 mm the results of the measurements under vegetation show an underestimation of the effective erosion potential, which is a result of the previously mentioned rim-effect. The correction function proposed by Hudson (1965) and used in Salles and Poesen (2000) or Cornelis (2004) is not applicable to our data, as we use cups of a different size.

Coalescing drops from leaves and branches (drips) are responsible for a notable spatial heterogeneity of throughfall erosivity compared to open rainfall although the amount of throughfall in forests is generally about 10-40 % less compared to the open field (Vis, 1986; Brandt, 1988; Nanko et al., 2004; Wei et al., 2005; Reid and Lewis, 2009; Ziegler et al., 2009). In our case on the average 64 % of total precipitation reached the forest floor as throughfall. Hence, about one third of the total throughfall dissipates along branches and stems (stemflow) or evaporates. If we assume spatial representativeness of our splash cup measurements, the effect of changes in drop characteristics for kinetic energy of throughfall is even more pronounced. The higher the erosion potential under forest, the more important is an intact shrub- and litter-layer to prevent soil erosion (Zhou et al., 2002). In forests on slopes, however, downhill litter movement may result in a patchy distribution of litter (Tsukamoto, 1991) and bare ground occurs which is prone to erosion by continuous drop impact from drips (Nanko et al., 2008).

The differences in throughfall erosivity between the observed successional stages can be explained with different falling heights of the throughfall drops from the canopies (e.g. Dohrenwend, 1977; Brandt, 1988; Styczen and Høgh-Schmidt, 1988; Zhou et al., 2002; Nanko et al., 2008). The difference in sand loss and throughfall amount between young and intermediate successional stages is more distinct than between intermediate and old successional stages. This circumstance can be related to the forest structure. A much higher coverage and lower tree height in the young successional stage result in a lower sand loss from splash cups and lower amount of throughfall because of a higher interception. Rainfall amount and energy are absorbed by the vegetation and, the shorter distance between the leaves and the ground in younger forests has the effect that drops are not likely to reach terminal velocity. Forests of intermediate and old age are more similar regarding canopy cover and tree height, which is clearly reflected in the results obtained by splash cup and throughfall measurements. Thus, forests of older successional stages may be more susceptible to splash induced erosion compared to early successional forests.

Throughfall is much more diverse in time and space than open rainfall as demonstrated by the standard deviations. This can be explained by the various components of throughfall (free throughfall, drip) that are controlled by the architecture of the canopy (e.g. Mosley, 1982; Vis, 1986; Calder, 2001; Hall and Calder, 1993; Nanko et al., 2004; Nanko et al., 2008). Differences in throughfall between the investigated tree species (*Schima superba*, *Castanopsis eyrei*) suggest that throughfall characteristics are strongly influenced by traits of those species, e.g. leaves of *Schima superba* (average size = 38.09 cm²) are about three times larger than the leaves of *Castanopsis eyrei* (average size = 12.92 cm²) (Fig. 5) (Kröber, 2010). Thus, *Schima superba* may collect more water with its leaves than *Castanopsis eyrei*.



Fig. 5: Leaf samples of *Castanopsis eyrei* (a) and *Schima superba* (b) (black line = 5 cm). (Kröber, 2010).

5. Conclusions

We studied rainfall and throughfall erosivity in a subtropical forest ecosystem using sand-filled splash cups. Our results show that splash cup measurements yield precise and reproducible results under both open field conditions and forest vegetation. Under open field conditions the measured sand loss corresponded well with rainfall amount, average rainfall intensity, maximum rainfall intensity and the average of the five highest five minute intensities.

The comparison of two devices for the measurement of precipitation (tipping-bucket rain gauge and Vaisala sensor) demonstrate that measurements of the Vaisala sensor (drop size detection) corresponded much better to sand loss of splash cups in terms of rainfall amount and erosivity than to measurements of the tipping-bucket rain gauge. The erosion potential of throughfall drops in forests was considerably higher (2.59 times) than under open field conditions and the spatial variability of the erosion potential was much more diverse in forests, caused by free throughfall and drip. By placing the splash cups under certain tree species it could be demonstrated that the erosivity of throughfall may depend on the species

and also on the successional stage of the forest stand. The splash cup measurements made clear that the erosivity and amount of throughfall depends on the forest structure (age, cover, height). Moreover, it could be shown that the ratio rainfall erosivity and throughfall erosivity is variable between different events (cf. Nanko, 2006).

Schima superba generated throughfall drops of higher erosivity than *Castanopsis eyrei*. We assume that one reason for this finding is the larger size of the leaves, resulting in larger throughfall drops and particularly drip. The erosion potential is also a function of stand height because throughfall drops are much more likely to reach terminal velocity under intermediate and old-growth forests. Therefore we conclude that the potential of throughfall to detach soil by splash is also related to the age of the specific forest stand: young forests have the lowest and old forests the highest erosion potential. This accentuates the importance of a shrub, herb and litter layer in forest ecosystems to protect the soil against erosion.

Our study showed that splash cups are an appropriate method for comparing rainfall and throughfall erosivity. Despite the valuable and encouraging results presented in this paper a comparison with other studies remains challenging. This is due to the necessity of standardization of measuring equipment being one general difficulty of experimental studies in soil erosion (Stroosnijder, 2005). Differences caused by the measurement technique like cup size, grain size of the unit sand are typical. Further, varying external meteorological factors (Nanko, 2006) have to be taken into account.

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Manuscript 5

Estimation of throughfall erosivity in a highly diverse forest ecosystem using sand-filled splash cups

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Abstract

Sand-filled splash cups were used to study the erosive power of rainfall and throughfall in the humid subtropics of Southeast China. The splash cup measurements yielded precise and reproducible results under both open field conditions and forest vegetation. The splash cups were exposed to specific forest stands of different ages and to selected species (*Schima superba*, *Castanopsis eyrei*, *Daphniphyllum oldhamii*, *Lithocarpus glaber*) in the Gutianshan (古田山) National Nature Reserve (GNNR). The results of the measurements under forest vegetation show that the erosive power of throughfall drops to be 2.59 times higher compared to the open field. This accentuates the importance of shrub, herb and litter layers in forest ecosystems to protect the soil against erosion. Coalescing drops from leaves and branches (drips) are responsible for this notable gain in erosive power. Moreover, differences in

sandloss between the investigated tree species (deciduous, evergreen) revealed that the erosion potential and the spatial heterogeneity of throughfall are species-specific. This highlights the importance of selecting specific species for afforestation projects considering the prevention of soil erosion.

Keywords: Biodiversity and Ecosystem Functioning BEF-China; biodiversity; soil erosion; soil erosion experiment; splash cup; throughfall erosivity.

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Introduction

In soil erosion research it is widely accepted that vegetation is a key control for the type and intensity of erosion (e.g., Morgan, 2005; Thornes, 1990; Hudson, 1971). The current paradigm is that natural or quasi-natural vegetation protects the soil against erosion while agricultural land use generally enhances erosion. However, even severe soil erosion may take place under forest vegetation with a well developed canopy but high amounts of bare ground due to the lack of a shrub or herb layer (Nanko et al., 2008; Zhao, 2006). Especially on steep slopes relocation of litter can result in a patchy distribution of plant residues and litter. Thus, parts of the forest floor may remain un-covered and unprotected (Tsukamoto, 1991).

Moreover, climate change induces a shift of the precipitation regime to exceptionally intense rainfall events. Key mechanisms of a vegetation cover in reducing or enhancing erosion potential are the modification of drop size distribution, retention of raindrop impact on the soil and changes in amount and spatial distribution of rainfall at the ground surface.

This study focuses on the application of sand-filled splash cups to study rainfall and throughfall erosivity in natural systems. We show the relationship of rainfall and vegetation characteristics to the sandloss measured by splash cups.

