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Carbon pools and sequestration in vegetation, litter dynamics and hydraulic anatomic properties in rainforest transformation systems in Indonesia

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Summary

Globally rising demand for cash crops such as oil palm, rubber, and cacao is driving the extensive conversion of natural rainforests in Southeast Asia with increasing speed. The consequences for humans and nature are immense and until today not thoroughly investigated.

In the present thesis the impact of natural rainforest conversion into intensively managed rubber and oil palm monocultures, and smallholder rubber and cacao agroforests on carbon storage and sequestration, litter dynamics and hydraulic anatomic properties in Indonesia was assessed and quantified. To fulfill the objectives, carbon and nutrient dynamics in phytomass of lowland rainforest transformation systems in two regions of Jambi Province on Sumatra were studied, while estimators of tree productivity and hydraulic anatomy patterns were investigated in cacao agroforests in Central Sulawesi.

The transformation of rainforest in our study area clearly resulted in significantly lower total carbon stocks in all investigated land-use types. According to our estimations, natural forests in this region store three times more carbon in biomass than even the extensively utilized jungle rubber system. The total carbon pools comprising aboveground tree biomass, dead wood debris as well as coarse and fine roots in rubber and oil palm monocultures consist of even less than 20 % of the natural forest C stocks they are replacing. Thus, compensating for the emitted carbon caused by land-use change on mineral soils may take hundreds of years or even be irreversible.

While oil palm monocultures showed the lowest carbon stock, we have measured the highest total net primary production (NPP) values in oil palm plantations followed by natural forest, jungle rubber and rubber monocultures. However, the carbon sequestration potential is reduced by forest conversion in the long term, as removal of major NPP fractions namely oil palm fruits, rubber latex and wood occurs. Since we found the carbon residence time in biomass to be longer in natural forest and jungle rubber, the establishment of oil palm or rubber plantations on former forest land does not enhance carbon sequestration potential despite the high total net primary production of oil palms. With predicted climate change associated with increasing mean temperatures and drought events, land-use intensification with introduced cash-crops is also expected to have influence on seasonal growth responses in moist tropical lowlands even with only moderately dry seasons. We found a higher coefficient of variance (CV)

following forest transformation for all examined components namely aboveground litterfall, fine root mortality, and aboveground woody production.

In addition to changes in the annual net primary production, element return to the soil via aboveground litterfall was significantly reduced for C, N, Ca, Fe, Mg, Mn and S in monoculture plantations, particularly for rubber. Due to crop removal, a high demand for fertilizer use was caused, which likely leaded to significantly lower nutrient use efficiencies (NUE) for all major nutrients in oil palm plantations. Decomposition rate was reduced in oil palm plantations compared to natural forest which further decelerated nutrient cycling.

Beside nutrient availability, a permanent water supply from roots to leaves is essential for effective plant growth. We found wood anatomical and derived hydraulic properties to be a good predictor for tree stem growth performance in the study on hydraulic architecture of the root, stem and branch wood in *Theobroma cacao* and five common shade tree species in agroforestry systems on Sulawesi. In contrast, neither wood density, nor empirically measured branch and root hydraulic conductivity, foliar $\delta^{13}C$ or foliar nitrogen content were good predictors for aboveground growth performance. A similar relationship was found between basal area increment and theoretical hydraulic conductivity in forest and rubber trees on Sumatra. Several wood anatomical patterns were observed to potentially follow drought adaptations strategies based on biogeographic origin. Hence, our results imply that future research on conceptual trade-offs of tree hydraulic architecture should consider that some of the long-established paradigms might not be uniformly applicable to all tree species.

Overall, the results of our study suggest that where natural forest cannot be conserved, agroforestry is the better land-use option in terms of long-term carbon storage and nutrient sustainability compared to rubber and oil palm monocultures. On the other hand, higher yields of monocultures and thus a potentially better income are decreasing the attractiveness of agroforests for local owners. Further depletion of carbon storage potential in the tropical lowlands may only be mitigated in cooperation with political and local institutions in the long term. Therefore, scientific evidence on the ecological costs and benefits of land-use change like presented in this study is aimed to guide political decision-making towards a more sustainable path in forest conservation and land management.

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General Introduction

1.1 General Introduction

We live in increasingly human-modified landscapes where natural habitats are pushed to their very borders driven by exponential population growth and rising per-capita resource consumption. While population dynamics in highly industrialized nations like Europe are stagnating (Ezeh et al., 2012), the population density as well as the annual growth in regions identified as biodiversity hotspots are about 30-40 % higher than the global rate (Cincotta et al., 2000, Williams, 2013). These biogeographic regions are characterized by exceptional biodiversity. They are mainly located in the tropics (Myers, 1988, Mittermeier et al., 2004) and at the present time have preserved only 14.9 % of their total area as natural intact vegetation (Sloan et al., 2014).

Between 1980 and 2000 more than 55 % of new agricultural land became available at the expense of intact forests across the tropics (Gibbs et al., 2010). Whereas 8000 years ago forests covered around half of Earth's surface (Fig. 1.1), nowadays this value is reduced to 30 % (Ball, 2001), while agriculture occupies about 38% of terrestrial surface (Ramankutty et al., 2008). Conversion of natural forests particularly in the tropics is one of the major environmental issues the world is currently facing as it is expected to have enormous adverse effects on both biotic and abiotic ecosystem functions worldwide (e.g. Tilman et al., 2001, Sodhi et al., 2004, Green et al., 2005, Fitzherbert et al., 2008). Tropical forests are strongly coupled to the climate system through physical, chemical, and biological processes. They play a crucial role in the global C cycle and carbon sequestration (Malhi et al., 2006, Adachi et al., 2011, Slik et al., 2013), and provide ecosystem services such as climate regulation via the hydrologic cycle and atmospheric composition (Bonan, 2008, Richardson et al., 2013). As a consequence, deforestation is likely not only to deplete biodiversity leading to loss of genetic plant and animal reservoirs with unknown results for potential new food, fiber and medicinal resources (Mendelsohn & Balick, 1995, Balick et al., 1996, Laurance et al., 2012). It may also affect water balance through disturbed recirculation and increased runoff (Medina, 1991) and lower the productive capacity of land due to soil erosion and reduced nutrient cycling (Pimentel et al., 1995). Furthermore, it may influence climate through the emission of atmospheric carbon and other greenhouse gases (Houghton, 2007). Due to large carbon densities in lowland rainforests (Malhi et al., 2006, Ruesch & Gibbs, 2008), changes in tropical land-use are evidently a source of carbon emission.

Figure 1.1: Historical forest loss and current extent of intact forest (Source: World Resources Institute 2009. Forest Landscapes Initiative)

Nowadays, the carbon released into the atmosphere through deforestation is an issue of growing concern due to its potential contributions to global climate change. World's tropical rainforests are located in the Amazon Basin (59 %), Central Africa (22 %) and Southeast Asia (18 %). While their total cover is less than 10 % of the Earth's land surface (FAO & JRC, 2012), they contain more than one third of the biomass in the terrestrial biosphere (Dixon et al., 1994, Meister et al., 2012) and collectively possess the largest annual rate of carbon sequestration among all terrestrial ecosystems (Pan et al., 2011) contributing about 30 % to global terrestrial net primary productivity (Del Grosso et al., 2008). Currently, peak deforestation rates have shifted from the Amazon Basin to Southeast Asia, with Indonesia showing the highest total primary forest loss (0.84 Mha in 2012) of all tropical countries (Miettinen et al., 2011, Margono et al., 2014).

Overall, an increasing number of studies (e.g Malhi et al., 2009, Chave et al., 2010, Laumonier et al., 2010, Malhi et al., 2011, Saatchi et al., 2011, Kho et al., 2013, Lewis et al., 2013, Ngo et al., 2013) are the basis for a well-founded scientific knowledge on carbon and nutrient cycling as well as productivity of natural rainforest underlining its global importance. In contrast, prevalent agricultural systems replacing primary tropical forest are seldom studied in comparable detail (Ziegler et al., 2012, Berenguer et al., 2014) reveling a severe lack of knowledge about consequences of progressing land-use change and its potential mitigation.

1.2 Land-use change in Indonesia

Until the end of the 19th century primary forests covered nearly all islands of Southeast Asia. These forests provide important ecosystem services for human well-being and are home to a stunning diversity of plants, animals and other biota. However, forests in the region are under increasing thread. The conversion to cash crop plantations is considered the main cause of forest loss (Fig. 1.2), while the role of shifting cultivation was classified as decreasing in Southeast Asia (Stibig et al., 2014). Indonesia harbors 44 % of all remaining natural forest cover of Southeast Asia. Even so it is concurrently the place where agriculturally driven land conversion is one of the severest worldwide. Forest cover disappears with a annually rate up to 5 % from 2000 to 2010 as observed for main conversion regions such as lowland Sumatra (Miettinen et al., 2011). Within the Central Sumatran provinces of Riau and Jambi, forest cover declined from 93 to 38 % between 1977 and 2009 (Ekadinata & Vincent, 2011). A trend that is projected to continue as 35 % (26.8 Mill ha) of Indonesia's remaining forests are located within industrial concessions (Abood et al., 2014).

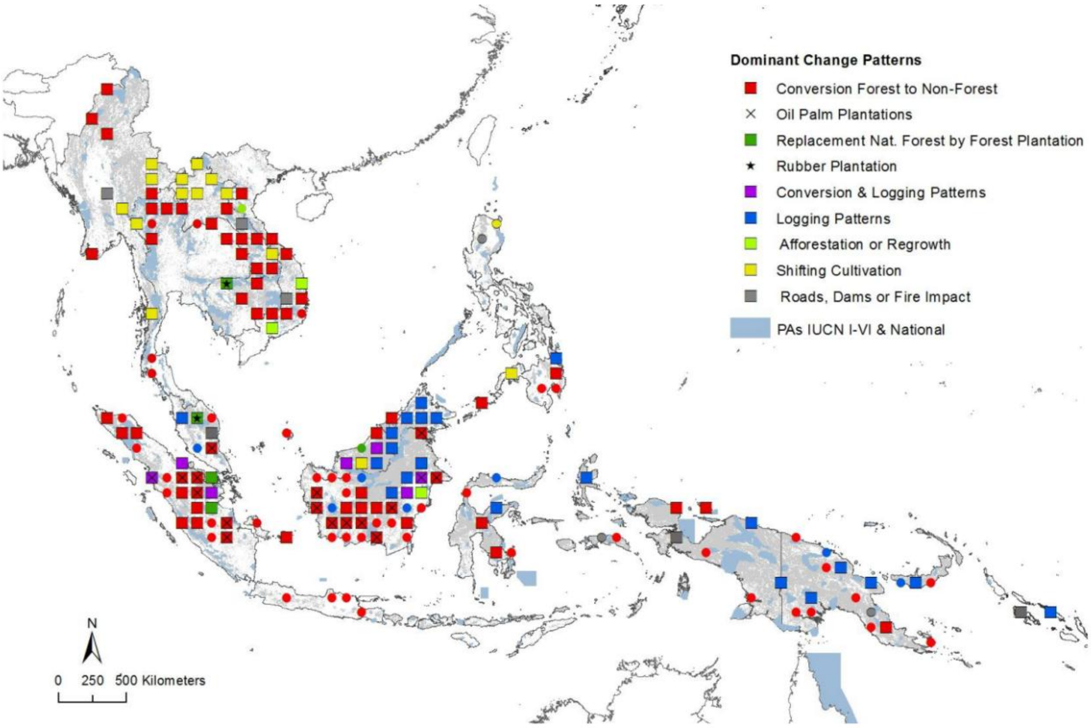

Figure 1.2: Patterns of dominant forest change types as visually identified from satellite imagery. Squares represent changes from 2000-2010, circles represent changes from 1990-2000 (Source: Stibig et al. 2014).

First historical valorization of forest resources by native tribes in Indonesia consisted of hunting and gathering activities, followed by slash and burn land-use associated with swidden cultivation of upland rice (Feintrenie & Levang, 2009). During the last three decades, the food crop-based cultivation systems were converted to small-scale rural agroforests in many regions as cash-crops begin to gain in importance (Wibawa et al., 2005). In general, agroforests are mixed systems with target species planted under remnants of natural forests and secondary forest regrowth (Huxley, 1999, Sinclair, 1999) or replanted after complete logging. Examples for these smallholders' plantations that are combining perennial cash crops such as rubber trees, coffee and cacao with other plants including timber and fruit trees, food crops, and medicinal plants (Michon & De Foresta, 1997, Michon et al., 2007) can be found in Sulawesi, Sumatra and other Indonesian islands. Due to the continuously increasing demand for rubber with the industrial revolution in Europe and North America in the second half of the nineteenth century, natural rubber (*Palaquium* spp. and *Dyera costulata*) was overexploited and Para rubber (*Hevea brasiliensis*) native to South America was introduced (Wibawa et al., 2005). Rubber agroforests spread over large parts of western Indonesia and particular Sumatra's eastern peneplains until the 1990s (Feintrenie & Levang, 2009).

On Sulawesi the widespread practice of slash-and-burn cultivation was curbed by the expansion of wet rice fields in the plains of the lowlands and the uplands, followed by cash-crops such as coffee (*Coffea* spp.), coconut (*Cocos nucifera*), cotton (*Gossypium* spp.) and clove (*Syzygium aromaticum*) leading to a heterogeneous and smallholder-dominated land-use (Weber et al., 2007). Around 1980 cacao (*Theobroma cacao*), native to tropical South America (Motamayor et al., 2008), was introduced to the Lore-Lindu region on Sulawesi by migrating Bugis traders. Due to the boom of cacao prices during the 1990s, immigration in Central Sulawesi reached a peak and cacao cultivation started to spread in the region replacing other crops (Weber et al., 2007). Nowadays, cacao monocultures dominate the landscape and agroforests are usually mixed stands of cocoa trees with legume shade trees (*Gliricidia sepium*, *Erythrina* ssp. and *Leucaena leucocephala*) or fruit trees such as coconut (*Cocos nucifera*), rambutan (*Nephelium lappaceum*) and mango trees (*Mangifera indica*) and are less frequently established under thinned rainforest cover (Rice & Greenberg, 2000). Harvesting is done continuously bi-weekly throughout the year. Cocoa pods are opened immediately and just the beans are removed from the site. Management includes cutting back the shade-trees and weeding between the crop plants. In contrast, rubber agroforests usually feature dense secondary forest vegetation that is left mostly unmanaged. While about 40 % of trees are rubber trees, most other trees are natural regrowth with several target species such as durian (*Durio zibethinus*) and other fruit trees planted by the farmer (Beukema & van Noordwijk, 2004). Usually agroforests are not fertilized. Both agroforestry types can maintain overall species richness and some ecosystem functions of near-primary forests. However, there is a trade-off between land-use intensity and farmers' profits as unshaded cacao monocultures may increase total income by at least 40 % (Steffan-Dewenter et al., 2007, Kohler et al., 2009). In the monoculture plantations rubber (latex) or palm oil is the only product. The undergrowth below the trees is suppressed by herbicide usage or by manual weeding to keep competition under control, while fertilizer is applied to stimulate growth and a high yield return. Tapping of monoculture rubber trees starts with the age of 5–6 years, while oil palm fruits can be harvested 3 years after planting.

Nowadays even agroforests are endangered in Indonesia, because their owners often choose the conversion to monospecific plantations of rubber or oil palm (*Elaeis guineensis*) (Ekadinata & Vincent, 2011). During the past few decades, the oil palm has become one of the most rapidly expanding equatorial crops and the palm oil is used for cosmetics, food and biofuel (FAO, 2015). From the late 1980s on Indonesia's government began to favor the expansion of large private oil palm companies by granting them huge concessions, often encroaching on state forest land or agroforest smallholdings leading to conflicts between the indigenous population, migrants and private companies (Casson, 2000, Jepson et al., 2001). Consequently, in 2008 Indonesia became the world's largest producer of palm oil surpassing Malaysia with more than 48 % of global annual production (26.9 M tons produced oil in 2013) (FAO, 2015).

1.3 Carbon storage in above- and belowground biomass

One of the main ecosystem services of intact tropical rainforest is carbon sequestration as they are estimated to store 55 % of the global forest carbon stock contributing a significant fraction of the Earth's carbon sink (Pan et al., 2011). Particularly forests of Indonesia and Malaysia are reported to have carbon densities ranging amongst the highest worldwide (Hertel et al., 2009, Saatchi et al., 2011), which is attributed to the occurrence of Dipterocarpaceae, a plant family with particularly tall trees of high wood densities (Slik et al., 2010, Saner et al., 2012). However, global environmental and land-use change can turn forests into a major source of CO_2 for the atmosphere (Achard et al., 2002, van der Werf et al., 2009). Tropical deforestation is the largest source of greenhouse gas emissions in most tropical countries and was estimated to have released roughly 1–2 billion tonnes of carbon annually in the 1990s, which is equivalent to 15–25 % of total annual global greenhouse gas emissions (Dixon et al., 1994, Malhi & Grace, 2000, Fearnside & Laurance, 2004, Houghton, 2005, van der Werf et al., 2009). Still, great uncertainties remain regarding the magnitude of these emissions as the quantity of carbon released to the atmosphere is mainly determined by the amount of carbon held in the biomass of the natural forest and the type of land-use conversion (Gibbs et al., 2007). To determine the quantity of the carbon pool components in tropical forest ecosystems on mineral soils, the living biomass of trees, understory vegetation and the dead mass of litter and woody debris is to be taken into account. The carbon stored in the aboveground living biomass of trees is typically the largest pool and the most directly impacted by deforestation and degradation. However, belowground biomass is estimated to account for at least 20% of the forest carbon stocks (Houghton et al., 2001, Mokany et al., 2006, Hertel et al., 2009, Ngo et al., 2013, Yuen et al., 2013)

Nonetheless, the majority of existing studies focus mainly on selected components of carbon sequestration in different stages of lowland rainforests, while studies on root systems and in oil palm and rubber plantations have rarely been conducted (Niiyama et al., 2010, Adachi et al., 2011, Yuen et al., 2013, Berenguer et al., 2014). Even for estimates of the relatively well studied aboveground carbon storage, considerable variations are reported. Results for old-growth forests vary between 164 to 250 Mg C ha^{-1} (Gibbs et al., 2007). The variation is even larger for rubber (25–143 Mg C ha^{-1}) and oil palm (17–69 Mg C ha^{-1}) plantations (Ziegler et al., 2012). Reasons for these uncertainties are the use of inadequate allometric equations and local variation in soil type, stand structure or plantation age as well as methodological differences (Baker et al., 2004, Basuki et al., 2009, Kenzo et al., 2009, Ziegler et al., 2012). In consequence, reliable in depth ground-based data are still highly in demand for up-scaling and modeling approaches as well as for informed decision making on forest conservation.

1.4 Net primary production

A systems potential to store carbon likewise depends on the process of net primary production (NPP) of the growing plants in the system. NPP is conventionally defined as the difference between total photosynthesis (gross primary production) and total plant respiration in an ecosystem or alternatively as the total new organic matter produced during a given interval (Clark et al., 2001). Consequently, estimated NPP is given by the amount of organic matter that was both produced and lost by the plants during the same interval, and the amount of new organic matter retained by living plants at the end of the interval. The measurement of all these components simultaneously in the field is difficult as they are subject to consumption, decomposition, mortality and exudation during the measurement interval. Instead, NPP is estimated based on a set of measurements and numerous underlying assumptions.

In forest or plantation ecosystems, these components are woody biomass increment, fine litterfall, leaf and root losses to consumers, emissions of biogenic volatile or leached organic compounds, increment of fine root biomass, root exudates, carbohydrates exported to mycorrhizal symbionts and any net increases in stores of non-structural carbohydrates (Clark et al., 2001). For practical reasons, most studies frequently measure aboveground woody biomass increment and fine aboveground litterfall and define their sum to be equated with aboveground net primary production (ANPP). The components of belowground net primary production (BNPP) such as coarse and fine root increment are seldom measured, but rather estimated as a proportion of aboveground production (Clark et al., 2001). While fine roots usually contribute little to total biomass in old-growth forest (Vogt et al., 1996, Cairns et al., 1997), they are considered to show high biological activity and turnover. Tropical rainforests may allocate between 30 to 50 % of their annual net primary production to fine roots (diameter ≤ 2 mm) (Vogt et al., 1996, Silver et al., 2005, Brunner et al., 2013). The precise estimation of root dynamics requires handling the challenge of distinguishing live from dead fine roots as well as choosing procedures from numerous calculation methods. Therefore, estimations comprise high uncertainties that are increased due to temporal and spatial variability in fine root biomass distribution and methodological uncertainties (e.g. Carvalheiro & Nepstad, 1996, Ostertag, 1998).