Materials and Methods

This study was conducted in the Gutianshan National Nature Reserve (GNNR), Zhejiang Province, China. The center of the GNNR is located at N29°14.657' and E118°06.805'. The elevation ranges between 320 and 910 m above sea level. The soils are predominantly Cambisols (cf. IUSS Working Group WRB, 2007) developed on granite with a more or less thick saprolite cover. The climate at the GNNR is typical for the humid subtropics with an annual average temperature of 15.3 °C and a mean annual rainfall of 1 963.7 mm (Bruehlheide et al., 2010; Hu and Yu, 2008). Rainfall data were obtained from an automatic weather station in the centre of the GNNR.

Modified Splash Cups

The modified splash cups have a diameter of 4.6 cm and a surface of 16.62 cm². They were developed based on the archetype of Ellison (1947). We measured the unit sand remaining inside the cup after single natural rainfall events.

By using unit sand with distinct properties (grain size: 125–200 µm), it is possible to focus on other factors such as the differing characteristics of open rainfall and throughfall (Salles and Poesen, 2000) or wind effects to rain (Cornelis et al., 2004). Sandloss, as the target variable, is calculated as the difference of the initial weight and resulting weight. For a detailed description and calibration results of the splash cups, see Geißler et al. (2010).

Experimental Design

The experimental design of the splash cup measurements under vegetation consists of two parts: forest stand-based and species-based. The specific forest stands were selected along a biodiversity and succession gradient. To calibrate the method a set of five splash cups (surface=83.10 cm²) was positioned in a pentagon next to the climate station under open field conditions. To reveal effects of a single tree species on the erosivity, three sets of five splash cups at a time were positioned under the target trees. A target tree represents a typical individual of one of the selected species (*Schima superba*, *Castanopsis eyrei*, *Daphniphyllum oldhamii*, *Lithocarpus glaber*). The splash cups were established 1 m above ground to avoid

disturbance by animals, forest floor vegetation and differing inclination of slopes. One rainfall collector (collecting area=13.40 cm²) was positioned per splash cup. An outlier test was applied both to the rainfall data and the splash cup measurements with standard deviation $\times 2 + \text{mean}$ as a criterion for exclusion

Results and Discussion

Simultaneous measurements under open field conditions (Fig. 1a) and in forest stands (Fig. 1b) of the three successional stages showed a remarkable difference in sandloss. Throughfall in all varied between 57% and 70% of total precipitation. The average sandloss under vegetation (44.69 g/m²) was 2.59 times higher than that under open field conditions (17.24 g/m²). There was a non-linear increasing sandloss with increasing successional stage: the difference between the young successional stage and the intermediate successional stage (16.71 g/m², factor 1.51) was much higher than that between the intermediate successional stage and the old successional stage (1.45 g/m², factor 1.03) (Fig. 2).

The resulting standard deviations between the measurement replicates can be considered in two ways: (i) for open field conditions the standard deviation is much lower than that for all successional stages, and (ii) the difference in standard deviation between the young successional stage and the intermediate successional stage was much higher than that between the intermediate and the old successional stage (Fig. 3). The standard deviation found under two common species (*Schima superba*, *Castanopsis eyrei*) was much higher than that under open field conditions. Nevertheless, there were distinct differences in splash potential represented by sandloss between *Schima superba* (55.54 g/m²) and *Castanopsis eyrei* (42.18 g/m²), although the average amount of throughfall was quite similar (24.77 mm for *Schima superba* and 23.22 mm for *Castanopsis eyrei*).



Fig. 1: Splash cup under open field conditions (a), and under forest vegetation (b).

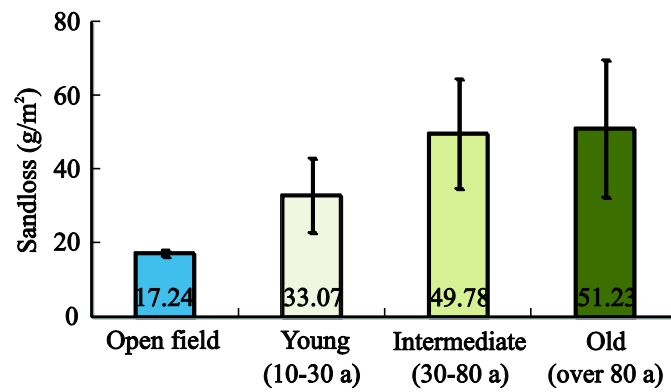


Fig. 2: Throughfall erosivity as measured by splash cups under open field conditions and three successional stages (solid lines=standard deviation).

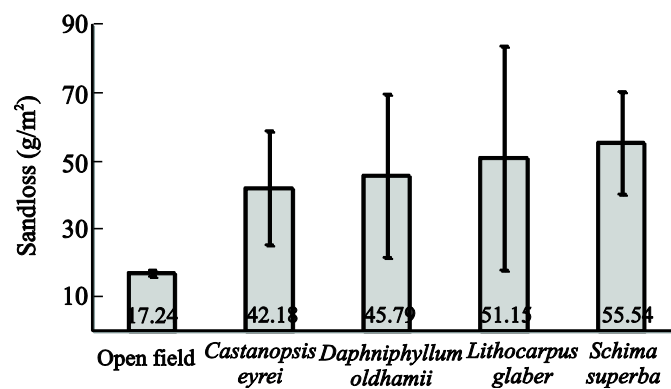


Fig. 3: Erosive power of throughfall as measured by splash cups for four tree species (solid lines= standard deviation).

The erosion potential of throughfall drops in forests was considerably higher (2.59 times) than that under open field conditions and the spatial variability of the erosion potential was much more diverse in forests, caused by free throughfall and drip. By placing the splash cups under certain tree species it could be demonstrated that the erosivity of throughfall depended on the species and also on the successional stage of the forest stand.

Schima superba, for example, generated throughfall drops of higher erosivity than *Castanopsis eyrei*. We assume that this is, amongst others, an effect of the larger size of the leaves of *Schima superba* which generates larger throughfall drops. The erosion potential is also a function of stand height because throughfall drops are much more likely to reach terminal velocity under old grown forests. Therefore, we conclude that the potential of throughfall to detach soil by splash is also related to the age of the specific forest stand: young forests have the lowest and old forests the highest erosion potential. This highlights the importance of a shrub, herb and litter layer in forest ecosystems to guard against soil erosion.

Conclusions

We studied rainfall and throughfall erosivity in a subtropical forest ecosystem using sand-filled splash cups. Our results show that the splash cup measurements yielded precise and reproducible results under both open field conditions and forest vegetation. The erosion potential of throughfall drops in forests was notably higher (2.59 times) than that under open field conditions and the spatial variability of the erosion potential was much more diverse in forests, caused by the two components of throughfall (free throughfall and drip). By placing the splash cups under certain tree species and specific forest stands it could be demonstrated that the erosivity of throughfall depended on the species and also on the successional stage. *Schima superba* generated throughfall drops of much higher erosivity than, for example, *Castanopsis eyrei*. We assume that this is, amongst others, an effect of the larger size of the leaves which generates larger throughfall drops, particularly drip. Tree diversity in forests may therefore also result in a higher variability of throughfall erosivity. The erosion potential is also a function of stand height because throughfall drops are much more likely to reach terminal velocity under old forests. Therefore, we conclude that the potential of throughfall to

detach soil by splash is also related to the age of the specific forest stand: young forests have the lowest and old forests the highest erosion potential. This accentuates the importance of a shrub, herb and litter layer in forest ecosystems to protect the soil against erosion.

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Manuscript 6

Biodiversity and throughfall kinetic energy in forest ecosystems in the humid subtropics of SE China – Effects of tree canopy structure, traits, and diversity

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Abstract

Throughfall kinetic energy (KE) and its variability in relation to biodiversity and other forest stand variables (tree canopy structure, tree canopy functional trait identity and tree canopy diversity) were studied in a secondary subtropical broad-leaved forest ecosystem. The overall aim was to contribute to the understanding of the mechanisms of the ecosystem service of soil erosion prevention in forests. Measurements were performed in the Gutianshan National Nature Reserve (GNNR), a biodiversity hotspot in the northern hemisphere with more than 60 woody species per km². For our study we focused on forest stands of contrasting biodiversity.