Additionally there is a lack of knowledge on factors controlling and limiting NPP in tropical rainforests and transformation systems. Even though in most parts of the Southeast Asian rainforests only short dry seasons with substantial variability between years occur (Malhi & Wright, 2004, Kumagai et al., 2006), it has been demonstrated that NPP reacts sensitive to precipitation (Schuur, 2003, Zhao & Running, 2010). Plants have developed drought-adaptive mechanisms linking the seasonality of stem, leaf and root growth with the seasonality of water availability (Guan et al., 2013). Despite the knowledge that key ecosystem processes such as nutrient cycling in these landscapes will be influenced by ongoing land-use change, still few in-detail studies on all main fractions of NPP in different transformation systems exist. It remains a question whether NPP in tropical rainforests and its transformation systems is limited by nutrients or can become constrained by water supply.

1.5 Nutrient return via aboveground litterfall, litter decomposition and nutrient use efficiency

All plant growth is either limited by water availability, energy or nutrient supply. Nutrients in forest ecosystems are cycling from weathering of parental material and nutrient mobilization in soils as well as atmospheric deposition and are incorporated in plant biomass. Through litterfall, stemflow, throughfall, exudations and root death these nutrients may partly be returned to the soil and decompositions releases them again into a new cycle. In forest ecosystems, litterfall and subsequent decomposition represent one of the major pathways of nutrient cycling (Vitousek, 1984, Barlow et al., 2007). Since particularly tropical forests grow on highly weathered soils, a major proportion of available nutrients is tied up in the living phytomass and organic matter breakdown will release the amount of nutrients required for nearly all biomass growth (Attiwill & Adams, 1993, Sayer & Tanner, 2010). Thus the nutrient return from forest trees to surface soil by aboveground litterfall and the subsequent nutrient release from decomposing litter by mineralization are the main processes regulating nutrient availability and the rate of forest growth and carbon sequestration (Yavitt et al., 2004, Sayer & Tanner, 2010). In order to release nutrients, the litter must be fragmented and decomposed by forest floor microorganisms and fauna. The litter decomposition rate is determined by substrate quality, water availability, microbial community, and climatic conditions such as the range and absolute temperature, (Aerts, 1997, Cornwell et al., 2008, Bakker et al., 2011). Hence, in ecosystems worldwide fine litter nutrient contents and their ratios as well as within-stand nutrient-use efficiency (NUE) have been used as indices of litter quality, nutrient availability, growth limitation, and soil fertility (van den Driessche, 1974, Vitousek, 1982, Lodge et al., 1994, Koerselman & Meuleman, 1996, Tessier & Raynal, 2003). In many lowland tropical forests, phosphorus (P) availability is low and is expected to be limiting to growth, while nitrogen (N) availability is relatively high (Vitousek, 1984, Vitousek & Sanford, 1986, Tanner et al., 1998). The primary sources of plant available P in lowland tropics are geologic parent materials and deposition of dust and ash (Walker & Syers, 1976). Therefore, heavily weathered soils are expected to be a poor P source. However, as global P cycling is very slow, efficient P recycling from organic matter is an essential mechanism for maintaining P stocks in tropical forests (Smil, 2000, Reed et al., 2011) as up to 60 % of the plant available P in the ecosystem is delivered from organically bound phosphorus (Zou et al., 1992). Phosphorus is part of the chemical structures of adenosine diphosphate (ADP) and triphosphate (ATP) and important for photosynthesis functions and energy transfer. In contrast, nitrogen occurs in large quantities in the atmosphere and can be biological fixated by microorganisms such as symbiotic soil bacteria and algae (Vitousek et al., 1997). Furthermore, increased wet and dry N deposition from the atmosphere driven by industrialization contributes to plant available N in the system (Vitousek et al., 1997, Galloway et al., 2008). On the other hand, plants require large quantities of N as nitrogen is a major constituent of amino acids, which are components of proteins, nucleic acids, chlorophyll, and enzymes. Other plant nutrients such as calcium (Ca), potassium (K), magnesium (Mg) and sulfur (S) are also essential for plant functioning such as cell wall building, stomata regulation and chlorophyll formation, and their low supply can lead to co-limitation of plant growth and decomposition in tropical rainforest (Kaspari et al., 2008).

Despite the generally high potential of nutrient leaching in humid tropical soils caused by high precipitation rates, undisturbed forest systems show relatively low nutrient losses due to high fine root biomass density near the surface (Leuschner et al., 2006, Hertel et al., 2007), low nutrient concentrations in leaf and other tissues (Peace and Macdonald 1981) and efficient nutrient retranslocation in plant tissue before leaf shedding (Chapin 1980). It is hypothesized that there is a trade-off between the production of either low-quality leaves at low energy costs, or high-quality leaves at high structural costs (Silla & Escudero, 2004). Since every plant species follow different physiological strategies, changes in species composition may largely alter litter quality and quantity. Therefore, human-induced land-use change not only leads to a severe loss of forest cover and associated ecosystem services, but also introduces non-native species to the environment that may further cause changes in the ecosystem's nutrient cycling of unknown extent. In response to potentially higher nutrient loss through biomass burning, crop removal, increased nutrient leaching and surface runoff, agricultural management has to include fertilizer application to counterbalance nutrient loss and increase productivity.

1.6 Relationship of wood hydraulic anatomy and tree growth performance

Although in moist tropical forests like the Southeast Asian rainforests the dry seasons are not pronounced or generally short, it has been demonstrated that net primary production reacts sensitively to precipitation (Schuur, 2003) and plants have developed drought-adaptive mechanisms linking the seasonality of stem, leaf and root growth with the seasonality of water availability (Guan et al., 2013). Ongoing land-cover change as well as global warming in the tropics are likely to influence not only fundamental ecosystem processes such as nutrient cycling but consequently also initiate biophysical and biogeochemical biosphere-atmosphere feedbacks (Tian et al., 1998, Cox et al., 2000, Huntingford et al., 2008). For all tropical regions including Southeast Asia strong warming as well as increased rainfall seasonality (Malhi & Wright, 2004, Feng et al., 2013), a delayed monsoon start (Loo et al., 2014), and locally increased droughts, wildfire or flooding events are reported (Silva et al., 2013, Cai et al., 2014). Therefore, drought stress might play an increasing role in these human-modified systems. How introduced species such as rubber or legume species in agroforests with different drought adaptations are coping with the situation and whether we can find different patterns of adaptations strategies compared to native species used to perhumid conditions was yet addressed by only few studies. In this work the question is addressed whether tree growth performance can be directly linked with wood hydraulic architecture or with wood density. Furthermore, it is analyzed whether this is a uniformly applicable pattern across different species.

Overall, water transport through the xylem is fundamental to compensate water loss during transpiration, deliver nutrients, and enable continued photosynthesis (Kramer & Boyer, 1995). Transpiration generates the driving force behind the tension that pulls water through the xylem as described by the cohesion-tension theory (Dixon & Jolly, 1894). An optimal water transport system in trees minimizes the investment of carbon in vascular structures while maximizing hydraulic conductance (McCulloh et al., 2003). Conduction efficiency in turn influences transpiration and carbon fixation rates, and ultimately growth (Tyree, 2003, Poorter et al., 2009). According to the Hagen-Poiseuille's law, the hydraulic conductance scales with the fourth power of the vessel radius. Therefore, wider vessels contribute a lot to larger hydraulic conductances while concurrently facilitating more photosynthetic carbon gain (Santiago et al., 2004). On the other hand, smaller vessels imbedded in a matrix of dense tissue lead to a higher hydraulic safety due to reduced risk of vessel implosion and cavitation (Hacke et al., 2001), as water is transported in a meta-stable state below its vapor pressure in vascular plants, which makes them vulnerable to the formation of gas embolism (Hacke et al., 2006). In consequence particularly wide vessels are the most conductive but also most prone to the risk of hydraulic failure in form of xylem embolisms (Maherali et al., 2006, Awad et al., 2010, Cai et al., 2010, Hajek et al., 2014). Hence, there is a trade-off between stem hydraulic efficiency and stem safety against cavitation and plants have developed ecosystem-specific adaptations to maximize their growth performance.

Trees widely differ in their vulnerability to drought-induced cavitation and the responses to drought are species-specific and depend on the tree's hydraulic strategy (Bréda et al., 2006). Plant hydraulic architecture has been linked to many ecological patterns such as water transport sufficiency, photosynthetic rates, growth form and carbon allocation (McCulloh et al., 2011). Also wood density has been related to a wide variety of important ecological and physiological characteristics (Santiago et al., 2004, Chave et al., 2009, Zanne et al., 2010) and it was observed that fast-growing pioneer species tend to have less dense wood than slower-growing species (Enquist et al., 1999, King et al., 2005, Poorter et al., 2009). Wood density is closely linked to the amount of fibres and tracheids and thus to the physical stability of woody tissues during high negative pressures caused by drought stress (Domec et al., 2009). Nevertheless, several studies, particularly from tropical environments, found wood density decoupled of hydraulic efficiency traits and growth performance (Zhang & Cao, 2009, Russo et al., 2010, Fan et al., 2012, Schuldt et al., 2013).

As one of the basic organizing principles of tree hydraulic architecture it has been postulated that the mean vessel diameter in the xylem tissue generally taper acropetally from roots to branches (Baas, 1982, Tyree & Zimmermann, 2002). Consistent with these predictions it has indeed commonly been observed that the largest vessels along the water flow path are found in roots of trees from temperate environments (e.g. Martinez-Vilalta et al., 2002, Domec et al., 2009). However, recent studies in tropical forests in South America (Fortunel et al., 2013) and Indonesia (Schuldt et al., 2013) have produced contradictory results regarding the paradigm of continuous vessel tapering. Schuldt et al. (2013) supposed that mechanisms reducing cavitation risk may not have been evolved in these moist or perhumid environments where drought stress is normally not apparent. Therefore, it is necessary to compare wood anatomical features not only between species, but also between different organs such as stem, branch and root wood to understand their hydraulic strategy fully.

1.7 Project framework and study areas

To investigate the effects of rainforest transformation on carbon sequestration, litter dynamics and net primary productivity as well as hydraulic-anatomical wood properties, this study was conducted within the framework of two interdisciplinary projects with the location in Indonesia resulting from the cooperation between the German University of Göttingen and three Indonesian universities (Tadulako University in Palu on Sulawesi; Bogor Agricultural University on Java, and University of Jambi on Sumatra).
The main part of the present investigations were embedded in the 'EFForTS'-project (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems on Sumatra, Indonesia) which is a DFG funded Collaborative Research Center aiming to provide knowledge-based guidelines on how to protect and enhance the ecological functions and services of tropical forests, forest remnants and agricultural transformation systems at a landscape scale, while simultaneously improving human welfare. This international, interdisciplinary research program investigates the impacts and forces responsible for deforestation, and evaluates the economic, social and ecological consequences in Jambi Province, Sumatra which belongs to one of the most severely and recently converted regions in Indonesia (Miettinen et al., 2011).

Jambi Province compromises 5 million ha (10 % of Sumatra's total area) of mostly lowlands and is located at the eastern part of central Sumatra between the Barisan Mountains with the highest summit of Sumatra (Mt. Kerinci 3805 m) and the Java Sea. Jambi's climate is tropical humid with a dry season from June to August during which monthly rainfall can fall below 100 mm in some months (Fig. 1.3). The meteorological station in Jambi city (Stasiun Klimatologi Jambi: N 1°62.1', E 103°53.1') measured a mean temperature of 26.5°C and an annual rainfall of 2364 mm per year in the 2007-2013 period.

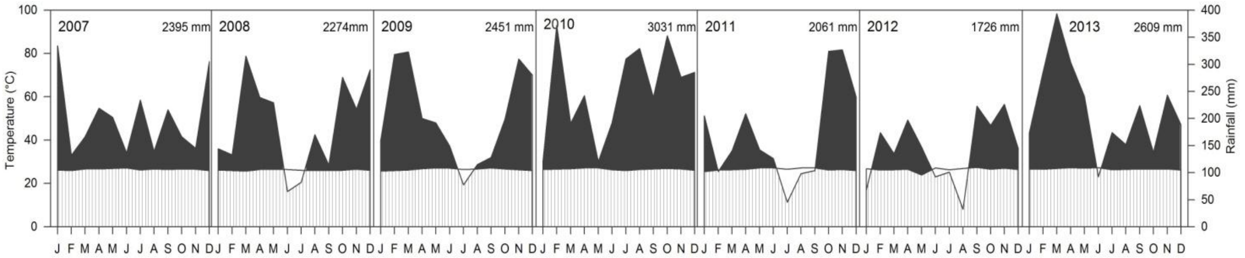

Figure 1.3: Climate diagram from Jambi climate station (Stasiun Klimatologi Jambi: N 1°62.1', E 103°53.1') over the period from 2007-2013.

The natural vegetation of the lowlands in Jambi Province is dipterocarp dominated lowland rainforests in the center and peat-swamp forests along the east coast (Laumonier, 1997). As investigation location two landscapes within the province have been chosen comprising large units of remaining lowland rainforest: National Park

Bukit Duabelas and Harapan Rainforest. The investigated transformation systems include old-growth lowland rainforest as reference sites, jungle rubber (extensive rubber plantations), and intensive monocultural rubber and oil palm plantations. Even though, pristine lowland rainforests without any kind of human interaction are no longer existent in Jambi Province, the selected rainforest reference sites represent forest in a close to natural state. In each of the two landscapes (comprising blocks in a randomized complete block design), four plots each 50 x 50 m of each of the four transformation systems (32 plots in total) were investigated (Fig 1.4).

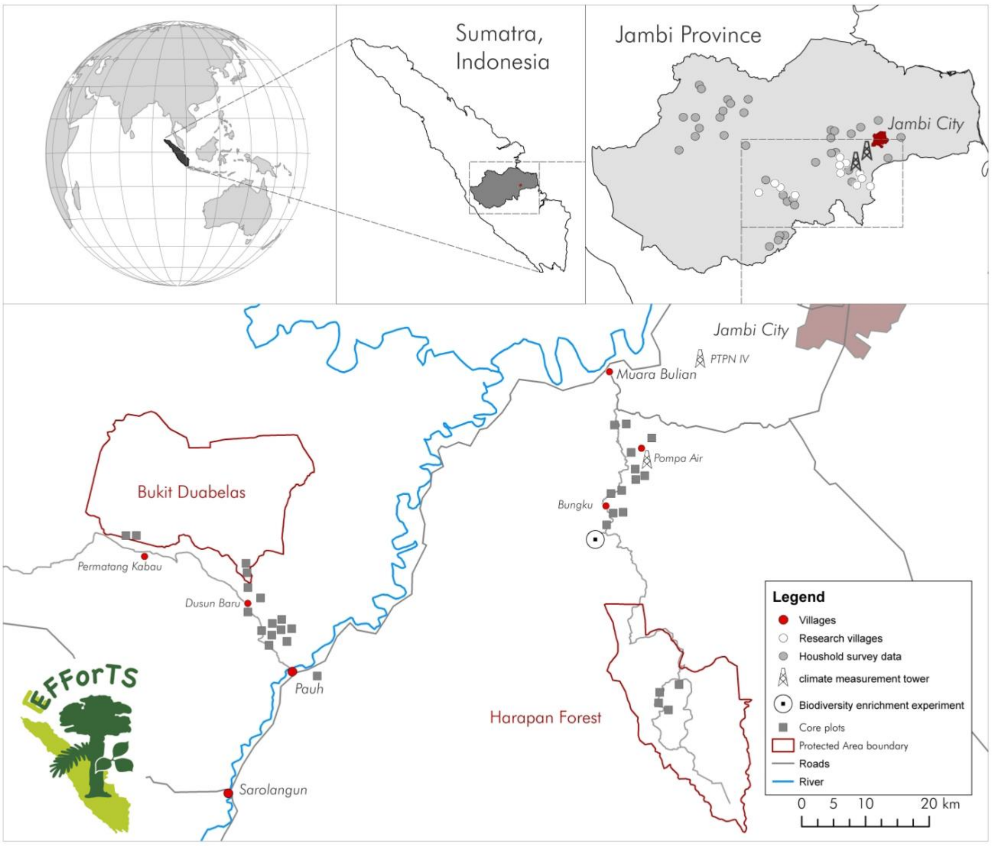

Figure 1.4: Location of study region and distribution of 32 research plot in Jambi Province, Sumatra (Source: Drescher et al. (in prep.))

The second part of the study was associated with the ELUC-project (Environmental and land-use change in Sulawesi, Indonesia) located in Central Sulawesi. The investigated system was cacao agroforestry in the Kulawi Valley, Bolabapu District, Central Sulawesi, Indonesia (S 01°55.9’ E120°02.2’, elevation 571 m a.s.l.). The climate of the study region is perhumid without a distinct dry season. Mean annual temperature recorded for the study area by Moser et al. (2010) is 25.5 °C and mean annual precipitation is 2092 mm between 2002 and 2006. For the study, a cacao agroforestry plot with multi-species shade tree layer was selected from a number of preselected cacao agroforestry plots that were found to be representative in terms of management, aboveground structure and topographical patterns for this region.

1.8 Study objectives and hypotheses

With the overall aim to understand effects and consequences of the recent intensive land-use change in Southeast Asia, the present work focuses on carbon sequestration, litter dynamics and net primary productivity as well as hydraulic anatomic wood properties in natural rainforests and their transformation systems. During a 20-months fieldwork period from 2012 to 2014, the above- and belowground carbon storage, production and plant functional traits like litter nutrient content and specific leaf area were investigated for natural old-growth forest, rubber agroforests under natural shade tree cover ('jungle rubber'), rubber monocultures, and oil palm plantations in Jambi Province, Sumatra. Furthermore, in a 2-months period in 2012 hydraulic wood architecture, conductivity features and leaf traits were studied in cocoa agroforests under mixed shade tree species in Kulawi valley, Sulawesi. The results of these investigations are essential to assess carbon allocation patterns and to understand the relationship between above- and belowground plant production in tropical rainforests and their transformation systems. They also illuminate the influence that land-use changes have on carbon storage, net primary productivity, and nutrient cycling in tropical forests. Furthermore, the results of this work can provide reliable estimates for informed decision-making in land-use planning and underline the importance of forest conservation.

Overall, following variables and processes were measured or estimated:

(i) All major above- and belowground tree biomass fractions (trees, palms, lianas, coarse roots, fine roots, and dead wood debris) were quantified, providing nearly complete estimates of the ecosystem phytomass C pool.

(ii) Net primary productivity with its main above- and belowground fractions (fine litterfall, aboveground woody increment, fine root productivity, and coarse root growth) was measured for quantifying changes in potential annual C sequestration.

(iii) All fractions of aboveground fine litterfall were analyzed for their nutrient content to quantify nutrient return to the soil and nutrient use efficiency of canopy on stand level.

(iv) Belowground fine root litter production was investigated using the sequential coring approach.

(v) Leaf litterfall in natural forest, as well as rubber systems and mature leafs of oil palm and cacao agroforest systems were scanned to obtain specific leaf area and relate it to plant functional traits such as foliar nitrogen content and $\delta\ ^{13}C$.

(vi) Samples of branch, stem, and root wood were analyzed for wood density and anatomic features such as hydraulic conductivity, vessel density and lumen area to relate them to tree growth performance.

The overarching hypotheses of the present dissertation were:

(1) The transformation of natural lowland rainforest into less divers land-use systems such as rubber and oil palm monocultures results in a large loss of carbon stored in above- and belowground tree biomass.

(2) Above- and belowground net primary production and carbon sequestration potential associated with biomass accumulation decreases from natural rainforest to jungle rubber, rubber and oil palm plantation.

(3) The stand-level nutrient use efficiency decreases with increasing level of land-use intensification along with carbon and nutrients return to the ecosystems cycle.

(4) Rainforest transformation negatively influences litter decomposability.

(5) Seasonality of net primary production is higher in intensively managed systems such as rubber and oil palm monocultures.

(6) Aboveground productivity across species is positively related to hydraulic conductivity but stem xylem hydraulic properties are unrelated to stem wood density.