Using a mixed model approach we could identify effects of tree canopy structure (height, LAI), diversity (rarefied species number) and functional trait identity (proportion of needle leafed species). KE increases with canopy height and biodiversity and decreases with increasing proportion of needle leafed species within a plot and an increasing LAI.

The results suggest that differences in KE between various forest stands are largely controlled by vegetation height as well as by redistribution and storage of rainfall within the canopy. The effect of higher KE in more diverse stands is compensated by higher total plant cover, keeping throughfall KE more or less constant and enhancing its variability with increasing diversity.

A higher total plant cover and biomass in species rich forests results in throughfall being much more likely to be re-intercepted or stored in the various canopy layers. The same mechanism enhances spatial heterogeneity in species rich forests. In our case, a higher diversity in species diminishes the effect of increasing stand heights with age which would cause a generally higher throughfall KE in older forests.

Keywords: Soil erosion; ecosystem functioning; ecosystem service; splash cups; BEF-China; Gutianshan National Nature Reserve.

1. Introduction

Biodiversity, ecosystem functioning and soil erosion

The term “Biodiversity and Ecosystem Functioning” (BEF) emerged beginning of the 1990s due to growing concern about a global loss of biodiversity. The basic question in biodiversity research deals with the relation of biodiversity to various ecosystem services (Scherer-Lorenzen, 2005). In forest ecosystems, regulating and supporting services like primary production, nutrient cycling, species conservation, soil formation, climate regulation and the prevention of soil erosion are of major interest (Bruehlheide et al., 2011).

Soil erosion and its prevention is a central topic in the subtropics, in particular in SE China (e.g. Thorp, 1936; Huang, 1987; Aldhous, 1993; Kolb, 2003; Shi et al., 2004; Cai et

al., 2005; Wang et al., 2005; Yu et al., 2006), where high rainfall rates cause severe and continuous soil losses and therefore enormous economic costs (Pimentel et al., 1995; Lal, 1998).

Forest ecosystems protect the soil very efficiently against erosion by water (e.g. Bechtle, 1974; Kwaad, 1977; Brooks et al., 1994; Aerts et al., 2006). This ecosystem function of erosion control (Hooper et al., 2005) is based on the effects of

- (1) a tree to keep away the direct impact of a raindrop onto the soil surface (particle detachment and aggregate breakdown) and
- (2) high infiltration rates of forest soils due to low bulk densities and high pore volumes.

Although soil erosion is generally reduced under forests (Smith, 1914), high sediment loads of rivers from forested catchments, especially in subtropical regions with high rainfall intensities, are often reported and related to climate change (Marks, 1998, Molnar, 2004).

It can be assumed that mechanisms controlling soil erosion under forest are very dynamic in space and time and may even increase soil loss with height growth due to changes of the kinetic energy (KE) of rainfall (Morgan, 2005). This has been proved for monocultures like acacia forest in Indonesia (Wiersum et al., 1979), beech forest in New Zealand (Mosley, 1982), tropical rain forest in Colombia (Vis, 1986), tropical rain forest in Brazil (Brandt, 1988), a forest plantation in Japan (Nanko et al., 2008) or a secondary forest in subtropical China (Geißler et al., 2010).

Variables considered to describe the variation of throughfall KE or throughfall redistribution in general under forest mainly refer to the characteristics of the rainfall event (e.g. Nanko et al., 2006; Levia and Frost, 2010), the age or height of the forest studied (e.g. Wakiyama et al., 2010), total plant cover or LAI (e.g. Gómez et al., 2001) or to leaf traits (Hall and Calder, 1993).

However, the role of biodiversity in this process system is not yet clarified although the relations between erosion processes and biodiversity are of great interest (Balvanera et al., 2006). Up to now studies on this topic remain scarce but it is suggested biodiversity having a negative effect on soil erosion. Körner (2002) e.g. suggests that a highly structured, diverse ground cover is the basis for soil erosion control on high mountain slopes. Pimentel (1998)

points out that soil erosion has a strong negative effect on biodiversity due to the loss of biomass from the ecosystem which results in reduced productivity. Consequently, soil erosion disturbs the stability of an ecosystem and can start a feedback loop. Up to now no study focused on the relation of soil erosion and biodiversity in forest ecosystems.

Objectives

Here we study the impact of tree canopy structure, functional trait identity and biodiversity on KE of raindrops in forests. The objective is to reveal the mechanisms of soil erosion in relation to biodiversity under forest in a species rich ecosystem in subtropical SE China.

Therefore, the aims of this study are:

- (i) to relate throughfall KE to rainfall KE
- (ii) to test for (inter-)relationships between biodiversity, tree canopy structure and KE of throughfall
- (iii) to test for effects of biodiversity and tree canopy structure on the variability of throughfall KE

2. Material and Methods

Study area

This study was conducted in the Gutianshan National Nature Reserve (GNNR), Zhejiang Province, P.R. China. The GNNR is located at N 29°14.657' and E 118°06.805' (center). The elevation ranges between 320 m and 910 m above sea level. The soils are predominantly Cambisols (cf. IUSS Working Group WRB, 2007) developed on granite with a more or less thick saprolite cover. The climate at the GNNR is typical of subtropical monsoon regions with an annual average temperature of 15.3 °C and a mean annual rainfall of 1963.7 mm (Hu

and Yu, 2008). The forest in the GNNR is extraordinary rich in species (Hu and Yu, 2008; Bruelheide et al., 2011).

In the framework of the BEF-China research group, a multidisciplinary research unit focusing the relationship between biodiversity and ecosystem services, 27 Comparative Study Plots (CSPs) were established in the GNNR stratified by successional stages (Bruelheide et al., 2011).

Throughfall KE measurements

Measurements of throughfall KE were conducted by the means of calibrated splash cups. The major advantage of splash cups is their easy handling and the high number of replications that can be obtained at reasonable costs. Moreover, they are able to measure the whole event rather than a short time span.

For measuring KE of throughfall “T Splash cups” were used in this study. These splash cups 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. For further information about the measurement procedure and the calibration results see Scholten et al. (2011) and Geißler et al. (2010).

Tree canopy and rainfall event related variables

The canopy related variables included in this study mainly refer to diversity of the studied plot, crown openness and leaf traits. Event related variables include rainfall amount and intensity as well as wind speed during the events. Individual variables were tested for collinearity before setting up the models. They were sorted by five hierarchical blocks in the order of their expected impact, namely event characteristics, age/ height of the vegetation, diversity measures, crown openness and leaf traits:

- (i) Event characteristics: Using an automatic weather station and splash cups, rainfall amount, rainfall intensity as well as rainfall KE and wind speed were measured in 5 min intervals for all events measured and included in the models.
- (ii) Age-height complex: Using three different tree canopy layers, we calculated a weighted average of canopy height by using tree layer cover as weight. Plot basal area was included as a measure of age of the plot studied.
- (iii) Diversity: We quantified tree canopy diversity using rarefaction curves (Sanders, 1968; Hurlbert, 1971). This method allows comparing sites with different numbers of tree individuals. As an alternative measure for biodiversity we used the functional diversity of tree leaf traits. We included specific leaf area, leaf size as well as presence absence of dentate, pinnate, or needle leaves of all individuals found in the plots. Based on tree species basal area in the plots, we calculated functional identity (see below) and functional dispersion of each plot (Laliberté and Legendre, 2010).
- (iv) Crown openness: Leaf area index (LAI) as a measure of crown openness was assessed using hemispherical photographs (Kundela, 2009). As a further measure of crown openness the estimated coverage values of the tree layers were included in the candidate models.
- (v) Leaf traits functional identity: Plot leaf trait functional identity was quantified as weighted mean of a leaf trait with basal area of the species used as weight. We considered the weighted mean of included specific leaf area and leaf size as numeric traits and coded presence/ absence of dentate, pinnate, or needle leaves as 0 and 1.

Experimental design

The experimental design of the splash cup measurements consists of a plot-based approach with 15 splash cups per plot (Fig. 1). From the 27 CSPs 15 plots of contrasting biodiversity were selected for this study. The splash cups were positioned randomly on the CSP according to a 1 m wide grid resulting in 900 possible positions. Consequently, the splash cups had a minimum distance of 1 m to each other. In case of a tree or any other obstacle being at the envisaged position, the splash cup was positioned at the next possible

position. The splash cups were numbered 1 to 15 and the positions remained constant during the events measured.

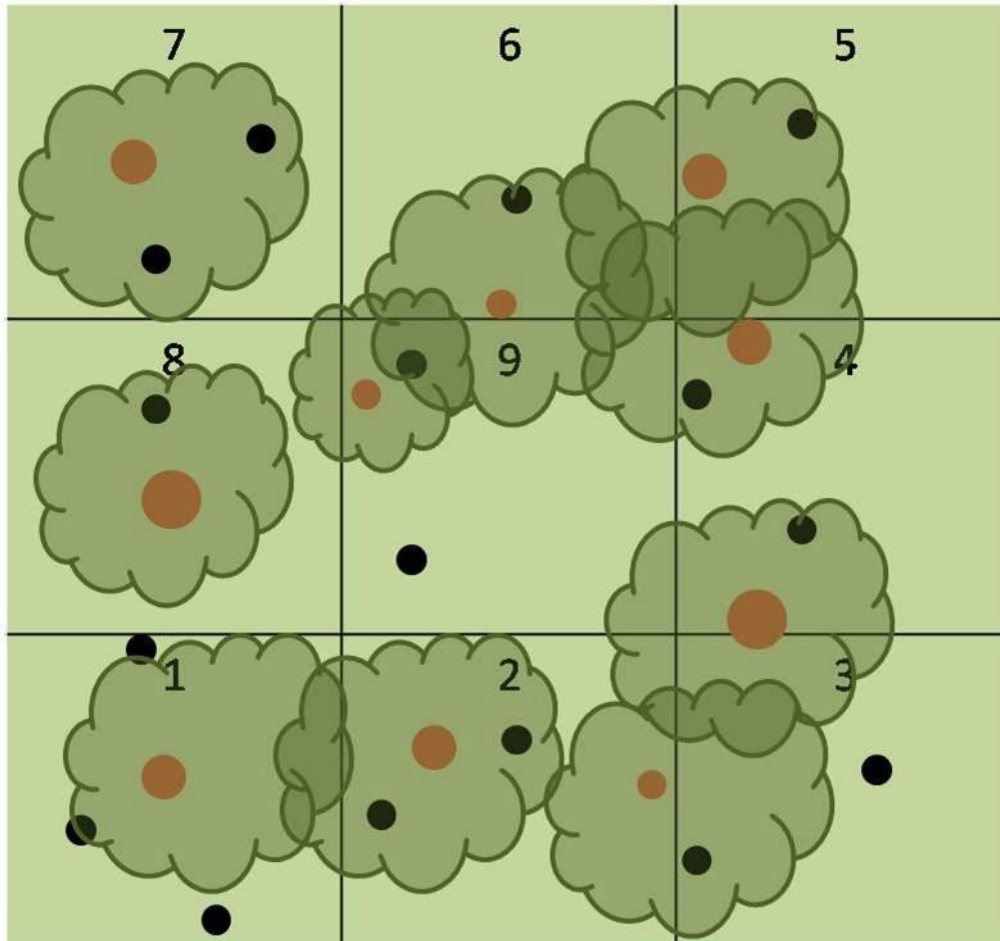


Fig. 1: Experimental design for the measurements under vegetation (brown circles = stems, black dots = splash cups).

Statistical analysis

The effect of forest structure on throughfall KE and the variability of throughfall KE was tested using mixed effects models. Analyses were performed using event and plot, as well as the positions of the splash cups within the plot, as random factors.

Due to the hierarchical design of splash cups nested in plots and plots measured at different rainfall events, we used mixed models with crossed random factors to assess the

impact of rainfall event and tree canopy related variables on throughfall KE and its variability. This approach allows us to test for the importance of splash cup identity (and thus spatial position of the splash cup) in explaining variance in throughfall KE using the variance component introduced by the splash cups.

Our candidate models all include one variable for each of the five blocks introduced above. Starting with the characteristics of the rainfall event, we used backwards selection to identify the most important variable in each of the groups (Seltman, 2010). We used a similar approach for the variability of KE. Since the lowest spatial level for variability of KE is the plot level, splash cup positions are not included in this model.

All analyses were performed using R 2.12 (R Development Core Team, 2010) together with the packages “lme4” (Bates et al., 2007) and “multcomp” (Hothorn et al., 2008). Functional trait measures were calculated using the “FD” package (Laliberté and Legendre, 2010).

3. Results

Relation between KE of open field rainfall and throughfall KE

The rainfall amounts for the events measured range from 1.80 mm up to 68.31 mm, while the maximum intensities range between 1.18 mm h⁻¹ and 55.73 mm h⁻¹ (Tab. 1). The lowest rainfall KE was measured during event 9 (13.13 J m⁻²) while the highest rainfall KE was measured during event 6 (717.02 J m⁻²) with an average rainfall KE of 297.25 J m⁻² over all events measured. KE of throughfall ranged from 62.71 J m⁻² for event 9 and 1237.04 J m⁻² for event 6 (average 685.10 J m⁻²). The ratio rainfall/ throughfall ranged from 1.37 for event 7 and 7.61 for event 11 (average: 3.79). The higher the rainfall amount (Fig. 2) and rainfall intensity (Fig. 3) are, the closer is the relationship between rainfall KE and throughfall KE.

Tab. 1: Characteristics of the rainfall events measured.

Rainfall event	Rainfall amount (mm)	Peak rainfall intensity (mm/h)	Peak wind speed (m/s)	Kinetic energy of rainfall (J/m ²)	Kinetic energy of throughfall (J/m ²)	Throughfall KE / rainfall KE
6	67.34	55.73	3.8	717.02	1237.04	1.73
7	68.31	33.79	2.2	701.46	958.26	1.37
8	26.15	8.98	1.9	137.45	646.31	4.70
9	1.80	1.18	1.1	13.13	62.71	4.78
10	33.95	18.65	5.8	273.16	837.93	3.07
11	3.80	5.23	5.5	26.27	199.77	7.61
12	55.11	32.98	1.9	413.24	1119.33	2.71
13	11.61	4.61	1.9	96.31	419.48	4.36
average				297.25	685.10	3.79

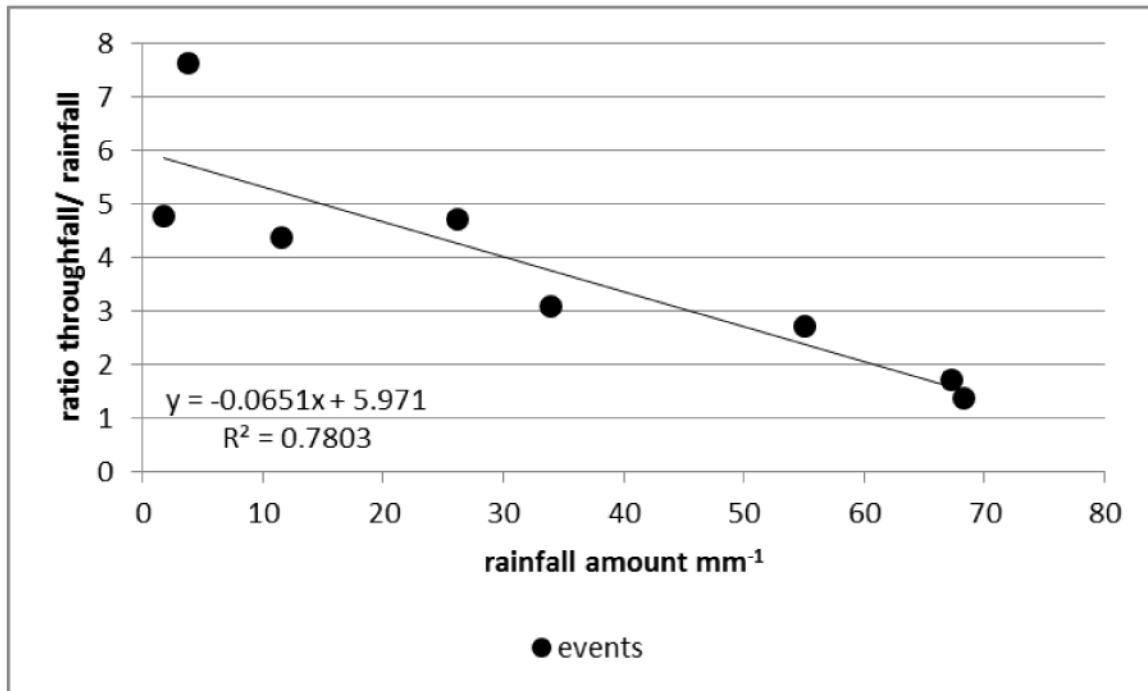


Fig. 2: Ratio between throughfall kinetic energy and rainfall kinetic energy in relation to rainfall amount.