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CHAPTER

2

Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia)

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Abstract

Natural forests in South-East Asia have been extensively converted into other land-use systems in the past decades and still show high deforestation rates. Historically, lowland forests have been converted into rubber forests, but more recently, the dominant conversion is into oil palm plantations. While it is expected that the large-scale conversion has strong effects on the carbon cycle, detailed studies quantifying carbon pools and total net primary production (NPP_{total}) in above- and belowground tree biomass in land-use systems replacing rainforest (incl. oil palm plantations) are rare so far. We measured above- and belowground carbon pools in tree biomass together with NPP_{total} in natural old-growth forests, 'jungle rubber' agroforests under natural tree cover, and rubber and oil palm monocultures in Sumatra. In total, 32 stands (eight plot replicates per land-use system) were studied in two different regions. Total tree biomass in the natural forest (mean: 384 Mg ha^{-1}) was more than two times higher than in jungle rubber stands (147 Mg ha^{-1}) and >four times higher than in monoculture rubber and oil palm plantations (78 and 50 Mg ha^{-1}). NPP_{total} was higher in the natural forest (24 Mg $ha^{-1}yr^{-1}$) than in the rubber systems (20 and 15 Mg $ha^{-1}yr^{-1}$), but was highest in the oil palm system (33 Mg $ha^{-1}yr^{-1}$) due to very high fruit production (15–20 Mg $ha^{-1}yr^{-1}$). NPP_{total} was dominated in all systems by aboveground production, but belowground productivity was significantly higher in the natural forest and jungle rubber than in plantations. We conclude that conversion of natural lowland forest into different agricultural systems leads to a strong reduction not only in the biomass carbon pool (up to 166 Mg C ha^{-1}) but also in carbon sequestration as carbon residence time (i.e. biomass-C:NPP-C) was 3–10 times higher in the natural forest than in rubber and oil palm plantations.

Keywords: Carbon stock, fine root production, land-use change, monoculture plantation, net primary production, oil palm, rubber, tropical rainforest

2.1 Introduction

Large-scale conversion of tropical rainforests into different land-use systems such as oil palm and rubber plantations is expected to have substiancial impacts on the global carbon cycle, causing major carbon dioxide emission, extensive environmental degradation, and loss of biodiversity (Tilman et al., 2001, Sodhi et al., 2004, Fitzherbert et al., 2008). While tropical rainforests cover less than 10 % of the Earth's land surface (FAO & JRC, 2012), they contain more than one third of the biomass in the terrestrial biosphere (Dixon et al., 1994, Meister et al., 2012) and contribute by about 30 % to global terrestrial net primary productivity (NPP) (Del Grosso et al., 2008). In most tropical countries, the largest source of CO_2 emissions is deforestation and land-use change (Gibbs et al., 2007, van der Werf et al., 2009). It contributes presumably 12-15 % of the annual global carbon emissions (Canadell et al., 2007, van der Werf et al., 2009) and deforestation is also affecting the future potential of forests to remove additional carbon from the atmosphere (Saatchi et al., 2011). Currently, old-growth rainforests in Indonesia have the highest annual deforestation rate of all tropical countries (Margono et al., 2014). Lowland rainforest on Sumatra has been replaced mainly by rubber *(Hevea brasiliensis)* agroforest systems in the past, while more recently oil palm (*Elaeis guineensis*) plantations are the most common land-use form (Dirjen & Perkebunan, 2013, Villamor et al., 2014). Oil palm has become one of the most rapidly expanding equatorial crops in the world (Carrasco et al., 2014) and Indonesia is the largest oil palm-producing country (USDA-FAS, 2010, Setiadi, 2011).

The carbon stocks and fluxes of agrosystems replacing forests in Southeast Asia remain poorly known (Pan et al., 2011, Saatchi et al., 2011). The majority of published studies focus on a single component of carbon sequestration, namely aboveground biomass in undisturbed or secondary lowland rainforests, whilst studies in oil palm and rubber plantations as well as investigations that take total belowground biomass and NPP into account, have seldom been conducted (Clark et al., 2001b, Niiyama et al., 2010, Adachi et al., 2011, Yuen et al., 2013, Berenguer et al., 2014). Even for estimates of the relatively well studied aboveground carbon storage, considerable variability was observed. Results for old-growth forests vary between 164 and 250 Mg C ha^{-1} (Gibbs et al., 2007), and the variation is even larger for rubber (25–143 Mg C ha^{-1}) and oil palm (17–69 Mg C ha^{-1}) plantations (Ziegler et al., 2012). Reasons for these uncertainties are the use of inadequate allometric equations and local variation in soil type, stand structure or plantation age as well as methodological differences (Kenzo et al., 2009, Ziegler et al., 2012). Since the amount of carbon released to the atmosphere resulting from land-use change is mainly determined by the amount of carbon held in the biomass of the converted forest (Gibbs et al., 2007), an expanded data collection is of particular importance. With the aim to understand cross-regional effects and consequences of the ongoing rapid land-use change in South-East Asia and to provide a reliable estimates for informed decision-making in land-use planning, in this detailed case study, we quantified all major above- and belowground tree biomass fractions providing nearly complete estimates of the ecosystem C pool and attempted to measure net primary productivity with its main above- and belowground fractions including root productivity for quantifying changes in potential annual C sequestration for natural old-growth forest and its transformation systems, namely rubber agroforests under natural shade tree cover ('jungle rubber'), rubber monocultures, and oil palm plantations in Jambi province, Sumatra. We explicitly wanted to test the hypotheses that (i) conversion of natural lowland rainforest into different land-use systems implies a large loss of carbon stored in tree biomass, both aboveground as well as belowground, (ii) this pattern of rainforest conversion is observed consistently in different Indonesian landscapes, and (iii) this conversion has major negative implications for the carbon sequestration potential through above- and belowground net primary production.

2.2 Material and Methods

Study area

The study was carried out in two lowland landscapes (peneplain) in Jambi Province, Sumatra (Indonesia) at elevations of 40-100 m a.s.l. Study plots were established in both landscapes; the Harapan ('HP') forest region ca. 50 km southwest of the province capital Jambi, and the Bukit Duabelas region ('B12') ca. 90 km west of Jambi. The natural vegetation in the study areas is mixed Dipterocarp lowland rainforest. The dominant four types of land-use systems were investigated in both study areas, namely old-growth natural forest as a reference system, complex multi-strata rubber agroforest (termed 'jungle rubber'), and simply structured crop systems such as rubber monoculture (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) plantations. In each land-use system and study area, four 50 m x 50 m plots were established resulting in a total number of 32 study plots. The selected plantation stands are representative of the specific production systems in the respective study area. Care was taken to ensure comparable soil and microclimatic conditions and a similar plantation age within a region. The age of the oil palm plantations varied between 8 and 15 years and that of the rubber plantations between 6 and 16 years. The age of the rubber trees in the complex multi-strata jungle rubber systems varied between 15 and 40 years. The management of both monoculture plantations included application of herbicides every 6 months and addition of 100-300 kg ha^{-1} yr^{-1} inorganic NPK fertilizer in rubber plantations and 300-600 kg ha^{-1} yr^{-1} in oil palm plantations. Tapping of rubber trees started at the age of 6-7 years. Natural rainforest plots with closed canopy cover and with a distance of least 200 m from disturbed forest were chosen as reference sites. All plots in a region were located at a minimum distance of 300 m to each other. The two study regions and the distribution of sample plots across the regions are presented in Figure 2.1.

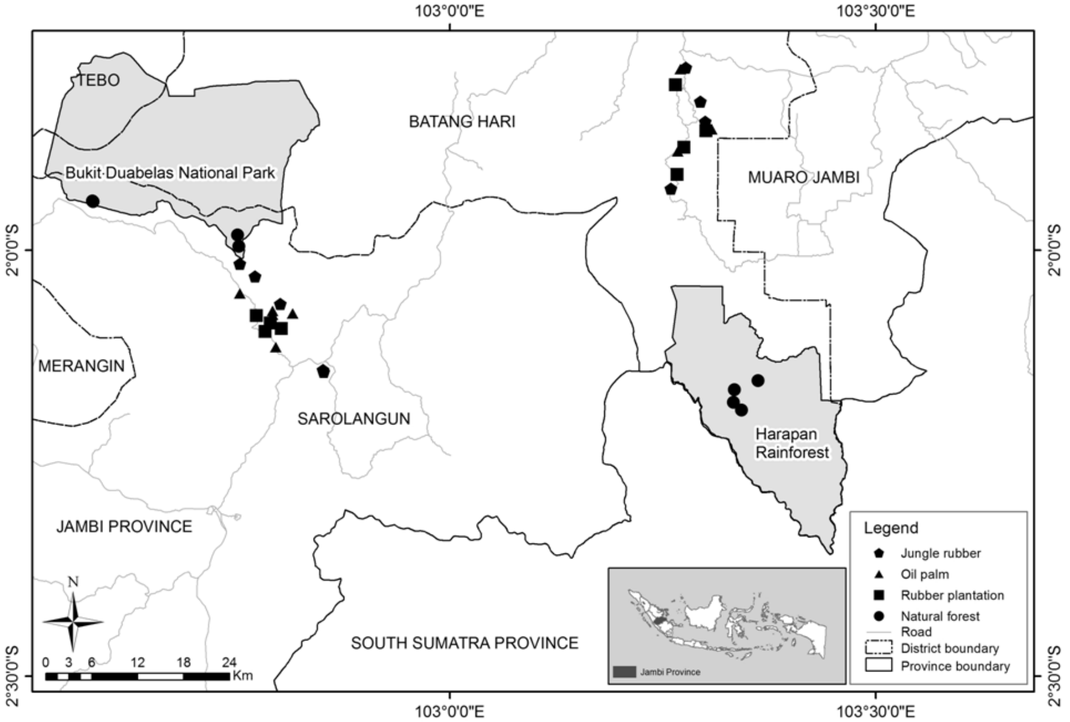

Figure 2.1: Location of the 32 plots in the two landscapes in Jambi, Sumatra (provided by Dian Melati).

The mean annual rainfall (average of 50 years, extracted from Worldclim Data Base) in both study regions of Jambi Province ranged from 2567 mm yr^{-1} in Harapan region to 2902 mm yr^{-1} in Bukit Duabelas region with a more or less distinct dry season occurring between May and September. The average monthly rainfall in the dry season (161 mm) was 62% of that in the rainy season's precipitation (261 mm). Temperatures are relatively constant throughout the year with an annual mean of 26.7 °C. In both study regions, the principal soil types are Acrisols: in the Harapan region, Sandy Loam Acrisols are the dominant soil type according to the WRB classification (2014), whereas in Bukit Duabelas the major soil type is Clay Acrisol. A summary of data on basic soil physical and chemical properties is given in Table 2.1 suggesting that the 32 study plots were well comparable with regard to soil properties.

Field data collection was conducted from August 2012 to March 2014; sample processing took mainly place in Jambi University, data analysis at the University of Göttingen.

Table 2.1: Soil parameters in the top soil (0-10 cm) of each of the four transformation systems in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra. Given are means ± SE (n = 4); soil texture: means ± SE (n = 3). Soil chemical data were provided by: pH and C/N ratio - Allen et al., unpublished data, soil texture - Kurniawan et al., unpublished data.

	Forest		**Jungle rubber**		**Rubber**		**Oil palm**	
Soil parameter	HP	B12	HP	B12	HP	B12	HP	B12
Soil texture								
Sand (%)	39.0 ± 8.0	35.9 ± 11.2	41.7 ± 19.2	26.6 ± 19.6	25.5 ± 13.5	34.7 ± 6.8	43.3 ± 13.6	11.2 ± 2.5
Silt (%)	38.5 ± 8.9	35.8 ± 6.8	25.0 ± 12.7	37.6 ± 9.9	38.5 ± 12.3	29.1 ± 3.8	33.9 ± 10.3	37.0 ± 8.9
Clay (%)	22.4 ± 1.1	28.3 ± 4.9	33.3 ± 6.8	35.8 ± 9.7	36.0 ± 14.3	36.2 ± 7.6	22.8 ± 3.3	51.8 ± 8.0
Soil pH	4.3 ± 0.04	4.2 ± 0.04	4.3 ± 0.03	4.5 ± 0.04	4.5 ± 0.1	4.5 ± 0.05	4.5 ± 0.06	4.4 ± 0.04
CN ratio	14.3 ± 0.2	13.1 ± 1.3	13.7 ± 0.8	13.0 ± 0.3	11.7 ± 0.7	14.3 ± 0.6	12.5 ± 0.5	13.5 ± 0.2
Organic layer (cm)	1.8 ± 0.1	1.9 ± 0.1	2.8 ± 0.3	2.0 ± 0.3	1.5 ± 0.2	1.2 ± 0.1	0.1 ± 0.1	0.02 ± 0.02

Stand structure, above- and belowground biomass

The tree aboveground inventory was conducted between August and September 2012 on all land-use system plots (n = 32). Within each 50 x 50 m plot, all trees, palms and lianas with diameter at breast height ≥ 10 cm (dbh at 1.3 m) were tagged, the dbh measured with a measuring tape (Richter Measuring Tools, Speichersdorf, Germany) and total height recorded using a Vertex III height meter (Haglöf, Långsele, Sweden). All height measurements were conducted by the same person previously trained with the instrument. For particularly high and not clearly visible trees, at least 3 measurements from different positions were taken and the maximum value used. For trees with buttresses or stilt roots, diameter was measured above stem anomalies. The diameter of rubber trees was recorded at 1.7 m or above the tapping mark since rubber harvest by cutting the bark influences tree diameter and growth rate (Silpi et al., 2006). Palm height was defined as the length from the base of the trunk to the base of the youngest leaf (Asari et al., 2013). For simplicity, we refer to palms as a 'tree' life form, although palm stipe growth form differs from that of trees.

To understand the contribution of small trees to total AGB, we established two 5 m x 5 m subplots in each plot, within which all stems between 2 and 10 cm dbh were inventoried.

To convert the recorded tree structural data into aboveground biomass, we applied the allometric equation developed by Chave et al. (2005) for tropical moist stands which uses diameter, height, and wood specific gravity as explicative variables. This allometric equation is currently the most prevalent model to estimate AGB across a broad range of tropical forest types because it has been based on an exceptionally large database of 2410 trees, directly harvested in 27 study sites across the tropics (Eq.1). During the preparation of this manuscript, a new equation model was published with a wider range of vegetation types and climatic conditions that are resulting in an even more reliable and robust estimates Chave et al. (2014). However, since the authors from the literature sources we compare our values to was using the Chave et al. (2005) equations as well (e.g. Djuikouo et al. 2010; Lewis et al. 2013; Day et al. 2014; Berenguer et al. 2014), we used the older version of the equation. A recalculation of the biomass for the forest plots with the new equation revealed a total difference of 2.8 % (mean of 8 plots) to the calculation method used in this paper. To calculate AGB of rubber trees, we used an equation by Wauters et al., (2008) based on 209 rubber trees destructively sampled in Brazil (Eq.2). For oil palms, aboveground dry mass estimation was based on the equation developed by Asari et al. (2013) and additionally validated on three felled and weighted oil palms from the region (Eq.3). AGB of all other unbranched and roughly cylindrical palms of other species was calculated using an equation based on cylinder volume, while assuming a wood density (ρ) for tropical palms of 0.31 g cm^{-3} given by Baker et al. (2004) (Eq.4). Finally, for lianas, AGB calculations were made using the equation of Schnitzer et al. (2006) (Eq. 5).

$$AGB = 0.0599 \times \rho D^2 H \qquad \text{(Eq.1)}$$

$$AGB = \frac{\exp\ (-6.748 + 2.723 \text{ x } \ln(C_{170}))}{0.487} \qquad \text{(Eq.2)}$$

$$AGB = 71.797\ H_{palm} - 7.0872 \qquad \text{(Eq.3)}$$

$$AGB = \pi\, r^2\, H_{palm}\, \rho \qquad \text{(Eq.4)}$$

$$AGB = \exp\ (-1.484 + 2.657 \ln(D)) \qquad \text{(Eq.5)}$$

AGB is the estimated aboveground biomass (in kg per tree, including stem and branch wood and leaf biomass), *D* the trunk diameter (dbh in cm), *H* total tree height (in m), C_{170} is stem circumference at 1.7 m height (in cm), H_{palm} palm stem height (in cm), *r* palm radius at 1.3 m (in cm), and ρ wood density (in g cm^{-3}). In the original equation for rubber trees, the carbon content of biomass is calculated with a factor of 48.7 %. To obtain dry aboveground biomass we divided the term by 0.487. Wood density values (dry mass per fresh volume in kg m^{-3}) were determined in cores extracted with an increment borer (Haglöf, Långsele, Sweden). Wood cores of 5-7 cm length were taken at 130 cm height of 10 trees per plot ($n_{\mathrm{total}} = 204$). Wood density values were calculated using the water-displacement method described in (Fearnside, 1997). Because this method is time-consuming and invasive, Chave et al. (2008) suggested using the Pilodyn 6J wood tester (PROCEQ SA, Zürich, Switzerland) to obtain wood density data in large-scale inventories. We thus measured the penetration depth of the Pilodyn pin into the stem wood of every tree (n = 3551) and calibrated the instrument on 204 trees, that were also cored for direct measurement of wood density. For these trees, wood specific gravity measured from cored wood samples varied between 0.199 and 0.963 g cm^{-3}. We found that wood density correlated strongly with the wood hardness as measured with the Pilodyn technique with the best predictive model ($r^2 = 0.72$) being:

$\ln(\rho) = 0.8711 - 0.5763 \ln(h)$ (Eq.6)

Here, h is defined as the penetration depth of the pin into the wood in mm. We applied this model on all inventoried trees where no wood cores were taken (n = 3347).
To account for trunk taper when diameter could not be measured at 1.3 m (or 1.7 in case of rubber trees), we developed a correcting equation. Diameter data were collected from forest trees without buttresses (n = 20, dbh 11 - 58.3 cm) as well as rubber trees (n = 20, dbh 14.1 – 23 cm) by measuring diameter every 10 cm from 1.3 m to 3 m height. Subsequently, an average taper slope using lme (nlme package, random effect = tree) was extracted and all tree diameters extrapolated to dbh using the form:

$dbh_{tree} = d - (h_d - 130) \times (-0.00647)\ (r^2 = 0.99)$ (Eq.7)

$dbh_{rubber} = d - (h_d - 170) \times (-0.0146)\ (r^2 = 0.98)$ (Eq.8)

where *dbh* is estimated diameter at breast height or 1.7 m for rubber in cm, respectively; *d* is the measured diameter at height h_d in cm.

The canopy cover of the 32 research plots was measured with a spherical densiometer. Readings were done in 4 directions, north, south, east and west at 16 locations per plot (see litter traps). The average of the four readings was used as one measurement.

Since the excavation of entire trees is very time- and labor-consuming and destructive, we did not measure the biomass of coarse roots and root stock in our study plots. To calculate total belowground biomass and coarse root production, we used vegetation-specific allometric equations based on excavated trees to acquire more accurate results compared to the usage of general root:shoot ratios as suggested by Mokany et al. (2006). For forest trees, we used the equation developed by Niiyama et al. (2010) from primary Dipterocarp forests on the Malayan peninsular based on 54 excavated trees (Eq.9):

$BGB_{forest} = 0.023\ \mathrm{dbh}^{2.59}$ (Eq.9)

For rubber trees, we used the equation introduced by Wauter et al. (2008) (Eq.10):

$BGB_{rubber} = \frac{\exp\ (-4.284+1.792\ln(C_{170}))}{0.487}$ (Eq.10)

For oil palm individuals, we used the equation given by Syahrinudin (2005) (Eq.11):

$BGB\ total_{oil\ palm} = 1.45\ age + 9.88$ (Eq.11)

BGB is the estimated belowground tree biomass (in kg per tree*), BGB total* $_{oil\ palm}$ is the estimated belowground biomass of oil palms (in Mg ha^{-1}*), dbh* is diameter at 1.3 m height (in cm), C_{170} the stem circumference at 1.7 m height (in cm), and *age* is plantation age.

The biomass of fine roots (< 2 mm in diameter) was investigated from June to December 2013. Due to the large number of samples and long processing time, we sampled the 32 plots in three campaigns in May 2013, September 2013, and January 2014 comprising a balanced number of plots from the four ecosystem types sampled in every campaign. Per plot 10 vertical soil cores (3.5 cm in diameter) were taken down to 50 cm soil depth including organic layer using a soil corer at least 40 cm away from the litter traps to avoid disturbance. The soil cores were divided into the 0-10 cm, 10-30 cm and 30-50 cm layers and stored in plastic bags at 5°C. All fine roots were extracted by washing the previously soaked soil cores over a sieve of 200 µm mesh size (Retsch, Haan, Germany). Fine root fragments longer than 1 cm were extracted manually with tweezers and separated under a stereomicroscope into live (biomass) and dead fractions (necromass). Indicators of root death vary between species, nonetheless disintegration of stele, pericycle and periderm, non-turgid cortex, differing root color and elasticity (Leuschner et al., 2001) can be attributed to dead roots with a practiced eye. Herb, fern and grass roots were distinguished from tree roots by their lack of visible suberinization, their color and their smaller diameter. In samples from the jungle rubber plots, rubber tree roots (living and dead) were separated from other tree roots by set of fine root morphological characteristics. After drying at 60 °C for 48 h until constant weight, all samples were weighed and the data were expressed as fine root mass (Mg ha^{-1}).