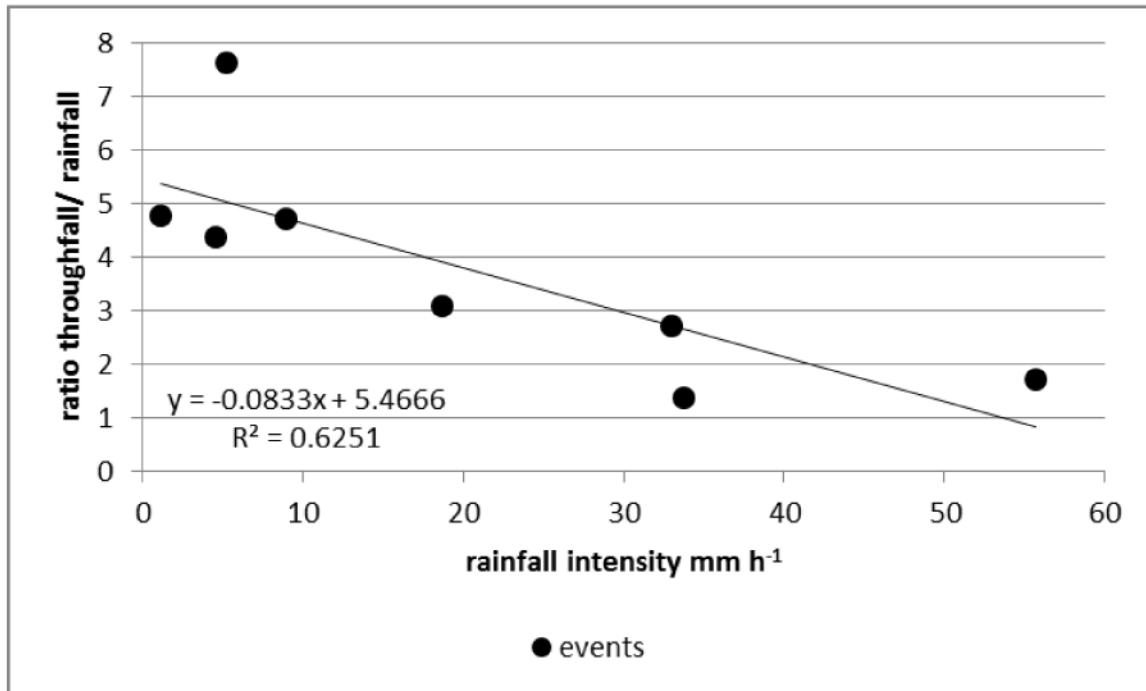


Fig. 3: Ratio between throughfall kinetic energy and rainfall kinetic energy in relation to rainfall intensity.

Relation between KE of throughfall, forest stand variables and biodiversity

In our experiment rainfall amount and weighted mean height of the tree layers as well as the interaction between both were the most important effects on throughfall KE for the eight events studied (Tab. 2). Rainfall intensity, rainfall KE and wind speed (block 1) all influenced model quality negatively and were therefore omitted. From block 2 weighted mean height of the vegetation improved model quality in contrast to age of the plot and plot basal area. Fig. 4 shows the relation between throughfall KE and the weighted mean height of the vegetation of the plot. Except for the event with the lowest magnitude (event 9), there is a general increase in throughfall KE with increasing weighted mean vegetation height.

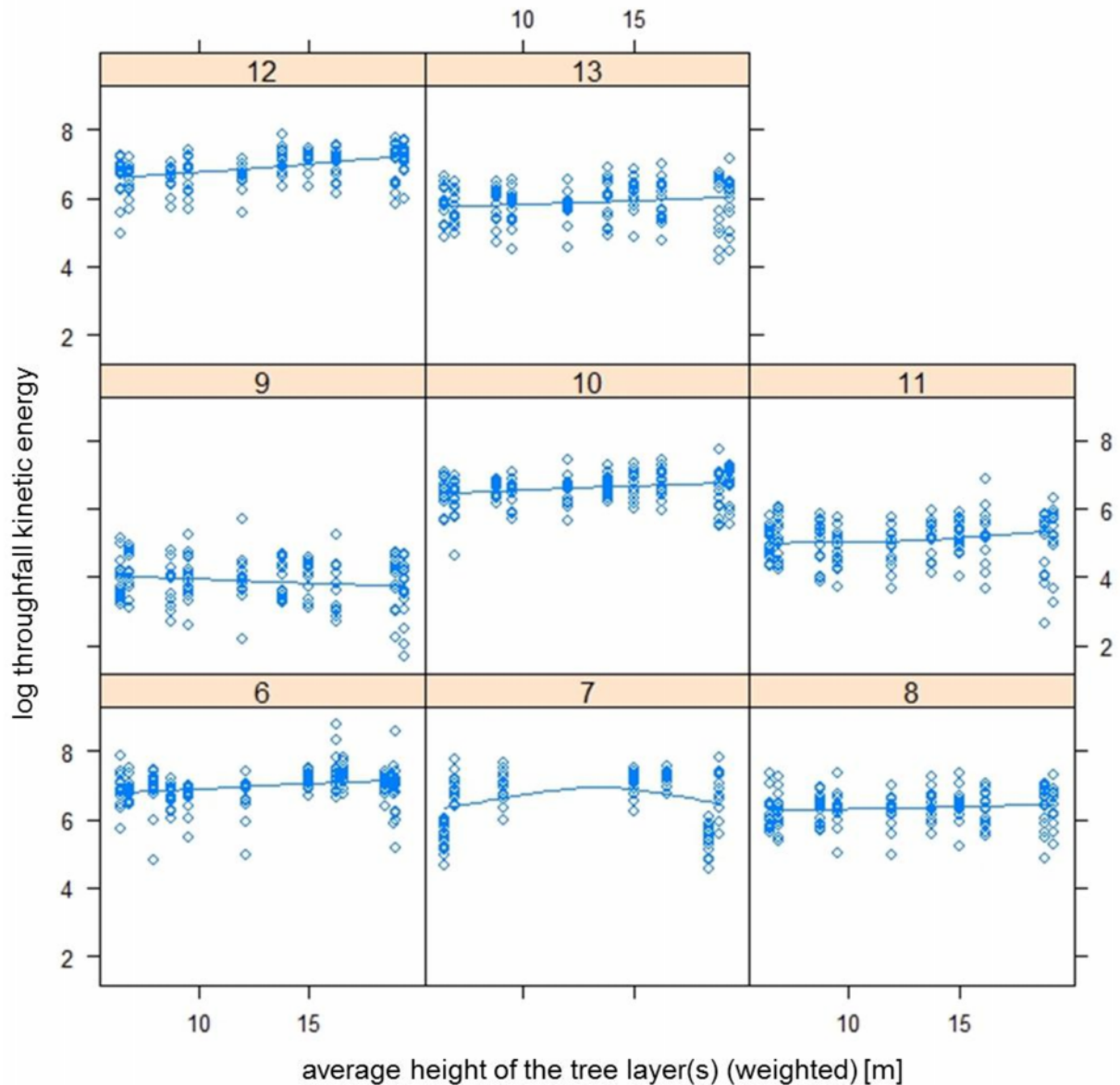


Fig. 4: Relation between log throughfall kinetic energy and average height of the tree layers for rainfall events 6-13.

In block 3 (diversity measures) biodiversity (rarefaction method) had a significant slightly positive effect on throughfall KE ($p = 0.0018$). In more diverse plots KE below the tree and shrub layers tends to be slightly higher than in less diverse plots (Fig. 5).

LAI (block 4: crown openness) had a significant negative effect on throughfall KE. The higher the LAI, the lower is the KE of throughfall. Except for the low magnitude event 9 there is a constant decrease in KE of throughfall with increasing LAI values (Fig. 6). Tree layer cover did not enter the final model.

Tab. 2: Effects influencing throughfall kinetic energy. Results of the simplified mixed effects model.

	Estimate	Std. Error	z value	Pr(> z)	sig.
(Intercept)	5.91915	0.2064	28.678	< 2e-16	***
rainfall amount	0.80111	0.19645	4.078	4.54E-05	***
weighted mean height of the vegetation	-0.13158	0.06255	-2.104	0.0354	*
biodiversity (rarefy 100)	0.12665	0.06434	1.968	0.0490	*
coniferousness (proportion of coniferous species)	-0.11717	0.05507	-2.127	0.0334	*
LAI	-0.11431	0.05788	-1.975	0.0483	*
rainfall amount:weighted mean height	0.09986	0.01407	7.099	1.25E-12	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Univariate p values reported)

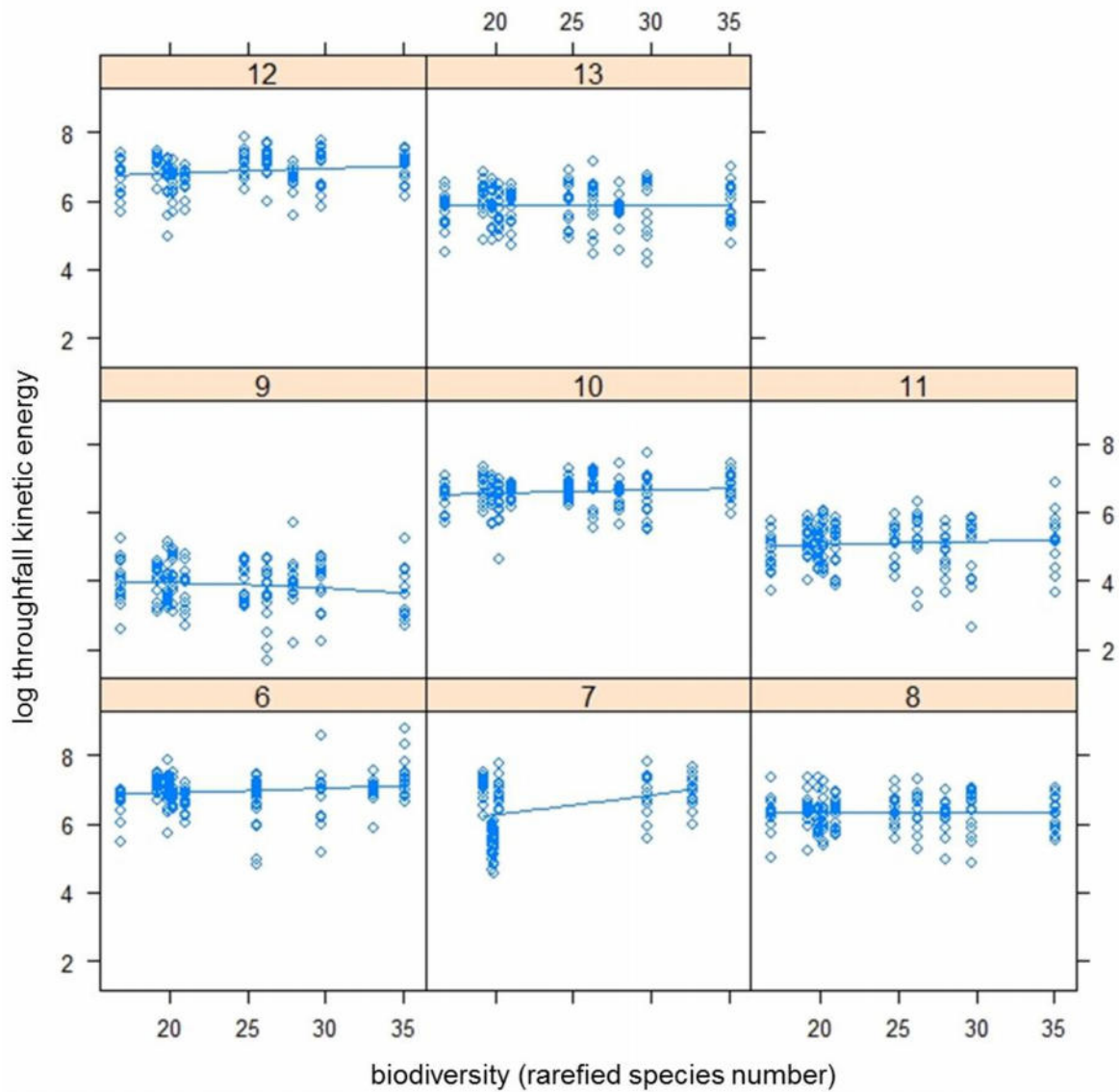


Fig. 5: Relation between log throughfall kinetic energy and biodiversity for rainfall events 6-13.

From block 5 (leaf traits) the proportion of coniferous species in a given plot had a significant negative impact on throughfall KE. Plots with a higher proportion of coniferous species in the tree layer generally receive less throughfall KE.