Even though the fraction of tree fine roots > 1 cm length is representing the major part of the living fine root mass, a substantial part of the dead fine root mass consists of decaying root fragments < 1 cm length (Bauhus & Bartsch, 1996). To record this fraction of dead rootlets, a method introduced by (van Praag et al., 1988) and modified by Hertel (1999) was applied to four out of the 10 samples. After the extraction of large root fragments (> 1 cm), remaining soil residues were evenly distributed on a large sheet of filter paper (730 cm²) subdivided into 36 squares. Six of the squares were randomly selected and all root material was collected under a stereomicroscope. The mass of small dead rootlets was extrapolated to the entire sample by means of the ratio of small rootlets to large dead roots (> 10 mm in length) that was established in a sub-sample for each plot and depth (Hertel et al., 2009a). Since the allometric equations for belowground biomass normally do not cover small-diameter roots, we added our measured fine root biomass numbers to the calculated total belowground biomass.

Plant biomass values were converted into carbon pool data based on the C concentrations in the respective fractions (stem wood, leaf litter, reproductive organs, branch litter, fine roots) detected with a CN elemental analyser (Vario EL III, elementar, Hanau, Germany). The content was calculated individually for each plot separating rubber from non-rubber trees. The carbon content for the four land-use types and organs is given in Table A 2.2. For the coarse root and root stock biomass values, the respective C concentration of the stem wood was used.

Above- and belowground net primary production

In order to quantify aboveground net primary production (NPP), we estimated all plant matter produced during a specified time interval. This total is considered as being equivalent to aboveground NPP (ANPP, Clark et al., 2001a). We collected data on aboveground litterfall, pruned oil palm fronds, rubber yield harvest as well as oil palm yield, and stem increment from March 2013 to April 2014. For litter collection, 16 litter traps (75 cm x 75 cm) made from PVC-tubed frames equipped with nylon mesh (mesh size 3 mm) mounted on 1 m-long wooden stakes were placed on all plots except oil palm plantations (n = 24) in the same randomly selected grid pattern. Litter sampling was done at monthly intervals for 12 months on all plots. Collected litter was sorted into different components (leaves, small woody material (diameter < 2 cm), propagules and inflorescences) and subsequently oven-dried for 72 h at 60 °C until constant weight. In jungle rubber systems, leaves and fruits of the rubber trees were separated from other forest tree components. We assumed that annual litter production was equal to the annual production of the respective tree organs, i.e. that the systems were in a quasi-equilibrium. In the oil palm plantations, all pruned oil palm fronds on the plots were counted, and an average dry weight per frond obtained from 16 harvested and dried fronds was used for the calculation of litter production in the context of managed-related pruning in the plantations. The yield of oil palm fruits and raw rubber (in kg dry mass per tree) was recorded through weighing of the fresh material separately for all trees of a plot. The dry weight was determined after oven-drying representative sub-samples of oil palm fruits (5 multiple fruits) and raw rubber (5 harvesting bowls) at 70°C to constant weight.

Annual aboveground tree biomass production (Mg d.m. $ha^{-1}yr^{-1}$) was calculated from stem increment data based on dendrometer tape readings (UMS, München, Germany) on 40 tree individuals per plot (n_{total} = 960 trees). The trees were chosen randomly from three size-class categories covering the range of wood densities. Care was taken to include a higher percentage of large trees since they account for the major portion of aboveground biomass in tropical forests (Berry et al., 2010, Sist et al., 2014). The cumulative biomass increment of each tree was calculated as the mass difference of a tree between March 2013 and April 2014, based on the allometric regression models used for biomass estimation as described above. If tree death occurred in the measurement interval and the intercensus interval was shorter than 6 months, the tree was ignored in the calculations. For the tree individuals not included in the dendrometer study, we applied mean increment rates per plot and tree species. A subsample of small trees (2-10 cm dbh) was re-measured with regard to their dbh and height in April 2014 and their mean increment rate was used to calculate small-tree growth.

For the estimate of fine root productivity, an ingrowth core experiment was conducted on all 32 plots using the method described by Powell and Day (1991) and Majdi et al. (2005). This approach quantifies the regrowth rate of fine roots into root-free soil. Compared to other techniques, this approach has been found to give rather conservative numbers of fine root production in temperate forests (e.g. Hertel & Leuschner, 2002, Hendricks et al., 2006, Finér et al., 2011). In March and April 2013, 16 ingrowth cores per plot were installed at random locations (30 cm from the litter traps). Soil cores were extracted from the topsoil down to 30 cm depth with a soil corer (3.5 cm in diameter), the soil material was cleaned by hand from all visible live and dead rootlets (> 1 cm length) and the root-free soil was replaced into the hole taking care to conserve structure and bulk density as much as possible. To mark the location as precise as possible, rubberized mesh wire (spacing 1 cm) was inserted 15 cm deep around the sampled core. Re-sampling of the cores was done after 8-10 months. The extracted soil cores were divided into the 0-10 cm and 10-30 cm layers and processed in the same manner as done in the fine root inventory in the laboratory at University of Jambi (see above), but only larger rootlets > 1 cm in length were considered. The fine root growth in the cores was extrapolated to one year and expressed in g dry mass produced per m^2 soil surface area and year to obtain data on annual fine root production, following Vogt et al. (1998). We assumed that fine root re-colonization started immediately after the installation of the ingrowth cores based on observations from earlier ingrowth core and mini-rhizotron approaches in tropical forests and that root mass losses due to root death and subsequent decomposition during the experiment were negligible (Harteveld et al., 2007, Leuschner et al., 2013).

We calculated the carbon residence time (C_{RT}) by dividing the total carbon in biomass (kg) by total carbon NPP (kg C yr^{-1}) as defined by Malhi et al. (2004). The C_{RT} is a measure of the quantity of carbon sequestered per unit of net primary production and therefore an indicator of slow versus fast carbon pools.

Woody coarse debris

Within all forest and jungle rubber plots, snags (dbh > 10 cm) and logs (mid-point diameter > 10 cm, length > 1m) were recorded. Three decay stages were used to characterize the woody debris: (1) not degraded (but loss of leaves), (2) medium degraded, (3) heavily degraded (Grove 2001). Biomass of the debris was calculated using the equations by Kauffmann and Donato (2012) and by applying the allometric equation by Chave et al. (2005) for calculation of aboveground biomass (AGB) of undegraded trees. The third decay class of downed dead wood was calculated using the formula of a cylinder.

Decay stage 1 = AGB – 2.5 % (Eq.12)

Decay stage 2 = AGB – 15 % (Eq.13)

Decay stage 3 = $\pi\ (D/2)^2 \times H \times \rho$ (Eq.14)

D is diameter in cm, H is height in cm, AGB is biomass as calculated by Eq.1 and ρ wood density (in kg cm^{-3}).

Data were converted to C stocks (Mg C ha^{-1}) by multiplying biomass with mean carbon content per decay stage as analyzed for subsamples of the debris with a CN elemental analyzer (Vario EL III, elementar, Hanau, Germany).

Statistical analysis

Each of the four plots per land-use system and landscape were treated as random replicates in the analyses. There was in general no significant influence of the factor 'landscape' (i.e. the two study regions) on our results; thus we present mean values for all 8 plots per land-use system as well. Data are presented as means ± standard errors. All analyses (except the PCA) were conducted using R 3.1.0 software (R Development Core Team, 2014). AGB, TB and NPP_{total} were log transformed to achieve normality and homoscedasticity of model residuals, according to Shapiro-Wilk and Bartlett tests. Relationships between AGB and stand parameters (stem density, mean dbh, basal area, canopy cover) were explored with Pearson’s correlation coefficients. The influence of land-use type and region on biomass, carbon stocks and NPP was tested using linear models (lm and aov, package: ‘stats’). Subsequently, multiple comparison tests between group means were tested in a post-hoc manner with Tukey HSD tests (glht package: ‘multcomp’). In case of heteroscedasticity an adjusted statistical framework for simultaneous inference and robust covariance estimators (Herberich et al. 2010) was used to account for different variances between groups. The Kruskal-Wallice test (kruskalmc, package: 'pgirmess') was used for the parameter wood density because normality of residuals was not given. All tests of statistical significance were based on a 0.05 probability level. A principal components analysis (PCA) was done to evaluate how stand parameters interrelate among different systems using the package CANOCO, version 4.5 (Biometris, Wageningen, the Netherlands).

2.3 Results

Aboveground structure

The four land-use systems showed distinct differences in aboveground structural variables (Table 2.2). Whereas natural forest contained significantly taller trees > 10 cm in dbh (ANOVA, Tukey HSD post-hoc test; $p < 0.05$) with wider average diameters than jungle rubber and rubber plantations, stem density was slightly higher in jungle rubber systems. Consequently, total basal area decreased significantly from natural forest (mean ± SE: 30.1 ± 0.9 m^2 ha^{-1}), jungle rubber (18.3 ± 1.1 m^2 ha^{-1}) to rubber monoculture (11.09 ± 1.05 m^2 ha^{-1}). Similarly, canopy cover decreased with decreasing naturalness of a land-use system from forest (92.1 ± 0.5 %) > jungle rubber (87.6 ± 0.8 %) > rubber monoculture (85.8 ± 0.9 %) > oil palm plantation (76.8 ± 1.0 %). Trees > 70 cm dbh were rarely present in any of the systems.

Differences between the landscapes in stand structural properties were not prominent. However, the natural forest in Harapan (HP) tended to contain taller trees as well as higher stem densities and therefore a higher basal area and canopy cover than the forest in Bukit Duabelas (B12) (Table 2.2). The situation was reversed in tendency in the jungle rubber systems, where higher rubber stem densities were found in B12 than in HP.

Table 2.2 Aboveground stand structural variables of the four transformation systems in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra. Given are means ± SE (n = 4). Lower case letters indicate significant differences between means of each landscape and land-use system according to Tukey HSD tests ($p < 0.05$). Only trees with dbh > 10 cm are considered.

	Forest		**Jungle rubber**		**Rubber**		**Oil palm**	
Structural variable	HP	B12	HP	B12	HP	B12	HP	B12
Mean tree height (m)	20.01 ± 0.63 d	16.97 ± 0.46 c	14.02 ± 0.22 b	15.19 ± 0.27 bc	13.42 ± 0.46 b	13.44 ± 0.11 b	4.88 ± 0.55 a	4.00 ± 0.29 a
Canopy height (m)	48.23 ± 1.57 d	42.53 ± 1.81 d	25.60 ± 1.34 c	27.58 ± 1.07 c	19.58 ± 0.73 b	17.65 ± 1.12 b	8.10 ± 1.78 a	5.43 ± 0.46 a
DBH (cm)	20.97 ± 0.54 b	23.01 ± 0.42 b	16.79 ± 0.48 a	17.25 ± 0.58 a	17.76 ± 1.24 a	15.20 ± 0.66 a		
Basal area (m^2 ha^{-1})	30.72 ± 0.97 d	29.39 ± 1.65 d	16.58 ± 0.43 bc	21.06 ± 1.43 c	12.23 ± 1.55 ab	9.95 ± 1.38 a		
Stem density (n ha^{-1})	658 ± 26.0 bc	471 ± 31.3 bc	525 ± 60.2 bc	685 ± 72.1 c	440 ± 81.7 b	497 ± 15.4 bc	140 ± 4.9 a	134 ± 6.0 a
Canopy cover (%)	92.89 ± 0.54 d	91.23 ± 0.78 cd	88.56 ± 0.55 bd	86.56 ± 1.32 bc	86.9 ± 0.73 bc	84.7 ± 1.58 b	78.83 ± 0.40 a	74.7 ± 1.44 a

Biomass and carbon pools in above- and belowground fractions

Total biomass with all above- and belowground components amounted for 388.6 ± 23.5 Mg ha^{-1} (mean ± SE) in natural forest and was significantly higher than in all other systems (ANOVA, Tukey HSD post-hoc test; $p < 0.05$) (Figure 2.2).

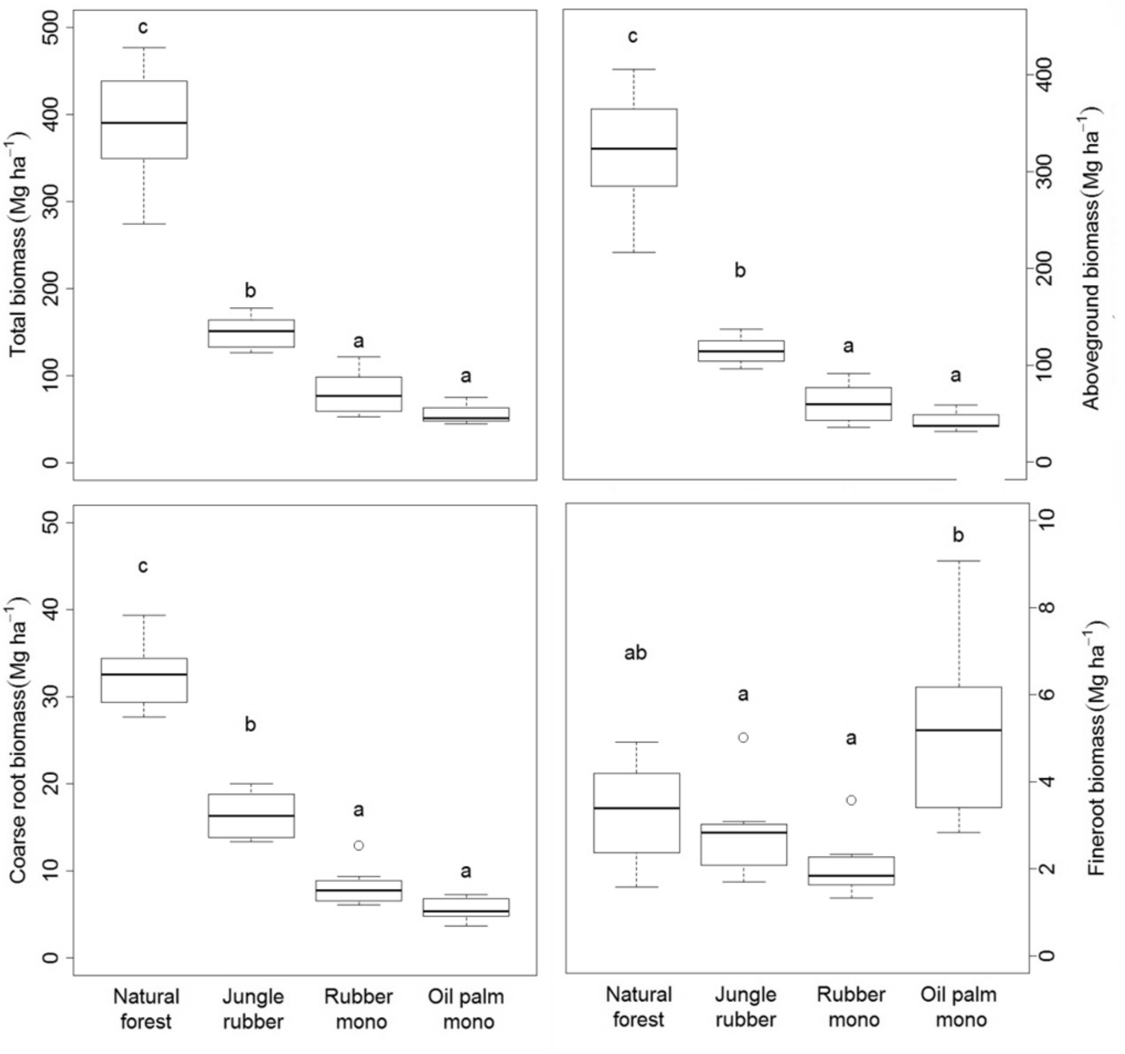

Figure 2.2: Total biomass, aboveground biomass, coarse root and fine root biomass (Mg ha^{-1}) of the four land-use systems in Jambi, Sumatra. Shown are means ± SE (n = 8). Lower case letters indicate significant differences between systems according to Tukey HSD post-hoc tests ($p < 0.05$).

Jungle rubber held less than 40 % of natural forest biomass (149.9 ± 6.7 Mg ha^{-1}) and rubber monoculture (80.6 ± 8.8 Mg ha^{-1}) and oil palm (55.7 ± 4.2 Mg ha^{-1}) less than 20 % (Table 2.3). Data for all 32 plots are provided in the Appendix (Table A 2.1). AGB was the largest component of carbon storage in biomass (79.5 ± 0.7 %), followed by coarse roots/root stocks (16.9 ± 0.8 %), aboveground dead wood (2.2 ± 0.4 %), fine root biomass (0.7 ± 0.1 %) and fine root necromass (0.7 ± 0.1 %) in the natural forest sites. Aboveground dead wood was noticeable only in the natural forest (4.5 ± 0.9 Mg ha^{-1}) and in jungle rubber (4.3 ± 2.2 Mg ha^{-1}) where it built 5.3 ± 2.5 % of the carbon stock. Carbon content varied substantially among land-use types and organs ranging between 37 % in rubber tree fine roots and 60 % in oil palm fruits (Table A 2.2).

Large trees > 40 cm dbh contributed only 11 % of the total number of tree individuals in natural forest, but accounted for the majority of basal area (52 % of total BA) and aboveground biomass (66 % of total AGB). Regional differences between the four land-use systems were not significant, except for fine root biomass and necromass, where oil palm plantations showed higher values in the Harapan than in the Bukit Duabelas region (Table 2.3).

Table 2.3: Above- and belowground biomass (Mg ha^{-1}) and carbon pools (in brackets Mg C ha^{-1}) by fraction in the four transformation systems in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra as estimated by aboveground structural inventories in combination with allometric equations, and fine root biomass inventories (down to 50 cm soil depth). Given are means ± SE (n = 4). Lower case letters indicate significant differences between means of each landscape and land-use according to Tukey HSD post-hoc tests ($p < 0.05$).
[a] including root stock.

	Forest				**Jungle rubber**				**Rubber**				**Oil palm**			
Biomass fraction (Mg ha^{-1})	HP		B12		HP		B12		HP		B12		HP		B12	
Aboveground biomass	351.7 ± 21.8 (171.2)	e	291.1 ± 33.2 (139.9)	e	103.8 ± 3.0 (48.9)	cd	126.8 ± 4.2 (60.4)	d	72.2 ± 8.6 (33.6)	bc	49.9 ± 9.6 (23.7)	ab	47.3 ± 6.0 (19.9)	ab	37.3 ± 2.1 (15.7)	a
Coarse root biomass [a]	62.3 ± 2.6 (32.1)	e	65.4 ± 4.5 (32.8)	e	27.1 ± 0.7 (14.0)	cd	36.6 ± 0.9 (18.9)	d	19.2 ± 3.0 (9.1)	bc	15.7 ± 1.5 (7.4)	ab	9.0 ± 0.7 (6.6)	ab	7.4 ± 0.5 (4.7)	a
Fineroot biomass	3.6 ± 0.5 (1.5)	a	3.0 ± 0.7 (1.3)	a	2.7 ± 0.2 (1.2)	a	2.9 ± 0.8 (1.2)	a	2.0 ± 0.3 (0.7)	a	2.14 ± 0.49 (0.8)	a	6.6 ± 0.9 (2.7)	b	3.7 ± 0.5 (1.4)	a
Fineroot necromass	4.1 ± 0.7 (1.8)	ab	2.2 ± 0.6 (0.9)	a	2.6 ± 0.2 (1.1)	a	2.0 ± 0.4 (0.8)	a	2.0 ± 0.2 (0.8)	a	2.0 ± 0.4 (0.7)	a	7.0 ± 0.2 (2.9)	c	4.8 ± 0.7 (1.8)	b
Dead wood	12.0 ± 1.3 (5.5)	b	7.54 ± 3.3 (3.5)	ab	15.6 ± 8.3 (7.2)	ab	3.0 ± 1.4 (1.3)	a								
Total biomass	417.6 ± 24.0 (212.0)	e	359.5 ± 38.1 (178.5)	e	133.5 ± 3.4 (72.4)	cd	166.3 ± 4.1 (82.6)	d	93.4 ± 11.7 (44.0)	bc	67.7 ± 10.8 (32.6)	ab	63.0 ± 6.5 (32.1)	ab	48.4 ± 1.9 (23.6)	a

Root:shoot ratios were estimated to vary between 0.20 ± 0.01 in forest and 0.30 ± 0.01 in jungle rubber, 0.33 ± 0.02 in rubber and 0.32 ± 0.03 in oil palm, respectively. Fine root biomass decreased with soil depth in all systems; in general, about 80 % of the fine root biomass in 0-50 cm was concentrated in the uppermost 30 cm.