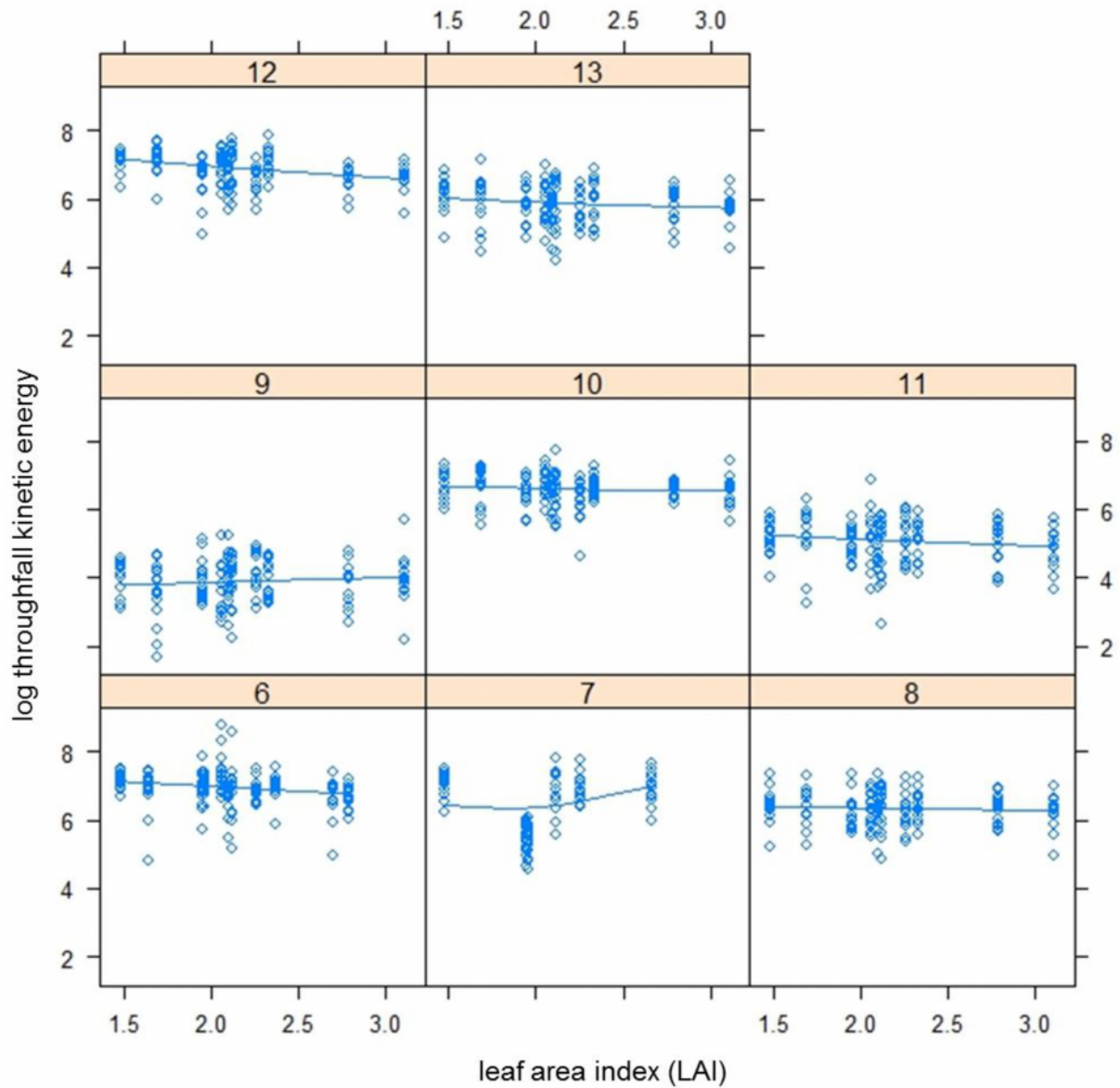


Fig. 6: Relation between log throughfall kinetic energy and leaf area index for rainfall events 6-13.

Variables not mentioned further here did not enter the final model.

Variability of KE of throughfall related to forest stand variables and biodiversity

The most important effects on the variation of throughfall KE were the significant effects of rainfall intensity and biodiversity (Tab. 3). Generally, variability of throughfall KE increases as the biodiversity of a given plot during a given event increases (Fig. 7).

Plot basal area, plot age, leaf area, LAI, weighted mean height and functional diversity did not enter the final model.

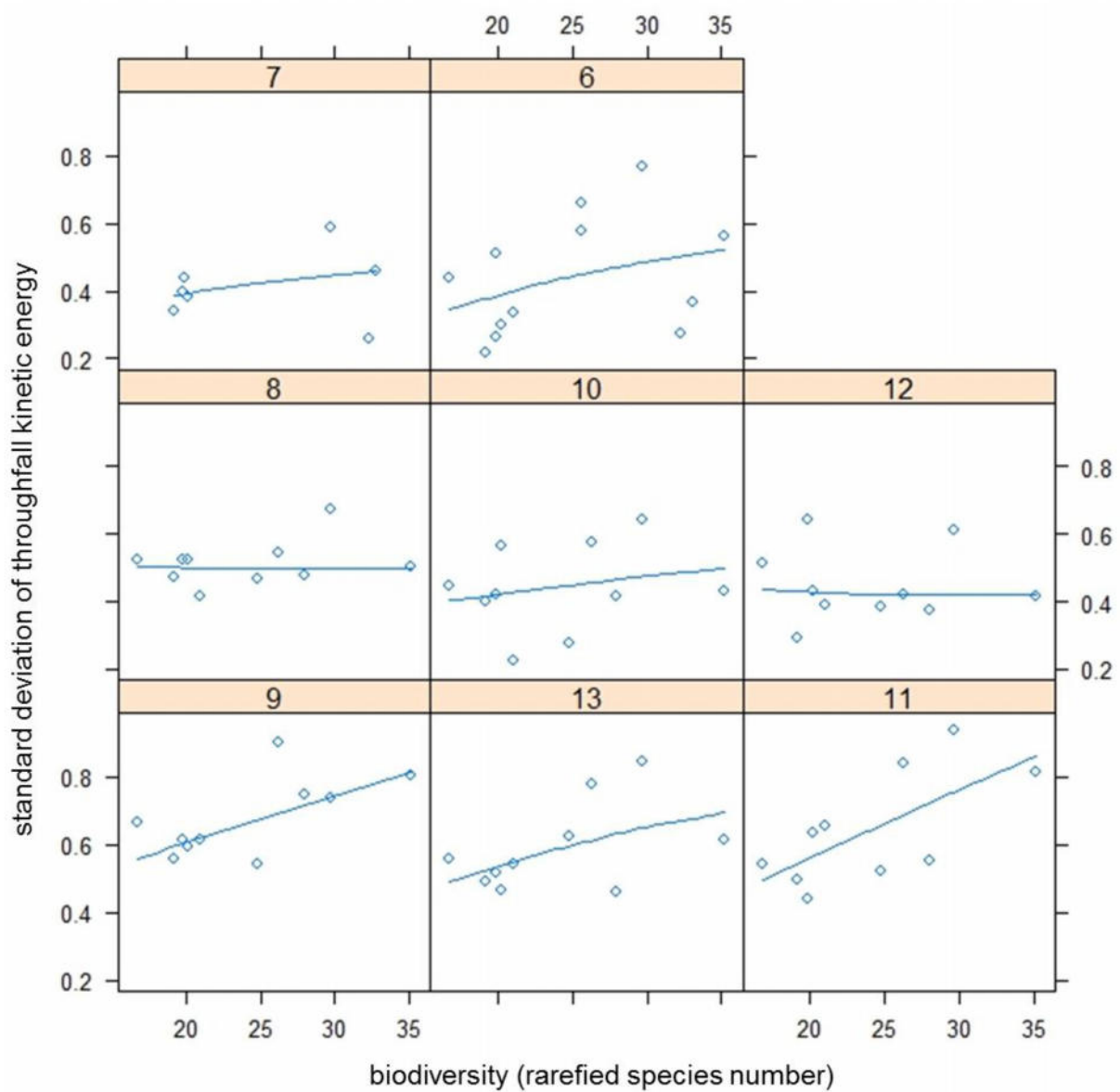


Fig. 7: Relation between standard deviation of throughfall kinetic energy and biodiversity for rainfall events 6-13.

Tab. 3: Effects influencing the standard deviation of throughfall kinetic energy. Results of the simplified mixed effects model.

	Estimate	Std. Error	z value	Pr(> z)	sig.
(Intercept)	0.53288	0.02595	20.531	< 2e-16	***
rainfall intensity	-0.08651	0.01506	-5.745	9.17E-09	***
biodiversity (rarefy 100)	0.05018	0.02371	2.116	0.0343	*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Univariate p values reported)

4. Discussion

A highly variable relation between KE of open field rainfall and throughfall KE

The results of the events measured show that the relation between rainfall KE and throughfall KE is highly variable in time depending on the amount and intensity of rainfall. This indicates that canopy storage has a substantial effect on throughfall KE. In low amount and low intensity events there is in general a higher chance of rainfall to be intercepted and accumulated on leaves and branches. Contrastingly, higher event magnitudes and intensity result in a lower storage capacity of the canopy. Calder et al. (1996), Levia and Frost (2006) and Nanko et al. (2006) explain this circumstance with larger raindrops hitting the canopy during high magnitude events, preventing a storage on leaves and branches and allow a subsequent release of small throughfall drops. However, in low magnitude events, water can converge on leaves and fall to the ground as large drops gaining high values of KE. This results in a large difference in KE between open field and forest (e.g. event 9). In high magnitude events, the permanent impact of large drops prevents the water to converge on leaves and water is released from the canopy more easily resulting in much smaller drops with less KE. The same process system described here is responsible for higher throughfall volumes in tropical than in temperate regions where generally precipitation events larger in magnitude and intensity occur (Levia and Frost, 2006). Although wind speed is also supposed to affect this process system through canopy vibration (Nanko et al., 2006), no relationship ($R^2 = 0.047$) could be found in our data.