Above- and belowground NPP and associated carbon sequestration

The estimated total NPP of all 32 plots ranged between 12.3 and 35.9 Mg ha^{-1} yr^{-1}. Oil palm fruit production in the Harapan region was slightly higher, but otherwise the two landscapes had similar NPP fractions. Total NPP in the oil palm plantations (mean ± SE: 31.7 ± 1.6 Mg ha^{-1} yr^{-1}) consisting by 54.0 ± 2.4 % of fruit production (yield) was significantly higher than in the natural forest (24.1 ± 1.3 Mg ha^{-1} yr^{-1}) and jungle rubber (20.0 ± 1.0 Mg ha^{-1} yr^{-1}) systems (Figure 2.3).

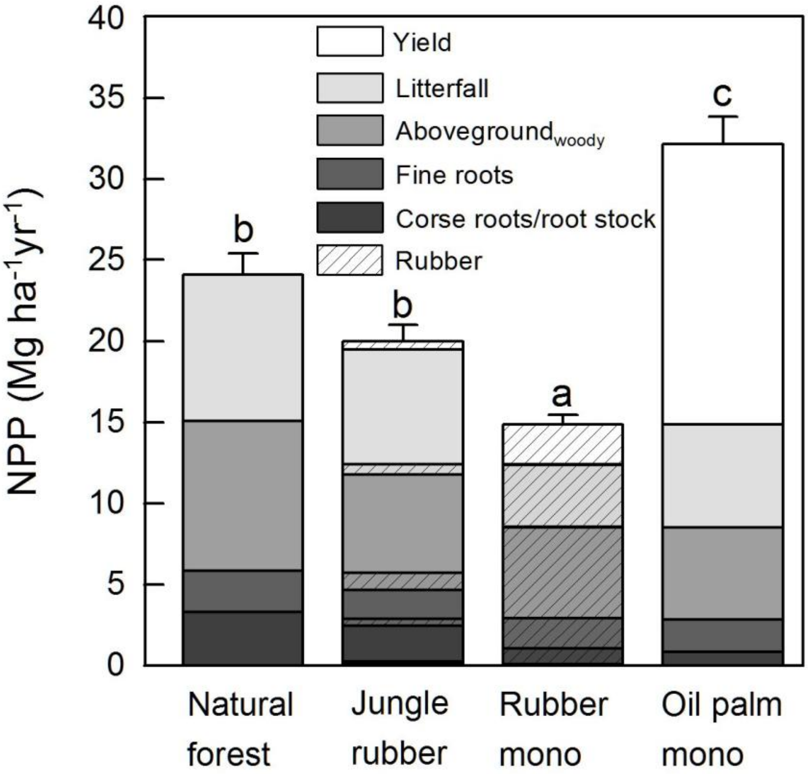

Figure 2.3: The net primary productivity (NPP) of the four ecosystems by fraction. The contribution of rubber is shaded. All values are means of both landscapes in Mg ha^{-1} yr^{-1} (n = 8). Lower case letters indicate significant differences between NPP_{total} values of the systems according to Tukey HSD tests ($p < 0.05$).

However, when only long-term C pools are considered, oil palm plantation productivity was lower than in forests. Rubber monocultures had the lowest total NPP (14.9 ± 0.6 Mg ha^{-1} yr^{-1}) (Table 2.4). While in oil palm plantations more than 50 % of carbon was allocated in the fruits, in natural forest and jungle rubber the components of tree biomass production were roughly equally divided to stem growth, aboveground litter and root productions. In rubber monocultures around 20 % of NPP was attributed to latex harvest, while a smaller percentage of NPP was allocated to leaf and root production. Total standing biomass was not related to total NPP across all systems (Pearson’s correlation coefficient; r = 0.013, p = 0.94), but when excluding yield from NPP, a positive correlation could be observed (r = 0.78, $p < 0.001$).

The carbon residence time (C_{RT}) was highest in natural forest and decreased significantly from rubber systems to oil palm plantations, where it reaches just 10 % of the forests’ values.

Table 2.4 Components of net primary productivity (NPP) (Mg ha^{-1} yr^{-1}) and carbon sequestration (Mg C ha^{-1} yr^{-1}) as well as the carbon retention time (C_{RT}) defined as biomass divided by total NPP (Mg Mg^{-1} yr) for the four land-use systems in the two landscapes in Jambi, Sumatra. No data are available for root exudation, transfer to mycorrhizal hyphae and consumption by herbivores. Leaf and reproductive part production was assumed to equal annual aboveground litterfall (NPP_{litter}). Fine root production ($NPP_{fineroot}$) was estimated from an ingrowth core approach. Given are means ± SE (n = 4). Lower case letters indicate significant differences between means according to Tukey HSD tests ($p < 0.05$).
a including root stock

	Forest		**Jungle rubber**		**Rubber**		**Oil palm**	
NPP fraction (Mg ha^{-1} yr^{-1})	HP	B12	HP	B12	HP	B12	HP	B12
NPP_{woody}	8.1 ± 0.1 (4.0) ab	10.3 ± 1.6 (5.0) b	6.9 ± 0.8 (3.3) ab	7.4 ± 0.4 (3.5) ab	6.1 ± 0.7 (2.8) a	5.2 ± 1.0 (2.4) a	4.4 ± 0.6 (1.9) a	6.2 ± 0.6 (2.6) a
NPP_{litter}	8.3 ± 0.5 (4.1) c	9.8 ± 1.4 (4.8) bc	7.7 ± 0.6 (3.8) bc	7.6 ± 0.6 (3.7) bc	3.6 ± 0.3 (1.8) a	4.1 ± 0.2 (2.1) a	5.5 ± 0.2 (2.5) b	7.2 ± 1.0 (3.3) ac
$NPP_{coarseroot}$ [a]	3.1 ± 0.3 (1.5) c	3.5 ± 0.2 (1.7) c	2.1 ± 0.2 (1.0) b	2.8 ± 0.2 (1.3) bc	1.0 ± 0.1 (0.5) a	1.1 ± 0.3 (0.5) a	0.8 ± 0.02 (0.3) a	0.8 ± 0.04 (0.4) a
$NPP_{fineroot}$	3.0 ± 0.3 (1.3) b	2.1 ± 0.5 (0.9) ab	2.1 ± 0.4 (0.9) ab	2.3 ± 0.6 (0.9) ab	1.8 ± 0.2 (0.7) ab	1.9 ± 0.3 (0.7) ab	2.8 ± 0.7 (1.1) ab	1.2 ± 0.1 (0.4) a
NPP_{yield}			0.8 ± 0.2 (0.7) a	0.3 ± 0.1 (0.2) a	1.8 ± 0.5 (1.5) a	3.1 ± 0.9 (2.6) a	19.9 ± 1.3 (11.5) c	14.7 ± 1.6 (8.5) b
NPP_{total}	22.5 ± 0.5 (10.8) c	25.7 ± 2.4 (12.3) cd	19.7 ± 1.5 (9.6) ac	20.2 ± 1.4 (9.7) bc	14.3 ± 0.6 (7.2) a	15.4 ± 1.1 (8.3) ab	33.4 ± 1.1 (17.3) d	30.1 ± 3.1 (15.1) cd
C_{RT} (yr)	19.6 ± 1.4 d	14.5 ± 1.2 d	7.6 ± 0.5 c	8.7 ± 0.8 c	6.2 ± 0.9 c	4.2 ± 1.0 bc	1.9 ± 0.1 ab	1.6 ± 0.2 a

Ordination of the plots according to the results of the principle components analysis (PCA) based on parameters of stand structure, AGB and NPP confirmed the differentiation among the four land-use systems (Figure 2.4). The first axis (eigenvalue = 0.50) of the PCA separated natural forest, jungle rubber, rubber plantation and oil palm plantation consecutively along a gradient of decreasing naturalness. Most parameters of biomass (AGB, $BGB_{coarseroot}$, TB) and NPP (NPP_{wood}, $NPP_{coarseroot}$) together with all interrelated structural variables like canopy height, canopy cover and WD were related to this axis. In the opposite direction, NPP_{yield} showed an interrelationship to this axis. The strongest influential factors on the second axis (eigenvalue = 0.25), which separated rubber systems from the other systems, were NPP_{total} as well as NPP_{litter} and fine root biomass. Root:shoot ratio was associated with the axis in the opposite direction.

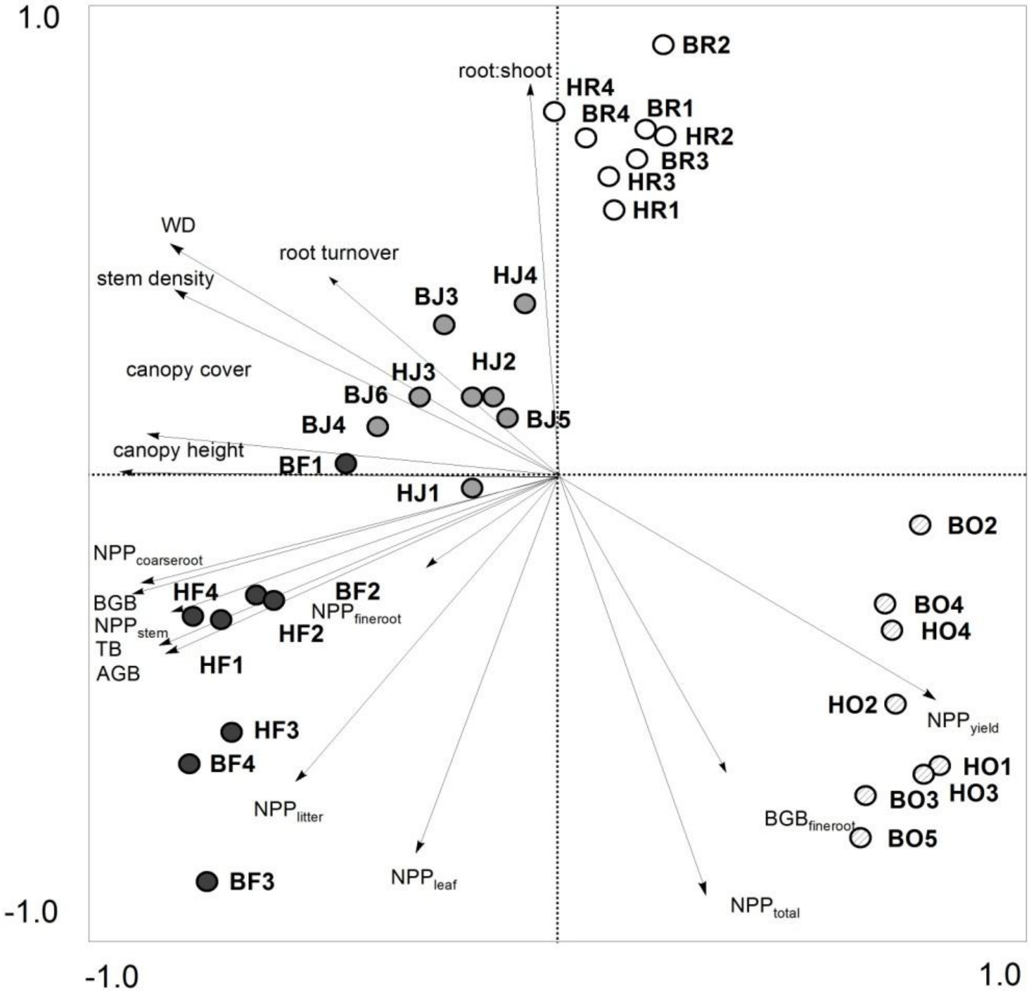

Figure 2.4: Plot showing the distribution of the 32 Plots in four transformation systems and two landscapes (HP = Harapan region, B = Bukit Duabelas region; F = natural forest, R= rubber monoculture, J = jungle rubber, O = oil palm monoculture) in PCA axes 1 and 2 with stand structural and biomass variables. Vector length and angle are proportional to the direction and degree of their correlation with the plot ordination scores.

2.4 Discussion

Effect of land-use change on carbon pools

Our study quantifies the high losses in carbon stocks which follow from the conversion of natural tropical lowland forests. We found that natural forests in this region store three times more carbon in the tree biomass than even the most extensively utilized conversion system (i.e. 'jungle rubber'). The total carbon pools of rubber and oil palm monocultures consist of less than 20 % of the natural forest C stocks they are replacing.

Converting natural forest to oil palm or rubber monocultures results in the reduction of the phytomass C stock by up to 170 Mg C ha^{-1} in this lowland area. Nowadays, the most common land-use change in the region is conversion of jungle rubber to oil palm plantations (Villamor et al., 2014), which still decreases biomass C storage by at least 50 Mg C ha^{-1}. Due to the short rotation time of efficient plantation use, carbon stocks in these monoculture systems can reach maximal double the values of the here reported mature phase before being felled (Syahrinudin, 2005, Morel et al., 2011, Maggiotto et al., 2014). Oil palm productivity per plant decreases at the age of 20 years (Asari et al., 2013), whereas rubber monocultures can efficiently be tapped during 40 years (Gouyon et al., 1993, Song et al., 2013).

Our study differs from most of the cited biomass studies in that we were able to estimate total, i.e. above- and belowground tree biomass. Furthermore, we have measured carbon content of all biomass components individually finding substantial differences and did not apply a simple conversion factor of 0.5 as in most studies (e.g. Gibbs et al., 2007, Saatchi et al., 2011, Saner et al., 2012, Berenguer et al., 2014). Using the 0.5 conversion factor may lead to a biased carbon estimate between 3-10 % for all land-use systems and even when applying a 0.48 conversion factor the carbon stocks in oil palm plantations are overestimated by 6 % compared to the usage of the correct carbon content. These findings are underlining not only the importance of using appropriate allometric equations, but also correct carbon content.

AGB as well as root biomass varied considerably between land-use systems with the differences largely explained by the stand variables canopy height, mean diameter and, to a lesser extent, by wood density and stem density. In the natural forest plots, average wood density was the highest of all systems. However, the density values varied largely between the species and we found in natural forest and jungle rubber plots soft-wooded and very hard-wooded species in the same stand, the latter mostly Dipterocarpaceae species (Basuki et al., 2009). In jungle rubber plantations, we found that rubber trees contributed 23 % to AGB, while the other 77 % referred to tree species remaining from the forest or invading fast-growing pioneer tree species. The lower C storage compared to natural forest can largely be explained by the absence of big trees, as individuals > 30 cm in dbh were nearly absent in agroforests. Even in natural forest sites we found an uncommonly low number of 1.9 trees > 70 cm dbh per hectare (Paoli et al., 2008).

Although the natural forest at our sites is protected by law, we found clear indication in the frequency distribution of tree diameters in the stands that can only be explained by selective tree extraction in these forest sites in the past. This might be one of the reasons why our total C stock estimates (195.2 ± 13.0 Mg C ha^{-1}) and AGB values (321.4 ± 21.7 Mg ha^{-1}) are lower than in other forests in Southeast Asia. Adachi et al. (2011) reported an AGB value of 226.3 Mg C ha^{-1} from a dry evergreen forest in Thailand, and Katayama et al. (2013) measured an even higher figure of 272.4 Mg C ha^{-1} in a Dipterocarp forest in Borneo. AGB stocks in African tropical lowland rainforests were found to range between 350 and 460 Mg ha^{-1} (Glenday, 2006, Djuikouo et al., 2010, Lewis et al., 2013, Day et al., 2014). The numbers recorded in our two study regions appear to be more similar to carbon densities found in over-logged forests in Sabah, Malaysia (167.9 Mg C ha^{-1}; Saner et al., 2012) and they are in the same magnitude as AGB densities reported for neotropical forests in the Amazon basin which range between 241 and 397 Mg ha^{-1} (Houghton et al., 2001, Cummings et al., 2002, Nascimento & Laurance, 2002, Malhi et al., 2006, Nogueira et al., 2008, Baraloto et al., 2011, Berenguer et al., 2014). Differences in soil characteristics as well as in rainfall that were observed among the regions could not explain much of the variation in biomass and consequently carbon stock fractions within a land-use system.

In accordance with other studies, we found that AGB accounted for 65-80 % of total plant C in all four land-use systems (Gibbs et al., 2007, Nogueira et al., 2008, Hertel et al., 2009b, Saner et al., 2012), followed by coarse roots, while dead wood (present only in natural forest and jungle rubber) contributed only a few percent with plot averages of 3-16 Mg d.m. ha^{-1}. Fine root biomass accounted for not more than 2 percent of total plant biomass in all systems except for oil palm, where it reached values close to the coarse root and root stock biomass due to the homorhiz root system structure of the monocotyledonous oil palm (Jourdan & Rey, 1997). It is reported that soil carbon storage is greater in ecosystems dominated by ectomycorrhizal-associated plants (Averill et al. 2014) such as formed by Dipterocarp roots in Southeast-Asian forests (Brearley 2012). However, we did not find ectomycorrhizal roots in substantial numbers in any site suggesting that these forests are relatively poor in mature Dipterocarp trees. Standing and lying dead wood reached higher values in relative terms in the jungle rubber systems compared to the three other land-use systems due to the species composition that consists of more short-lived pioneer species (Remboldt et al., unpublished data) and former disturbance effects like timber extraction or death of rubber trees following intensive tapping and fungal infections (Gouyon et al., 1993, Schroth et al., 2004). Nevertheless, our dead wood figures are low in comparison to data from other tropical forests. For example, over two times higher dead wood masses were reported for natural forests in Venezuela (Delaney et al., 1998) and Peru (Gurdak et al., 2014) or even 10 times higher figures from eastern Brazil (Rice et al., 2004). One hypothesis is that dead wood may have been harvested by the local inhabitants. We did not observe dead wood in rubber monoculture or oil palm systems, because in case of tree death, the wood is either used as firewood or usually burned directly in case of oil palm plantations.

Variation in net primary productivity and its components

We estimated total NPP (above- and belowground) to be 24.1 ± 1.3 Mg d.m. ha^{-1} yr^{-1} in the natural forest sites and even higher in the oil palm monocultures (31.7 ± 1.6 Mg ha^{-1} yr^{-1}). In contrast to our relatively low biomass values in the natural forests, we have measured rather high total NPP values for our forest plots compared to other published figures from tropical forests (Clark et al., 2001b, Kitayama & Aiba, 2002, Hertel et al., 2009b, Girardin et al., 2010). However, recent comprehensive data compilations from several Amazonian sites (Aragao et al., 2009, Malhi et al., 2009) as well as several forests in the Southeast Asian tropics (Kho et al., 2013) revealed similar total NPP figures ranging between 18.6 and 34.0 Mg ha^{-1} yr^{-1}. Similar to biomass inventories, studies investigating all major components of NPP with full consideration of belowground fractions are still rare and probably result in underestimation of reported means (Clark et al., 2001b, Hertel et al., 2009b). The yield of oil palm fruit bunches and rubber latex production were investigated as well. Parameters such as leaf and root herbivory, carbohydrate transfer to mycorrhiza and rhizodeposition, however, were not taken into account as they are still too difficult to measure. In addition, tree recruitment and mortality were not measured due to the short duration of our study. Therefore, we still might have underestimated actual NPP in the natural forest and jungle rubber stands to a certain extent. On the other hand, if old-growth forests have a mortality rate higher than the recruitment rate, this would lower NPP, but it is not considered here. Despite these assumed methodological shortcomings, the observed relative differences between the four studied systems are large and thus may be robust as identical methods were applied at all sites (except for litter production measurement in oil palm plantations where the pruned, and not fallen, palm leaves were collected).

Different from all other three land-use systems, oil palm plantations have a particularly high fruit production with about half of the NPP invested in reproductive organs. The measured relatively high values of aboveground woody NPP, particularly in the B12 forest, support our assumption of former forest disturbance of these study sites (Kho et al., 2013). In the aftermath of selecting logging, aboveground wood production is reported to increase due to increased light availability (Figueira et al., 2008, Malhi et al., 2009). Similarly, wood increment in the jungle rubber plots was not significantly lower than in the forest plots even though total AGB and canopy cover were much smaller. While the leaf:fine root production ratio was not significantly different between natural forest and rubber systems, oil palm plantations showed higher allocation to total aboveground components and also larger investment in leaves than in roots. Regional variation in clay content could be a factor influencing the aboveground:belowground allocation ratio of the trees and palms. The higher clay content in the B12 region could have led to decreased investment in fine roots due to lower soil penetrability and increased water holding capacity as compared to the more drought-affected sandier soils in the Harapan region (Metcalfe et al., 2008, Aragao et al., 2009).

Average fine litterfall in the natural forest (9.0 Mg ha^{-1} yr^{-1}) and in the jungle rubber (7.7 Mg ha^{-1} yr^{-1}) are in the range reported by Aragao et al. (2009), Chave et al. (2010), and Malhi et al. (2011). Our data support earlier reports that fine litter production can be used as a fairly good predictor for total NPP (Aragao et al., 2009, Girardin et al., 2010, Malhi et al., 2011), because a very large fraction of the litter (78 % in the natural forest and 80 % in the jungle rubber) refers to leaf mass.

While the variation in aboveground biomass stocks and aboveground NPP across the different components revealed similar patterns, fine roots play a negligible role in the total carbon stock, but are more prominent in their contribution to productivity (Vogt et al., 1996, Hertel et al., 2009b). The annual fine root production in the forests of this study was estimated with the ingrowth core approach to be 2.6 Mg ha^{-1}yr^{-1} what is equivalent to 1.4 Mg C ha^{-1}yr^{-1}. This figure is in the range of reported values from other tropical forests (Vogt et al., 1996, Hertel et al., 2009a, Leuschner et al., 2013). However, as fine roots can reach much greater depth then studied by us, these values will certainly underestimate the profile total (Nepstad et al., 1994).

Jungle rubber plantations are a heterogeneous transition system between forest and rubber monocultures as also indicated by the results of the PCA and they have the potential to provide smallholders with noteworthy income while still maintaining some important ecosystem functions of the forest (Schroth et al., 2004). Additionally, other timber and non-timber products such as fruits can be extracted from jungle rubber stands (Gouyon et al., 1993, Montagnini & Nair, 2004) and the forest is never clear-cut, retaining a large fraction of its carbon stock. The production of wood, branches, coarse and fine roots as well as the C flux with leaf litter is comparable to that in a natural forest. In contrast to the extensively utilized and unfertilized jungle rubber, oil palm plantations are highly managed systems where competition by other plants is suppressed and that are heavily fertilized usually twice a year by synthetic NPK fertilizer or urea. This management is one of the main causes of the high NPP values recorded in this system. However, long-term carbon sequestration through biomass accumulation does only occur at a much reduced rate in this system as the main component – fruit bunches – is regularly removed from the system. Consequently, the amount of annually sequestered carbon through biomass accumulation is three times higher in the natural forest than in the oil palm plantation. With the same net production rate oil palm plantations would sequester 90 % less carbon in biomass than natural forest. This pattern is better captured by the carbon residence time (C_{RT}), as the anthropogenic managed systems show a much faster carbon pool than natural forest and we can assume that the carbon stored in very short lifespan pools will be released rather quickly. Furthermore, a crop rotation period of around 20 years with burning or rapid decay of the felled palm biomass results in a low long-term C sequestration potential.

In conclusion converting tropical lowland forests or structurally diverse agroforests into rubber or oil palm monocultures does not only reduce the biomass C stock greatly, but it also lowers the carbon sequestration potential. It thus will take hundreds of years to compensate for the emitted carbon which is caused by conversion from a forest- or agroforest-dominated landscape to oil palm monocultures (Henson, 2008). High-yield farming is expected to allow more species to persist on spared land (Green et al., 2005) and protecting forests may offer a cost-effective way of reducing carbon emissions (Schrope, 2009) as promoted by the REDD+ initiative. However, the financial opportunity costs of oil palm plantations on mineral soil preceded by logging of forest in Indonesia currently represent a strong economic incentive (Koh & Ghazoul, 2010, Irawan et al., 2013) and the oil palm case suggests that improvements in tropical crop yields will further transfer agricultural production from temperate to tropical regions, leading to more tropical deforestation (Carrasco et al., 2014). Our analysis further shows that neither logged-over forest nor extensively managed agroforest systems are coming close to replacing the full amount of carbon that was present in the primary forest, but these extensively used systems have the potential of sustaining some forest ecosystem functions while additionally providing valuable products and food to local people.

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2.5 Appendix

Table A 2.1. Above- and belowground biomass, net primary production (NPP) by components, and carbon pools in 32 plots in four transformation systems (F = natural forest, J = jungle rubber, R= rubber monoculture, O = oil palm monoculture) in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra as estimated by aboveground structural inventories in combination with allometric regression equations, and fine root biomass inventories. Fine root production ($NPP_{fineroot}$) was estimated from an ingrowth core approach. Crop yield (NPP_{yield}) included latex and oil palm fruit harvest. NPP_{woody} and $NPP_{coarseroot}$ were accessed based on allometric equations. Aboveground litter production (NPP_{litter}) was assumed to equal annual leaf litterfall.*The age of jungle rubber plantations refers to the age of the oldest rubber trees planted.

Region	**System**	**Plot**	**Age** years*	**AGB** Mg ha^{-1}	**BGB** Mg ha^{-1}	**$NPP_{fineroot}$** Mg $ha^{-1}yr^{-1}$	**NPP_{yield}** Mg $ha^{-1}yr^{-1}$	**NPP_{woody}** Mg $ha^{-1}yr^{-1}$	**$NPP_{coarseroot}$** Mg $ha^{-1}yr^{-1}$	**NPP_{litter}** Mg $ha^{-1}yr^{-1}$	**TB** Mg C ha^{-1}	**NPP_{total}** Mg C $ha^{-1}yr^{-1}$
B12												
	F	BF1		216.49	58.15	2.07		5.76	3.13	8.76	132.10	9.38
	F	BF2		277.78	62.70	1.01		12.85	4.04	7.28	165.86	11.94
	F	BF3		292.68	71.63	3.21		10.85	3.60	13.81	183.48	15.25
	F	BF4		377.52	81.03	2.25		11.84	3.17	9.29	232.34	12.98
	J	BJ3	17	118.40	41.67	1.65	0.33	7.31	2.87	6.83	82.54	9.08
	J	BJ4	25	122.62	37.28	2.69	0.17	8.25	3.26	9.07	77.87	11.09
	J	BJ5	24	137.79	39.56	1.09	0.66	6.51	2.14	6.59	86.28	8.20
	J	BJ6	39	128.33	39.71	3.63	0.00	7.32	2.96	7.94	83.52	10.42
	O	BO2	12	37.98	11.13	1.07	11.45	4.46	0.71	5.10	23.12	11.57
	O	BO3	11	41.77	11.65	0.84	17.25	6.78	0.85	8.81	25.95	17.52
	O	BO4	10	31.55	13.08	1.38	12.22	6.67	0.85	5.98	22.51	13.47
	O	BO5	8	37.75	8.79	1.35	17.69	6.89	0.89	9.06	22.65	18.05
	R	BR1	15	77.50	21.46	1.36	3.10	2.70	0.61	4.56	47.52	6.71
	R	BR2	7	39.36	15.71	1.63	5.30	4.81	1.04	3.45	26.59	9.50
	R	BR3	6	36.19	16.61	2.87	3.24	5.95	1.24	4.09	25.40	9.17
	R	BR4	7	46.65	17.39	1.81	0.87	7.24	1.39	4.22	30.97	7.63

Table A 2.1. (continued) Above- and belowground biomass, net primary production (NPP) by components, and carbon pools in 32 plots in four transformation systems (F = natural forest, J = jungle rubber, R= rubber monoculture, O = oil palm monoculture) in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra as estimated by aboveground structural inventories in combination with allometric regression equations, and fine root biomass inventories. Fine root production ($NPP_{fineroot}$) was estimated from an ingrowth core approach. Crop yield (NPP_{yield}) included latex and oil palm fruit harvest. NPP_{woody} and $NPP_{coarseroot}$ were accessed based on allometric equations. Aboveground litter production (NPP_{litter}) was assumed to equal annual leaf litterfall.*The age of jungle rubber plantations refers to the age of the oldest rubber trees planted.

Region	**System**	**Plot**	**Age** years*	**AGB** Mg ha^{-1}	**BGB** Mg ha^{-1}	**NPP$_{fineroot}$** Mg ha^{-1}yr^{-1}	**NPP$_{yield}$** Mg ha^{-1}yr^{-1}	**NPP$_{woody}$** Mg ha^{-1}yr^{-1}	**NPP$_{coarseroot}$** Mg ha^{-1}yr^{-1}	**NPP$_{litter}$** Mg ha^{-1}yr^{-1}	**TB** Mg C ha^{-1}	**NPP$_{total}$** Mg C ha^{-1}yr^{-1}
HP	F	HF1		352.95	63.26	2.78		7.92	3.29	8.45	209.37	10.68
	F	HF2		299.46	59.76	3.82		8.06	2.36	8.35	181.11	10.88
	F	HF3		348.20	70.14	2.78		8.28	3.13	9.39	214.57	11.49
	F	HF4		406.27	70.34	2.50		8.20	3.57	6.97	243.11	10.38
	J	HJ1	17	110.28	31.81	2.39	1.22	7.72	2.34	9.18	87.61	11.21
	J	HJ2	16	96.40	29.80	2.94	0.70	6.19	1.91	8.39	62.77	9.87
	J	HJ3	15	106.68	28.34	1.66	0.61	8.68	2.56	6.68	71.61	9.66
	J	HJ4	16	101.73	29.10	1.38	0.62	5.10	1.74	6.63	67.74	7.57
	O	HO1	15	59.23	16.33	0.95	23.72	4.63	0.77	5.79	37.21	19.06
	O	HO2	13	56.27	16.26	3.28	18.67	3.47	0.78	5.32	36.00	16.38
	O	HO3	11	36.89	17.27	2.47	19.31	5.97	0.76	5.73	29.63	17.65
	O	HO4	11	36.97	12.64	4.49	18.02	3.68	0.69	4.99	25.55	16.43
	R	HR1	13	77.15	20.59	1.45	1.52	6.90	1.09	3.58	45.20	7.08
	R	HR2	14	50.54	15.07	1.70	2.39	4.16	0.68	4.27	31.36	7.04
	R	HR3	16	69.25	19.19	2.06	2.65	6.24	1.02	3.82	42.14	8.15
	R	HR4	14	91.84	29.91	2.03	0.53	7.18	1.30	2.75	57.37	6.56

Table A 2.2 Carbon content of the biomass and net primary production components in four transformation systems in the two landscapes (HP = Harapan region, B12 = Bukit Duabelas region) in Jambi, Sumatra. Given are mean values ± SE (n = 9 – 40 for stem samples; n = 30 − 48 for fine root samples; n = 5 – 32 for litter samples).

	Natural forest		**Jungle rubber**		**Rubber mono**		**Oil palm mono**	
C content (%)	HP	B12	HP	B12	HP	B12	HP	B12
Stem wood								
Forest trees	48.6 ± 0.1	48.0 ± 0.2	47.3 ± 0.2	47.6 ± 0.5				
Plantation trees			46.8 ± 0.2	48.2 ± 0.2	46.7 ± 0.2	47.3 ± 0.2	42.1 ± 0.3	
Fine roots inventory								
Forest trees	42.5 ± 0.4	42.6 ± 0.5	43.0 ± 0.6	40.7 ± 0.4				
Plantation trees			41.3 ± 0.8	37.4 ± 0.7	36.8 ± 0.6	37.9 ± 0.5	41.2 ± 0.4	37.5 ± 0.4
Fine roots ingrowth cores								
Forest trees	39.9 ± 0.6	39.4 ± 0.5	41.1 ± 0.6	39.6 ± 0.5				
Plantation trees			40.2 ± 0.9	38.2 ± 0.5	37.8 ± 0.4	37.4 ± 0.6	37.2 ± 0.8	37.2 ± 0.4
Leaf litter								
Forest trees	50.0 ± 0.4	49.4 ± 0.4	48.0 ± 0.6	48.3 ± 0.4				
Plantation trees			51.6 ± 0.3	51.7 ± 0.3	51.0 ± 0.1	50.3 ± 0.2	46.6 ± 0.2	45.7 ± 0.3
Branch wood litter								
	50.1 ± 0.4	49.4 ± 0.2	48.6 ± 0.3	48.3 ± 0.4	48.4 ± 0.4	47.9 ± 0.5		
Fruit								
	49.4 ± 0.5	48.7 ± 0.7	49.6 ± 0.7	49.3 ± 1.1	50.7 ± 1.0	52.4 ± 1.4	60.1 ± 5.4	
Flower								
	48.7 ± 0.3	48.7 ± 0.5	48.7 ± 0.3	48.7 ± 0.5	51.5 ± 1.2	52.2 ± 0.4		

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CHAPTER

3

Conversion of tropical lowland forest reduces nutrient return through litterfall, and alters nutrient use efficiency and seasonality of net primary production

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Abstract

Tropical landscapes are not only rapidly transformed by ongoing land-use change, but are additionally confronted by increasing seasonal climate variation. There is an increasing demand for studies analyzing the effects and feedbacks on ecosystem functioning of large-scale conversions of tropical natural forest into intensively managed cash crop agriculture. We analyzed the seasonality of aboveground litterfall, fine root litter production, and woody biomass productivity ($\mathrm{ANPP}_{\mathrm{woody}}$) in natural lowland forest, rubber agroforests under natural tree cover ('jungle rubber'), rubber and oil palm monocultures along a forest-to-agriculture transformation gradient in Sumatra. We hypothesized that temporal fluctuation of litter production increases with increasing land-use intensity, while the associated nutrient fluxes and nutrient use efficiency (NUE) decreases. Indeed, the seasonal variation of aboveground litter production and $\mathrm{ANPP}_{\mathrm{woody}}$ increased from the natural forest to the plantations, while aboveground litterfall generally decreased. Nutrient return with aboveground litter was mostly highest in the natural forest, however significantly lower only in rubber plantations. NUE for N, P and K was lowest in the oil palm plantations, with natural forest and the rubber systems showing comparably high values. Root litter production was generally lower than leaf litter production in all systems, while the root-to-leaf ratio of litter C flux increased along the land-use intensity gradient. Our results suggest that the nutrient and carbon cycles in species-poor agricultural systems are more directly affected by climate seasonality than species-rich forests and therefore might be more susceptible to inter-annual climate fluctuation and climate change.

Keywords: Land-use change, oil palm plantation, rubber plantation, nutrient cycling, leaf litterfall, root litter, growth seasonality

3.1 Introduction

Human population growth and increasing demand for agricultural products is driving rapid land-use change in the tropical rainforest biome (Tilman et al., 2001, Baudron & Giller, 2014). Many of these regions are hotspots of biodiversity (Sodhi et al., 2004, Koh & Wilcove, 2007), play a crucial role in the global carbon (C) cycle (Malhi et al., 2006, Adachi et al., 2011, Slik et al., 2013) and provide important ecosystem services such as climate regulation by influencing the hydrologic cycle and the trace gas concentration of the atmosphere (Bonan, 2008, Richardson et al., 2013). The ongoing land-cover change in much of the tropical zone in conjunction with global warming has the potential to alter fundamental ecosystem functions such as carbon and nutrient cycling (Tian et al., 1998) which may feed back on the atmosphere (Cox et al., 2000, Huntingford et al., 2008).

In many regions of Southeast Asia, the key driver of deforestation is the establishment of oil palm plantations (*Elaeis guineensis*) (Koh and Wilcove 2008). Indonesia is not only the number one in palm oil production (FAO 2015) and one of the main cultivation areas of rubber trees (*Hevea brasiliensis*), it is also the tropical country with the highest deforestation rate in recent time (Margono et al. 2014). One of the focal places of land-use change is Sumatra which once harbored vast lowland rainforests (Laumonier 1997). Conversion of the natural forest to agricultural systems is known to have large impacts on ecosystem carbon storage and the C sequestration potential with primary production (Jandl et al. 2007). However, precise data on how productivity patterns and nutrient cycling are affected by the transformation of rainforest to oil palm and rubber plantations are scarce. Intact tropical rainforests are thought to have the highest annual productivity of all terrestrial ecosystems on earth (Pan et al. 2011), and many tropical forests have developed tight nutrient cycles between plant biomass and soil in order to reduce nutrient losses and maintain high productivity on nutrient-poor soils (Jordan and Herrera 1981). The nutrient return from tree biomass to the soil with leaf litterfall and the subsequent nutrient release from decomposing litter are key processes that regulate nutrient availability and thus the rate of forest growth and carbon sequestration (Yavitt et al. 2004; Sayer and Tanner 2010). Reduced species diversity in agricultural systems is likely to alter amount of litter production, litter quality and litter decomposition affecting soil nutrient availability, soil water storage capacity and ultimately plant productivity (Lawrence 2005). The rate of nutrient return with leaf litterfall is intimately linked to the nutrient use efficiency (NUE) of the plants, i.e. the amount of litter mass produced per nutrient content in the leaf litter, or the inverse of nutrient concentration in litter mass according to the definition of Vitousek (1982). A second, but less well studied, process of carbon and nutrient cycling is the death and subsequent decomposition of root biomass which represents a major source of C, and probably also of nutrients, in the soil. In tropical forests on poor soil, where a major part of the nutrient capital is tied up in the living biomass (Herrera et al. 1978; Hedin et al. 2009), these two processes of litter production should play a key role as determinants of forest productivity.

Even in wet non-seasonal tropical regions such as Sumatra where only short irregular drier periods are occurring (Kumagai et al. 2006), aboveground litterfall in forest ecosystems often follows a distinct seasonal rhythm. It has been demonstrated that the net primary production of tropical moist forests responds sensitively to alteration of precipitation amounts (Schuur 2003) and that moist forest trees possess drought adaptation mechanisms which link the seasonality of stem, leaf and root growth to the seasonality of water availability (Guan et al., 2013). Seasonal and inter-annual variation in light intensity and water availability likely are triggering the growth rhythms of many tropical trees (Clark & Clark, 1994), with different organs probably responding to environmental change in a different way (Brando et al., 2008). In Amazonian trees, leaf and wood growth seem to have high priority during the wet season, while carbohydrate allocation to fine roots may be promoted primarily during drier periods (Rowland et al., 2014a). Studies in tropical forests with distinct dry season indicate that leaf fall peaks at the beginning of the dry season which would be economic in order to avoid drought damage to the canopy (Wieder & Wright, 1995, Rice et al., 2004, Chave et al., 2010). However, in other studies, leaf litterfall was found to be unrelated to critical soil moisture levels (Wright & Cornejo, 1990, Cavelier et al., 1999) suggesting that elevated radiation intensities may be more decisive in controlling leaf phenology (Kim et al., 2012). It is not well understood how the seasonality of growth is affected by the dramatic rainforest transformation process which currently takes place in Sumatra and elsewhere in the tropical forest biome. The lack of knowledge is particularly severe with respect to root activity in tropical forests and transformation systems (Vogt et al., 1996, Clark et al., 2001b, Harteveld et al., 2007, Leuschner et al., 2013, Yuen et al., 2013).

With the aim to better understand the functional consequences of the large-scale transformation of tropical lowland forest to agricultural systems in Southeast Asia, we established a comprehensive case study with 32 plots to examine changes in seasonal C sequestration through aboveground net primary productivity, and in nutrient return with above- and belowground litter production in natural old-growth forests and three transformation systems, i.e. rubber agroforests under natural shade tree cover ('jungle rubber'), rubber monocultures, and oil palm plantations in the lowlands of eastern Sumatra. We tested the hypotheses that (1) conversion of natural lowland forest to highly or moderately intense managed agricultural systems leads to reduced nutrient return to the soil with litter production, (2) nutrient use-efficiency (N, P, Ca, K, Mg) is higher in natural forest than in agricultural systems with fertilization, (3) the seasonality of leaf and fine root litter production, and of aboveground productivity in general, is higher in the agricultural transformation systems than in the species-rich natural forest, and (4) increasing land-use intensity rises the relative importance of fine root litter input as compared to aboveground litter input as a carbon flux to the soil (cf. Hertel et al. (2009a). The study is part of a more comprehensive investigation on the drivers and functional consequences of forest conversion in Sumatra (Collaborative Research Centre 990 – Ecological and socioeconomic functions of tropical lowland rainforest transformation systems).