Species richness keeps KE values constant during succession

As expected, rainfall amount is the most important variable concerning throughfall KE. Rainfall amount showed a highly significant positive effect on throughfall KE which is unsurprising (see 4.1; e.g. Levia and Frost, 2006) as there is generally a strong linear relationship between rainfall amount (mm) and KE (J m^{-2}) (e.g. Scholten et al., 2011). Numerous researchers found a dependency of throughfall amount on rainfall amount (e.g. Stogsdill et al. 1989, Filoso et al. 1999, Carlyle-Moses et al. 2004). This suggests throughfall KE being largely controlled by rainfall amount arriving at the canopy. Over the rainfall events measured rainfall amount was the variable describing by far most of the variability of throughfall KE.

The weighted mean height of the vegetation proved to have a significant effect on throughfall KE as well. The height effect has been recognized by Chapman as early as 1948 and confirmed thereafter by numerous authors (e.g. Tsukamoto, 1966; Mosley, 1982; Wiersum, 1985; Vis, 1986; Brandt, 1988; Brandt, 1989; Nanko et al., 2004; Nanko et al., 2008). Nevertheless, weighted mean height is only marginally significant (at the 0.5 level) although it is supposed to be a rather strong effect on throughfall KE. The cause for this circumstance is probably the vertical layering of the forest which is incorporated in weighted mean height through the coverage values for every layer. This is also the substantial difference to many other studies of throughfall KE which were performed mainly in (young) forest plantations, where height of the vegetation in a given plot remains rather constant (Chapman, 1948; Tsukamoto, 1966; Nanko et al., 2008; Wakiyama et al., 2010). Through vegetation layering the height effect gets less clear than one would expect (Wiersum, 1985).

The interaction between rainfall amount and weighted mean height of the vegetation also showed to be significant. This indicates that during forest growth the relation of rainfall KE to throughfall KE changes (which affects the measured values for KE). For example in a dense young forest cover values are the highest (74% in our case) decreasing with increasing age or height of the vegetation (down to 50% in our case). This again affects canopy storage.

The slightly positive relationship between throughfall KE and biodiversity can be attributed to the increase of species richness with growing stand age in the forests studied. With increasing forest age species accumulate through random immigration of recruits during succession (Bruelheide et al., 2011). Due to the gain of height with increasing forest age one

would expect a substantially higher throughfall KE in species rich (and therefore mostly late successional) forests. However, throughfall KE remains rather constant with increasing species richness (Fig. 6). This means that species rich forests achieve to keep throughfall kinetic energy low, although maximum falling height of the drops is generally higher. However, in species rich forest ecosystems plant biomass and total plant cover is much higher than in species poor forests (Loreau et al., 2001; Scherer-Lorenzen 2005; Hooper et al., 2005; Balvanera et al., 2006). Additionally, in species rich forests, ecological niches are better exploited and consequently throughfall drops are much more likely to be re-intercepted by lower vegetation layers. Brandt (1988) and Wiersum (1985) have shown that a highly structured forest ecosystem keeps throughfall KE at low values despite of a total gain in height of the forest stand.

From block 5, LAI showed to have a significant negative effect on throughfall KE. With increasing LAI throughfall KE decreases. Basically, LAI is a measure of crown thickness and canopy openness. Therefore, higher LAI values should result in higher canopy storage, e.g. a smaller amount of throughfall or throughfall KE reaching the forest floor (e.g. Park and Cameron, 2008). Again, on the one hand this implies differences in throughfall KE being largely controlled by an alteration of the spatial distribution of the amount of throughfall. On the other hand also throughfall KE is lowered independently of rainfall amount under thicker canopies through the process of re-interception. Falling drops in thick canopies are much more likely to be re-intercepted and splitted by lower parts of the canopy (Nanko et al., 2008b) which has a negative effect on throughfall KE.

The significant negative impact of the proportion of coniferous species (block 5: leaf traits) on throughfall KE can be attributed to differences between throughfall drop generation and leaf shape. Drops released from needle shaped leaves generally have less KE than drops from broad-leaved species as the storage capacity of needle shaped leaves is relatively small (Armstrong and Mitchell, 1988; Nanko et al., 2006). According to this, regarding KE of throughfall a certain proportion of coniferous species in a specific forest has beneficial effects for the forest ecosystem by lowering throughfall erosivity.

Species richness enhances spatial variability of throughfall KE

Concerning the variability of throughfall KE only variables from block 1 (event characteristics) and from block 3 (diversity measures) showed significant trends. During model selection rainfall intensity appeared to describe variability of throughfall KE better than rainfall amount and rainfall KE. According to our data, increasing rainfall intensity seems to lead to a decreasing variability of throughfall KE. As described above KE under forest is closely connected to rainfall amount and many related variables (e.g. LAI, crown openness, weighted mean height) are responsible for re-distributing rainfall by temporary canopy storage. Nevertheless, concerning higher rainfall intensities storage on leaves is reduced because of two reasons resulting in canopy vibration:

(1) permanent impact of large drops and

(2) high wind speeds often associated with high rainfall intensities (e.g. Nanko et al., 2006).

Therefore, for higher rainfall intensities it is less likely for a given position within the forest being in a rain-shadow and thereby enhancing spatial variability of throughfall KE.

The significant positive relationship between variability of throughfall KE and biodiversity is reasonable as both the variability of throughfall KE and biodiversity are measures of heterogeneity. With increasing biodiversity of a forest stand, also the variability of throughfall increases substantially.

As mentioned above, biodiversity in the GNNR is closely related to the successional stage of a specific forest stand (Bruelheide et al., 2011) and one might argue the variability of throughfall just being a function of forest age. Nevertheless, through backward model selection none of the parameters describing the age or height of a specific forest stand (block 2: successional stage, basal diameter, weighted mean height) showed to have any significant influence on the variability of throughfall.

Moreover, as it is supposed that both throughfall volume and KE are species specific (Hall and Calder, 1993; Levia and Frost, 2006; Nanko et al., 2006; Geißler et al., 2010). Hence, a higher number of species in a given plot should result in a more heterogeneous pattern of throughfall amount and KE. In more diverse plots a high number of species is

occupying several ecological niches (Hutchinson, 1957) thereby increasing total plant cover in different heights. Consequently, in a highly diverse forest plot, throughfall is very likely to be intercepted in e.g. different heights or to a different extent resulting in a more heterogeneous pattern of throughfall amount and KE.

5. Conclusions

Rainfall and throughfall erosivity were studied in a secondary subtropical broad-leaved forest in SE China using calibrated splash cups. It could be shown that the decrease of the rainfall KE/ throughfall KE ratio with increasing rainfall amount and intensity is related to canopy storage capacity during a given event. In high magnitude rainfall events, the storage capacity of the canopy is reduced as permanent drop impacts prohibit the filling of the reservoirs on the leaves which would result in a periodic release of large, highly erosive drops.

It could also be shown that a variety of variables describes the alteration of rainfall into throughfall in a highly diverse forest ecosystem. Basically, the differences between rainfall KE and throughfall KE are supposed to be controlled by the redistribution of rain water within the canopy as every species or individual has its own capacity to store water in the canopy. Basic measures describing this redistribution and alteration are biodiversity, LAI, weighted mean height of the vegetation and the proportion of coniferous species within a plot.

Biodiversity affects throughfall KE through a higher total plant cover which results in a more structured and diverse cover at different heights. This keeps – despite increasing stand heights – throughfall KE more or less constant. Finally, through varying rainfall amount and -intensity this process system of redistribution and storage is controlled and influenced externally.

6. References

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Curriculum Vitae

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Scientific publications and conference contributions

Scientific papers (peer reviewed)

- Geißler, C., Lang, A. C., von Oheimb, G., Härdtle, W., Baruffol, M., Scholten, T. (under review): An experimental test of the effectiveness of young trees to reduce the kinetic energy of rainfall – Importance of stand density, tree architecture and species identity. *Agricultural and Forest Meteorology*.
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Conference contributions and other publications

Geißler, C., Kühn, P., Scholten, T. (2010): Soil erosion potential under forest vegetation in the humid subtropics of southeast China. IUSS World Congress 2010, Brisbane, Australia.

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