3.2 Material and Methods

Study area

The sampling was carried out in the lowlands of Jambi Province, Sumatra (Indonesia) in 2013 and 2014. This region has already undergone large-scale conversion of the original dipterocarp-rich rainforest. We investigated four of the major types of land-use systems in eightfold replication in two different landscapes (n = 32 study plots), namely old-growth natural forest as reference system, complex multistrata rubber agroforest (rubber planted under remaining natural forest tree cover, called 'jungle rubber') and two high intensity crop systems i.e. rubber monoculture (*Hevea brasiliensis* (Willd. ex A.Juss.) Muell. Arg.) and oil palm plantations (*Elaeis guineensis*, Jacq.). Oil palm being a monocotyledon from the Palmaceae family originating from West Africa is the most productive oleaginous plant (Wahid et al., 2005). *H. brasiliensis*, on the other hand, is a brevi-deciduous tree in its native habitat of Amazonian tropical rainforests (Wycherley, 1992), which is reported to show different intensities of synchronous leaf shedding depending on the grade of seasonal climatic variation (Chen et al., 2010). Seasonally leaf-shedding trees were also observed in the natural forest where they contributed a minor percentage of canopy cover (personal observations).

The 32 study plots of 50 m x 50 m were located in two landscapes in the Jambi Province, Indonesia, i.e. the Harapan ('HP') forest region (N 2°13’ E 103°37’) and the Bukit Duabelas region ('B12') (N 1°94’ E 102°58’) at elevations of 40-100 m a.s.l. The plots were carefully selected so that the soil and climatic conditions were comparable and they were representative for the two study regions; the stand age of the respective land-use systems was comparable among replicate plots. Natural rainforest plots with closed canopy cover and with a distance of at least 200 m from disturbed forest were chosen as reference sites. The age of the oil palm plantations varied between 8 and 15 years and that of the rubber plantations from 7 to 16 years. Rubber trees in the jungle rubber systems were between 15 and 40 years old. All plantations were owned and managed by smallholders (up to 50 ha of landholdings) and the monoculture plantations were directly converted from either natural forest or jungle rubber agroforest systems as indicated by remaining tree stumps in the plantations. The management of the plantations continued with intensities typical for the respective land-use system and included application of herbicides circa every 6 months and addition of 100-200 kg ha^{-1} yr^{-1} inorganic NPK fertilizer in the rubber monocultures and 300-600 kg ha^{-1} yr^{-1} in the oil palm plantations, which is equivalent to 48–88 kg N, 21–38 kg P and 40–73 kg K ha^{-1}year^{-1} (Allen et al., 2015). However, fertilizer application intervals varied among smallholders with rubber plantations sometimes not being fertilized a whole year (personal communication of plot owners). Jungle rubber systems are usually neither fertilized nor treated systematically with herbicides. All plots were located at a minimum distance of 300 m to each other.

The mean annual rainfall (Worldclim Data Base: http://www.worldclim.org; average of 50 years) of the two investigated landscapes in Jambi Province was ~2567 mm y^{-1} in the Harapan region and ~2902 mm y^{-1} in the Bukit Duabelas region. In both regions, May to September represented a markedly drier season in comparison to the rainy season between October and April (Figure 3.1).

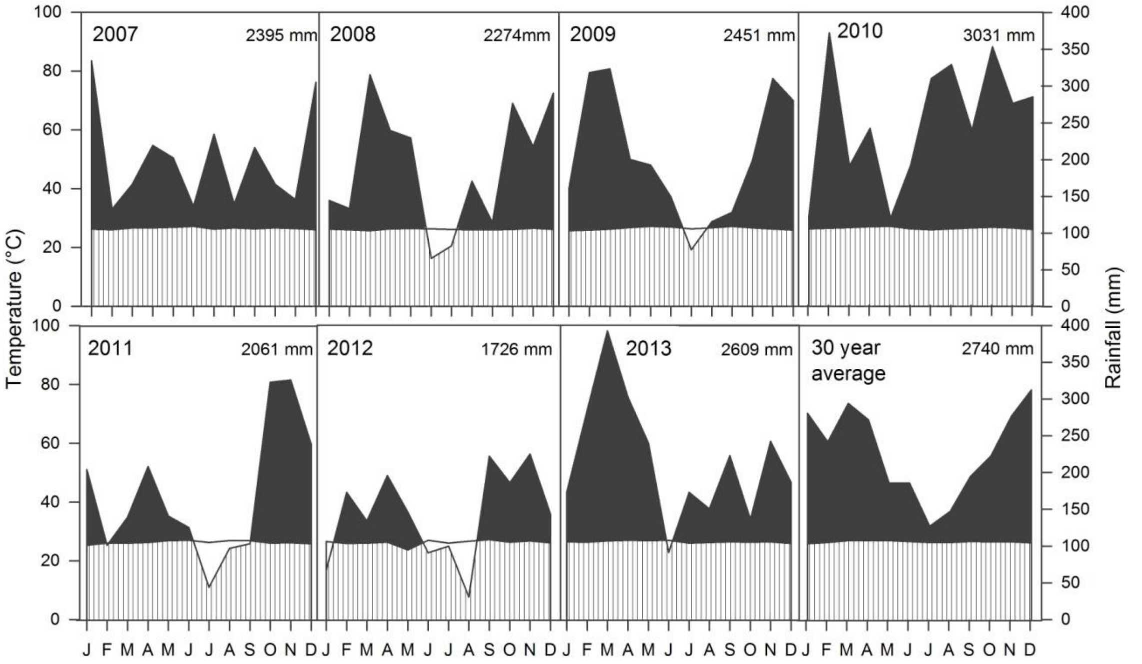

Figure 3.1: Mean monthly precipitation (mm) and temperature (°C) from Jambi climate station (Stasiun Klimatologi Jambi: N 1°62.1’, E 103°53.1’) over the period from 2007-2013 and of the study region with long-term data extracted from wordclim.com (30 year average).

Nevertheless, all months receive on average more than 100 mm of rain in this perhumid climate. The average monthly rainfall in the dry season (161 mm) is 62% of that in the rainy season (261 mm). In the study years, however, monthly rainfall was somewhat below 100 mm in June and August 2013 in both regions, as well as in February and March 2014 in the Harapan region. Air temperature is relatively constant throughout the year with an annual average of 26.7 °C (Fig. 3.1). On-site data on precipitation were collected at four reference stations, two located close to the forest plots in each landscape and two in the centre of the plantations of each region.

In both study landscapes, the soil type is Acrisol. In the Harapan region, the dominant soil type is sandy loam Acrisol, whereas in Bukit Duabelas the major soil type is clay Acrisol (Allen et al., 2015). Except for a higher sand content in the soils of the oil palm and jungle rubber plots of the Harapan region, basic soil physical and chemical properties varied independently from the land use system and in general were more or less comparable across the 32 plots. pH values (measured in water at 1:4 ratio) in the upper mineral soil ranged between 4.2 and 4.5, C:N ratio was between 11.7 – 14.3, and base saturation at the cation exchangers ranged between 10.6 % in forest soils on loam Acrisol and 37.5 % in oil palm plantations on clay Acrisol (soil chemical data were provided by Allen et al., 2015; soil texture - Kurniawan et al., unpublished data) .

Aboveground litterfall

Aboveground fine litter was collected on every plot using 16 litter traps (75 cm x 75 cm aperture) that were placed in a randomly selected grid pattern (n = 24 plots; no samplers in the oil palm plantations). They were made of PVC-tubed frames on 1m-long wooden stakes with nylon-mesh (mesh size 3 mm) fixed to it. The fallen litter was collected at monthly intervals from March 2013 to April 2014. The litter was sorted into the components leaves, small woody material (diameter < 2 cm), and propagules and inflorescences, and oven-dried for 72 h at 60°C until constant weight. In jungle rubber stands, leaves and fruits of rubber trees were separated from other forest tree components. To calculate the litter production of oil palm which refers to the pruning by man, all pruned oil palm fronds were counted at each harvest date. Then we multiplied the number of fronds by an average dry weight per frond obtained from 16 harvested and dried fronds from each plot. The yield of oil palm fruit in kg was recorded through weighing of the fresh material separately for all trees per plot. The dry weight was determined after oven-drying representative sub-samples of oil palm fruits (5 multiple fruits) at 60°C to constant weight.

To calculate the element content in the litter and total nutrient return to the soil, four samples of each litter fraction per plot at two sampling dates (July 2013 for the drier season and December 2013 for the rainy season) were analyzed with a CN gas chromatographic auto-analyzer (Vario EL III, Hanau, Germany) at the University of Göttingen. Analysis of the P, S, Ca, K, Mg, Mn, and Fe concentrations of the same fine leaf litter material was conducted after HNO_3 digestion by ICP-OES analysis (Perkin Elmer Optima 5300 DV). Litter C:N as well as N:P ratios were calculated based on mean values per plot, season and litter fraction and then a weighted average per plot was calculated. The nutrient use efficiency (NUE) of the canopy representing the NUE on an ecosystem level was calculated for the prominent elements N, P, K and Ca by dividing annual aboveground litter dry mass by the respective nutrient amount in the litter following (Vitousek, 1982, Vitousek, 1984, Harrington et al., 2001). In case of oil palm, shed fronds did not exist and we instead analyzed the oldest (lowermost) fronds which often showed signs of senescence.

To obtain specific leaf area (SLA in g cm^{-2}) all leaves from 16 litter traps per plot collected in March 2013 were scanned with a flat bed scanner, and the leaf area analyzed using WinFolia 2000a (Régent Instruments, Quebec, Canada) dividing oven-dried mass by the total area.

Aboveground woody biomass production

Aboveground woody biomass production (ANPP$_{woody}$, Mg ha^{-1} yr^{-1}) was calculated from stem increment data based on manual dendrometer tapes (UMS, München, Germany) mounted on 40 tree individuals per plot (n$_{total}$ = 960 trees) that were read in March 2013, July 2013, October 2013, January 2014 and April 2014. The trees were chosen randomly across the range of measured wood densities and species considering the specific size-class distribution on the plot. Care was taken to include a higher percentage of large trees (> 40 cm dbh) if present on the plot, since they are known to account for the major portion of aboveground biomass in forests (Berry et al., 2010, Sist et al., 2014). The ANPP$_{woody}$ of a tree was calculated as the pairwise difference in tree biomass between the measurement dates, based on allometric regression models used to calculate wood biomass from dbh, tree height and wood density. For forest trees we used the allometric equations developed by Chave et al. (2005) for tropical moist stands based on 2410 directly harvested tree individuals across the tropics (Eq.1). To calculate the AGB of rubber trees, we used a modified equation by (Wauters et al.,2008) based on 209 rubber trees destructively sampled in Brazil (Eq.2). For oil palms ANPP$_{woody}$ results from stem height growth as measured for all individuals every six months with a Vertex III height meter (Haglöf, Långsele, Sweden). Here, aboveground dry weight estimation was based on equations developed by Asari et al. (2013) (Eq.3).

$$AGB = 0.0599 \times \rho D^2 H \qquad \text{(Eq.1)}$$

$$AGB = \frac{\exp\ (-6.748 + 2.723 \text{ x } \ln(C_{170}))}{0.487} \qquad \text{(Eq.2)}$$

$$AGB = 71.797\ H_{palm} - 7.0872 \qquad \text{(Eq.3)}$$

AGB is the estimated aboveground biomass (in kg per tree, including stem and branch wood), *D* the trunk diameter (dbh in cm), *H* total tree height (in m), C_{170} is stem circumference at 1.7 m height (in cm), H_{palm} palm stem height (in cm), and ρ wood density (in g cm^{-3}). Wood density values (dry mass per fresh volume in kg m^{-3}) were determined in cores extracted with an increment borer (Haglöf, Långsele, Sweden). Wood cores of 5-7 cm length were taken at 130 cm height of 10 trees per plot (n$_{total}$ = 204). Wood density values were calculated using the water-displacement method described in (Fearnside, 1997). Since this method is rather destructive and may influence tree growth, we used the Pilodyn 6J wood tester (PROCEQ SA, Zürich, Switzerland) to obtain estimated wood densities on trees where no wood cores were taken. We measured the penetration depth of the Pilodyn pin into the stem wood of every tree ($n = 3551$) and calibrated the instrument on 204 trees, that were also cored for direct measurement of wood density. Measured wood density correlated strongly with the wood hardness as measured by the Pilodyn with the best predictive model ($r^2 = 0.72$) being: $\ln(\rho) = 0.8711 - 0.5763 \ln(h)$. With h defined as the penetration depth of the pin into the wood in mm.

If tree death occurred in the measurement interval and the intercensus interval was shorter than 6 months, the tree was ignored in the calculations. As we found that absolute stem diameter increment is related to dbh with dissimilar trends for diameter classes, we calculated a plot based relative stem diameter increment per season (each 3 months) and applied this mean increment rates to calculate the $ANPP_{woody}$ of tree individuals not covered by the dendrometer measurements.

Fine root litter production

To estimate litter production by fine roots (i.e. roots < 2 mm in diameter), we applied the sequential coring method (Persson, 1979) which is a widely used standard approach to determine fine root productivity of woody plants (Vogt et al., 1998). Subsequently, we applied the calculation scheme of Yuan & Chen (2013) based on the decision matrix (Table 3.1) introduced by McClaugherty et al. (1982) and corrected by Fairley & Alexander (1985) to calculate annual fine root mortality (which is assumed to equal fine root production) for these tropical land-use systems following Röderstein et al. (2005).

Table 3.1: Simplified decision matrix for calculating fine root mortality based on sequential soil coring. Δ = changes in fine root biomass or necromass, L = live mass, D = dead mass, M = mortality. Vertical bars indicate the absolute values. The first left column indicate conditions on the values of changes in fine root biomass and necromass, on which the suggested equations right column are given for calculating fine root mortality.

If	M =
$\Delta L + \Delta D \geq 0$ & $\Delta D \geq 0$	ΔD
$\Delta L \geq 0$ & $\Delta D \leq 0$	0
$\Delta L \leq 0$ & $\Delta L + \Delta D \leq 0$	$\lvert\Delta L\rvert$

We considered all temporal differences in root biomass and necromass between sampling dates, regardless of statistical significance, since it appeared unlikely that there exist extended time periods during the year in which no root death occurs. These data allowed us to analyze the seasonality of root litter production. As these equations do not include root exudation and carbon transfer to mycorrhiza, it is considered an underestimate of actual carbon investment in fine root production (Clark et al., 2001a). Since root samples are heavily washed before analysis to remove attached soil, mobile cations may be lost from the sample. Therefore, we did analyze only carbon content of fine root samples and did not consider other nutrients. Furthermore, the decomposition process changes nutrient contents in roots rapidly and analysis of partly decomposed fine roots is likely to bias estimates of nutrient content.

The sampling campaigns took place in April 2013, July 2013, October 2013 and January 2014. Due to the large number of samples and long processing time, we sampled only one representative plot per system (n = 4). Per plot 16 vertical soil cores (3.5 cm in diameter) were taken down to 30 cm soil depth including the organic layer using a soil corer at least 40 cm away from the litter traps to avoid disturbance. Repeated coring took place 20 cm away from the former coring place in a quadrangular shape. The soil cores were divided into the 0-10 cm and 10-30 cm layers and stored in plastic bags at 5°C. All fine roots were extracted by washing the previously soaked soil cores over a sieve of 200 µm mesh size (Retsch, Haan, Germany). All fine root fragments longer than 1 cm were extracted manually with tweezers and separated under a stereomicroscope into live (biomass) and dead fractions (necromass). Rubber tree roots (living and dead) were separated from other tree roots in samples from the jungle rubber plots. Indicators of root death vary between species; nonetheless, alteration in periderm color, disintegration of stele, pericycle and periderm, non-turgid cortex and root elasticity could be used to determine dead roots after some practice (Persson, 1979, Leuschner et al., 2001, Hertel & Leuschner, 2002). Herb, fern and grass roots were distinguished from tree roots by their lack of visible suberinization, their finer branching and their smaller diameter. To record the fraction of dead rootlets < 1 cm length, a method introduced by (van Praag et al., 1988) and modified by Hertel (1999) was applied to six out of the 16 samples. After the extraction of large root fragments (> 1 cm), remaining soil residues were evenly distributed on a large sheet of filter paper (730 cm²) and subdivided into 36 squares. All root material was then collected from six randomly selected squares under a stereomicroscope. The mass of small dead rootlets was extrapolated to the entire sample by means of the ratio of small rootlets to large dead roots that was established for each plot and each depth (Hertel et al., 2009a). After drying at 60 °C for 48 h until constant weight, all samples were weighed and the data were expressed as fine root mass (Mg ha^{-1}).

Statistical analysis

To examine the effect of monthly precipitation, landscape, transformation system and season on total monthly litter production, linear mixed-effect models were performed using the ‘lme’-function (package ‘nlme’) that fits the model by restricted maximum likelihood (REML), to allow for the unbalanced design as in some months not all litter traps in a plot were functional. To account for variability among the litter traps of a plot we used ‘plot’ as a random factor in the model. The other variables were treated as fixed factors. Model assessment followed Zuur et al. (2009) by starting with a full model and subsequently dropping each non-significant interaction term and then non-significant main effects. Similar tests were performed to assess effects of landscape, transformation system and season on nutrient contents and nutrient ratios of the different litter components. Where only one value per plot was available as in case of coefficients of variance (CV), element return to soil, nutrient use efficiency (NUE) and $\mathrm{ANPP}_{\mathrm{woody}}$, we used simple linear models (‘lm’) subsequently for visually testing linearity of the response. When necessary to achieve normality and homoscedasticity of model residuals, we $\log_{10}$ transformed the raw data before further analysis. The influence of land-use type on structural parameters, CV, nutrient input and NUE was tested using linear models (‘lm’ and ‘lme’, package: ‘stats’). Subsequently, multiple comparison tests between group means were analyzed post-hoc with Tukey HSD tests (‘glht’, package: ‘multcomp’). In case of heteroscedasticity, an adjusted statistical framework for simultaneous inference and robust covariance estimators (Herberich et al., 2010) was used to account for different variances between groups. In general, data are presented as means ± standard errors. Relationships between litterfall, $\mathrm{ANPP}_{\mathrm{woody}}$, SLA, canopy cover and nutrient parameters (C:N, N:P and NUE) were explored with Pearson’s correlation coefficients with a Bonferroni correction for comparison of multiple means. All analyses were conducted using R 3.1.0 software (R-Development-Core-Team, 2014) and tests of statistical significance were based on a 0.05 probability level.

3.3 Results

Aboveground structure

The aboveground stand and tree structural variables showed distinct differences among land-use systems (Table 3.2). Natural forests had a higher canopy cover and thicker litter layer on the soil than both rubber and oil palm monoculture plantations (‘lme’, Tukey HSD post-hoc test; $p < 0.05$). The specific leaf area of leaf litter (SLA) was highest in rubber plantations and lowest in oil palm trees; stem density was significantly smaller only in the oil palm plantations compared to the three other systems. Jungle rubber systems were intermediate in all parameters and were statistically indistinguishable from natural forest in terms of their mean SLA and stem density while they showed similar values to rubber monoculture in canopy cover.

Table 3.2: Stand structural variables of the four transformation systems in Jambi, Sumatra. Given are means ± SE (n = 8). Lower case letters indicate significant differences between the means of the land-use system according to Tukey HSD tests ($p < 0.05$).
* SLA of oil palms excluding frond rachis.

	Natural forest	Jungle rubber	Rubber	Oil palm
Structural variable				
Stem density (n ha^{-1})	565 ± 40.1 *b*	605 ± 53.0 *b*	469 ± 40.0 *b*	137 ± 3.8 *a*
Canopy cover (%)	92.1 ± 0.5 *c*	87.6 ± 0.8 *b*	85.8 ± 0.9 *b*	76.8 ± 1.0 *a*
SLA (g cm-2)	87.3 ± 5.7 *b*	106.6 ± 4.0 *b*	156.4 ± 4.2 *c*	68.9 ± 1.7* *a*
Litter layer (cm)	1.86 ± 0.06 *c*	2.45 ± 0.24 *c*	1.32 ± 0.11 *b*	0.04 ± 0.03 *a*
Litterfall (Mg ha^{-1} yr^{-1})	9.04 ± 0.75 *c*	7.66 ± 0.4 *bc*	3.84 ± 0.2 *a*	6.23 ± 0.86 *b*

Seasonal patterns in aboveground litterfall

Mean annual aboveground litterfall in natural forest was not significantly different from jungle rubber. However, the plot with highest litterfall (13.8 Mg ha^{-1} yr^{-1}) was in the natural forest. Overall, the litterfall of the forest and jungle rubber plots did not show a relationship with neither stem density nor basal area. Rubber monoculture and oil palm plantations showed lower annual litter production when excluding oil palm fruit yield. Leaf litter made the greatest contribution to total litter mass (around 80 %), whereas inflorescence and diaspore material made the smallest contribution (5 - 7 %), except oil palm plantations where the multiple fruits contributed more than 70 % to total aboveground litter production (Fig. 3.2).

Leaf litter made the greatest contribution to total litter mass (around 80 %), whereas inflorescence and diaspore material made the smallest contribution (5 - 7 %), except oil palm plantations where the multiple fruits contributed more than 70 % to total aboveground litter production. Factors influencing overall aboveground litter mass were land use system, season, and their interaction (‘lme’, F-value: 101.3, 17.9, and 22.6, respectively with $p < 0.001$). Neither region nor its interactions did have a significant effect and thus were excluded as a parameter from further analysis. Monthly litterfall in natural forest and jungle rubber did not significantly correspond to rainfall seasonality. In contrast, aboveground litterfall in rubber plantations was negatively correlated with precipitation (‘lme’, F-value: 33.3, $p < 0.001$) showing a distinct peak during the drier season and furthermore a minor increase in February and March 2014 (Fig. 3.2), when precipitation in the region dropped abnormally < 100 mm.

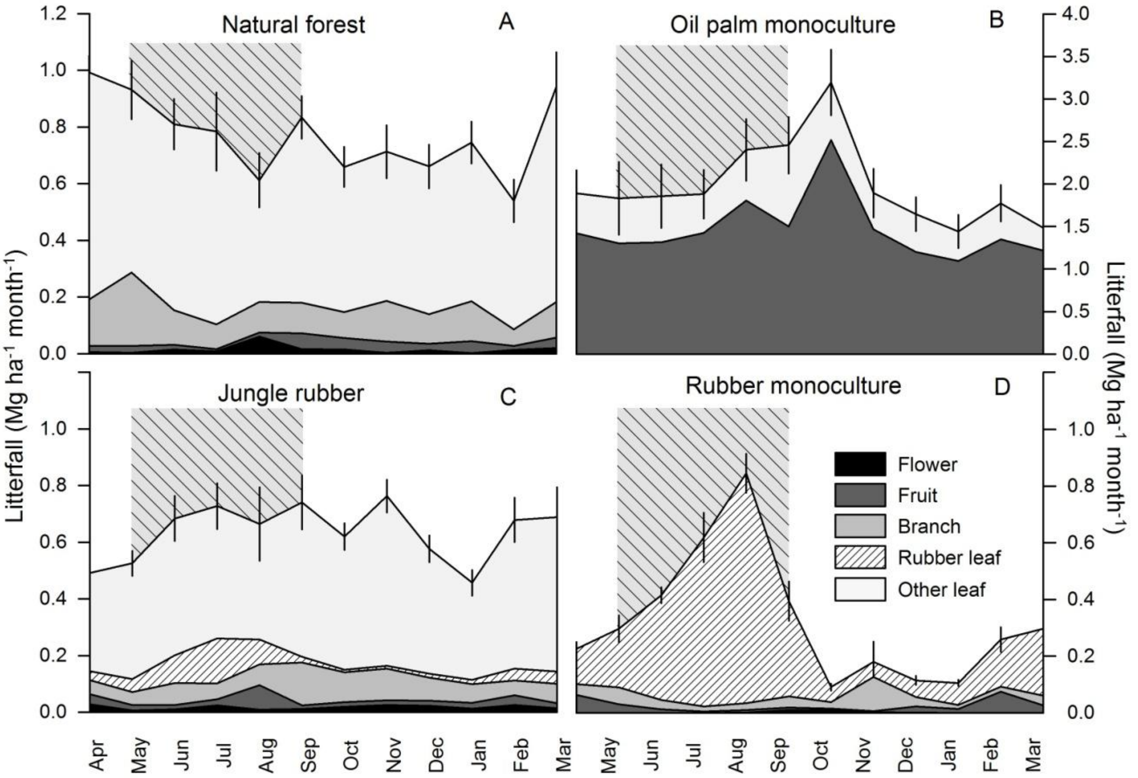

Figure 3.2: Seasonal patterns of aboveground litterfall (Mg ha^{-1} $month^{-1}$) with the fractions leaf, branch, fruit, and flower in the four transformation systems (period April 2013 – March 2014) (A) natural forest, (B) oil palm monoculture (C) jungle rubber, and (D) rubber monoculture. Given are means ± SE (n = 8 plots each). Grey shading indicates months with long-term monthly precipitation < 200 mm.

Monthly total aboveground litter mass was higher in the drier season than in the wet season only for rubber monoculture systems (514 ± 18 and 181 ± 19 kg ha^{-1} $month^{-1}$, respectively). Rubber trees followed the same pattern in the jungle rubber systems; however, the increase was less pronounced (Fig. 3.2). Natural forest tended to show a divergent pattern with lowest leaf litterfall during months with low precipitation (Aug'13 and Feb'14). However, at the peak of the drier season, flowering in natural forest and fruiting in jungle rubber took place with 35 % of annual fruit/flower production occurring in August. These patterns are also reflected in the coefficient of variance (CV) as a measure of variability within a year. The CV of total litter mass was significantly highest in rubber monocultures (0.81) followed by oil palm (0.41), jungle rubber (0.31) and natural forest (0.30), respectively (Table 3.3). As oil palm plantations are highly anthropogenic and continuously managed systems, aboveground litterfall did not occur in a natural way but was induced by pruning. Therefore, leaf removal is continuously ongoing during the harvest process and no dependency on rainfall could be observed. Conversely, we found oil palm fruit production to be nearly twofold higher at the end of the drier season compared to the annual average (Fig. 3.2).

Table 3.3: Coefficient of variance (CV) of the temporal variation of net primary production with the components of aboveground litterfall, fine root litter and aboveground woody biomass production ($ANPP_{woody}$) of the four transformation systems (period March 2013 – April 2014). Given are means ± SE (n = 8) except fine root litter, where only one plot per system was investigated. Lower case letters indicate significant differences between the means of land-use systems according to Tukey HSD tests ($p < 0.05$).

	Natural forest		**Jungle rubber**		**Rubber**		**Oil palm**	
Litter total	0.30 ± 0.05	*a*	0.31 ± 0.05	*a*	0.81 ± 0.04	*b*	0.41 ± 0.03	*a*
Leaf	0.31 ± 0.04	*ab*	0.28 ± 0.04	*a*			0.70 ± 0.19	*b*
Rubber leaf			1.03 ± 0.04	*a*	1.01 ± 0.05	*a*		
Branch	0.69 ± 0.11	*a*	0.69 ± 0.15	*a*	0.92 ± 0.17	*a*		
Fruit	1.15 ± 0.14	*b*	1.07 ± 0.20	*b*			0.40 ± 0.03	*a*
Rubber fruit			2.20 ± 0.23	*a*	1.77 ± 0.23	*a*		
Flower	1.62 ± 0.12	*a*	0.99 ± 0.20	*a*	2.41 ± 0.29	*b*		
NPP_w total	0.27 ± 0.06	*a*	0.48 ± 0.08	*ab*	0.49 ± 0.06	*ab*	0.58 ± 0.05	*b*
Forest tree	0.27 ± 0.06	*a*	0.26 ± 0.04	*a*				
Rubber tree			0.70 ± 0.10	*a*	0.49 ± 0.06	*a*		
Fine root total	0.79		0.88		0.85		0.84	
Forest tree	0.79		0.91				0.84	
Rubber tree			0.84		0.85			

Element return with aboveground litterfall

Although annual aboveground litter production was highest in oil palm systems (23.6 Mg ha^{-1} yr^{-1}) due to the fruit production, this yield was removed from the system and elements were not returned to the nutrient cycle. Therefore, annual C return to the soil via litter was highest in natural forest (4.5 Mg ha^{-1} yr^{-1}) followed by jungle rubber, oil palm and rubber (3.7; 2.9; and 1.9 Mg ha^{-1} yr^{-1}, respectively) (Table 3.4). Significantly higher nutrient return in the natural forest was also recorded for S, while the values for N, K, Fe, Mg and Mn were not significantly different from jungle rubber and oil palm. For Ca, significantly highest return rates were observed in jungle rubber systems. Return of P via leaf litter was nearly twofold larger in oil palm plantations than in the other systems. Rubber monocultures had the lowest element return rates of all systems; the fluxes represented only about 50 % of the element return measured in the natural forests (Table 3.4).

Table 3.4: Annual rate of element return to the soil with litterfall (in kg ha^{-1} yr^{-1}) for C, N, P, K, Ca, Fe, Mg, Mn and S, and the associated C:N and N:P ratios in aboveground litter of the four transformation systems. Given are means ± SE (n = 8) for the period March 2013 – April 2014. Lower case letters indicate significant differences between the means of the land-use systems according to Tukey HSD tests ($p < 0.05$). In case of oil palm, the total nutrient flux with fruit bunches and foliar litter (green pruned fronds) and the return to the soil with foliar litter are listed.

	Natural forest	**Jungle rubber**	**Rubber**	**Oil palm**	
Elements in litter *(kg ha^{-1} yr^{-1})*				total	return to soil
C	4568 ± 378 *c*	3668 ± 181 *bc*	1881 ± 106 *a*	13559 ± 1156 *d*	2887 ± 412 *b*
N	112.9 ± 8.3 *b*	84.3 ± 4.2 *b*	48.0 ± 2.5 *a*	211.4 ± 20.0 *c*	89 ± 12.3 *b*
P	2.9 ± 0.4 *b*	2.1 ± 0.2 *ab*	1.3 ± 0.1 *a*	17.2 ± 2.9 *d*	5.1 ± 0.8 *c*
K	17.6 ± 2.4 *b*	14.9 ± 1.7 *b*	7.9 ± 1.0 *a*	13.2 ± 147.2 *c*	18.2 ± 2.6 *b*
Ca	52.4 ± 8.5 *a*	63.4 ± 10.5 *ab*	40.1 ± 4.6 *a*	98.3 ± 11.2 *b*	45.3 ± 8.8 *a*
Fe	1.3 ± 0.2 *ab*	0.9 ± 0.1 *ab*	0.6 ± 0.1 *a*	1.6 ± 0.4 *b*	1.1 ± 0.4 *ab*
Mg	16.8 ± 1.4 *b*	19.0 ± 1.6 *b*	9.6 ± 1.0 *a*	51.6 ± 4.3 *c*	10.7 ± 2.0 *a*
Mn	3.0 ± 0.5 *a*	4.3 ± 1.1 *ab*	1.4 ± 0.2 *a*	3.5 ± 1.1 *a*	2.7 ± 0.7 *a*
S	12.4 ± 0.8 *c*	10.9 ± 0.6 *bc*	6.1 ± 0.3 *a*	25.8 ± 3.6 *d*	7.8 ± 1.2 *ab*
C:N ratio	40.6 ± 1.7 *bc*	43.6 ± 0.6 *c*	39.3 ± 1.1 *b*	64.6 ± 1.3 *d*	32.4 ± 1.5 *a*
N:P ratio	44.0 ± 4.5 *c*	42.6 ± 3.3 *c*	38.7 ± 3.8 *c*	13.2 ± 0.9 *a*	17.7 ± 0.6 *b*

The element concentrations in aboveground litter mass showed a significant effect of organ and system (‘lm’, organ: F-value = 48.8, $p < 0.001$; system: F-value = 13.5, $p < 0.001$), an only low influence of season (F-value = 6.7, $p < 0.05$), but no significant influence of the region and its interactions. Leaf litter of rubber trees tended to contain the highest Ca concentrations, whereas in oil palm fronds the highest concentrations in K, N and P were found (Table A 3.1). Noteworthy, seasonal differences in nutrient concentrations could only be detected for Ca in rubber fruit, rubber leaf and other fruits in the jungle rubber and rubber monoculture systems as well as for N and P in rubber fruits. However, reproductive organs contribute with less than 7 % to the nutrient flux with litterfall in all systems except oil palm plantations.

While monthly return rates for all elements in natural forest, jungle rubber and oil palm plantation were similar in the drier and rainy season, in rubber monocultures 70 - 80 % of nutrients were returned in the dry season months (Table A 3.1). The only exception is Fe, where we found 85 % of the annual Fe return in the drier season in natural forest and 70 % in oil palm monocultures (data not shown). Overall, leaf litter inputs in rubber monocultures were more than doubled in the drier season while rubber fruit input was higher in the rainy season: P input via fruit was even 10fold increased. In natural forest, jungle rubber and oil palm, the nutrient input to the soil was evenly distributed throughout the year with the exception of fertile components, where we found a reverse pattern of higher N, P, K inputs for flower in the drier season and lower values for the dry season input of fruits in the forests; and vice versa in the jungle rubber systems (Table A 3.1).

Oil palm fruits showed high C:N ratios (195 ± 16) compared to the 'Other fruits' component of rubber plantations (88 ± 14), jungle rubber (51 ± 5) and forest (35 ± 4), respectively (data not shown), while the C:N ratio of palm fronds (32 ± 1) was lower than that of rubber (36 ± 1) and forest tree leaves (39 ± 2). Due to the large contribution of oil palm fruits to total litter, the mass-weighted mean of the C:N ratio was significantly highest in oil palm plantations and decreased in the sequence jungle rubber > natural forest > rubber, while N:P ratios decreased from natural forest > jungle rubber > rubber to oil palm plantation (Table 3.4).

Nutrient use-efficiency (NUE) for the elements N, P, K and Ca was significantly lower in oil palm monocultures than in all other systems (Table 3.5). Except for NUE_{Ca}, rubber monoculture, jungle rubber and natural forest were not significantly different with regard to NUE figures. However, jungle rubber tended to show the highest NUE for these four elements followed by natural forest.

Table 3.5: Annual mean nutrient use efficiency (calculated as aboveground litter production / nutrient loss with aboveground litter; unit: g g^{-1}) for N, P, K, and Ca in aboveground litterfall of the four transformation systems. Given are means ± SE (n = 8). Lower case letters indicate significant differences between the means of the land-use systems according to Tukey HSD tests ($p < 0.05$). Because the analyzed oil palm fronds were not fully senescent, it is likely that the given NUE figures are underestimates of true NUE in this species.

	Natural forest		**Jungle rubber**		**Rubber**		**Oil palm**	
NUE								
N	80.2 ± 2.8	*b*	92.1 ± 5.6	*b*	80.4 ± 2.8	*b*	34.1 ± 6.9	*a*
P	3563 ± 428	*b*	3899 ± 333	*b*	3105 ± 325	*b*	457 ± 103	*a*
K	551.5 ± 51.4	*b*	549.4 ± 52.1	*b*	531.1 ± 58.3	*b*	10.0 ± 48.9	*a*
Ca	199.5 ± 25.2	*c*	141.4 ± 19.4	*c*	103.7 ± 10.5	*b*	74.3 ± 15.3	*a*

Fine root litter production

Estimated fine root litter production (i.e. fine root mortality) showed coherent patterns for all four land-use systems with higher values recorded during the wet season than the drier season. An exception was found in case of the oil palm plantations where the peak of root mortality was recorded end of the drier season in July – October 2013. The CV was similar in all four systems (Fig. 3.3).

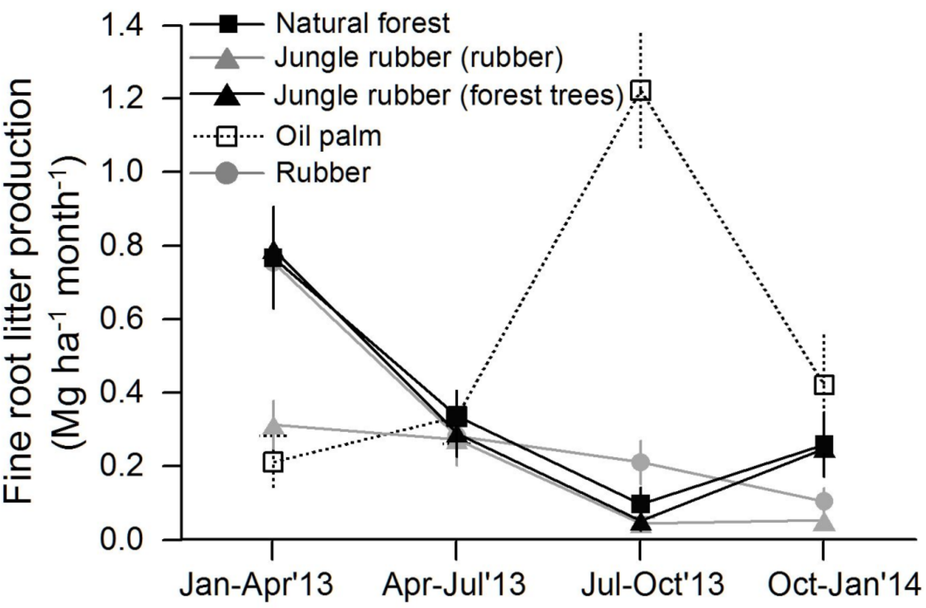

Figure 3.3: Seasonal patterns of fine root litter production (Mg ha^{-1} month^{-1}) in natural forest, 'jungle rubber' forest trees, 'jungle rubber' rubber trees, rubber monoculture trees and oil palms. Given are means ± SE (n = 16 replicate corings, one plot per land use type).

The amount of carbon transferred annually to the soil via fine root mortality ranged between 0.67 and 1.15 kg C ha^{-1} yr^{-1} and was higher in the oil palm plantation and jungle rubber than in the natural forest and rubber monoculture, while leaf litter C input was highest in the natural forest (Table 3.6).

Table 3.6: Mass and carbon fluxes with fine root litter and leaf litter (kg ha^{-1} yr^{-1}), and the ratio of C flux with fine root mortality and leaf litterfall in four rainforest transformation systems. Given are means ± SE. The ratio of root to leaf litter C fluxes shows a strong negative non-linear correlation with canopy cover (hence with increasing forest use intensity) at $r^2 = 0.99$, $P < 0.05$.

Fluxes to the soil (kg ha^{-1} yr^{-1})	**Natural forest**	**Jungle rubber**	**Rubber**	**Oil palm**
Fine root litter mass	4.37 ± 1.01	4.61 ± 0.80	4.04 ± 0.80	6.56 ± 1.32
Fine root litter C	1.86 ± 0.43	1.87 ± 0.32	1.51 ± 0.30	2.58 ± 0.52
Leaf litter mass	9.86 ± 0.92	5.36 ± 0.42	3.48 ± 0.12	8.81 ± 1.53
Leaf litter C	4.98 ± 0.46	2.58 ± 0.20	1.73 ± 0.06	4.04 ± 0.71
Sum C flux (fine root + leaf)	6.84	4.45	3.24	6.62
Ratio of root to leaf C flux	0.37	0.72	0.87	0.64

The leaf litter C flux exceeded the estimated C flux with fine root litter in all systems. Rubber monocultures showed the highest contribution of fine root mortality to total C flux (aboveground litter and fine roots), as nearly 50 % of total C input was returned via fine root litter compared to 30 % in natural forests. The total C flux with root and leaf litter production showed a U shaped pattern across the land-use intensification gradient with highest total litter C inputs in natural forests and oil palm plantations, while a reverse pattern was visible for the ratio of root to leaf litter C input (Table 3.6). We found a strong linear increase in the ratio of root to leaf C flux to the soil with decreasing canopy cover (thus, with increasing land-use intensity) for the land-use systems natural forest, jungle rubber and rubber ($r^2 = 0.98$, $p < 0.05$).

Seasonal variation in aboveground net primary production

Aboveground net primary production of the trees ($ANPP_{woody}$) showed highest monthly rates in the natural forest during the first quarter of the rainy season from October to January 2014 (Fig. 3.4). In rubber monoculture, $ANPP_{woody}$ followed a similar temporal trend but generally lower productivity and a more distinct peak during the rainy season. Oil palms tended have the highest productivity of their stem biomass during the drier season from July to October. While rubber trees in jungle rubber plantations contributed more than 35 % of the stems in these systems (data not shown), their $ANPP_{woody}$ accounted for only 18 % of the system's total. $ANPP_{woody}$ was most variable in rubber monocultures and oil palm plantations while temporal CV values of NPP were lowest in natural forest trees (Table 3.2). The jungle rubber system showed overall intermediate $ANPP_{woody}$ variability; however, rubber trees in this land-use type had the highest CV values of all systems.

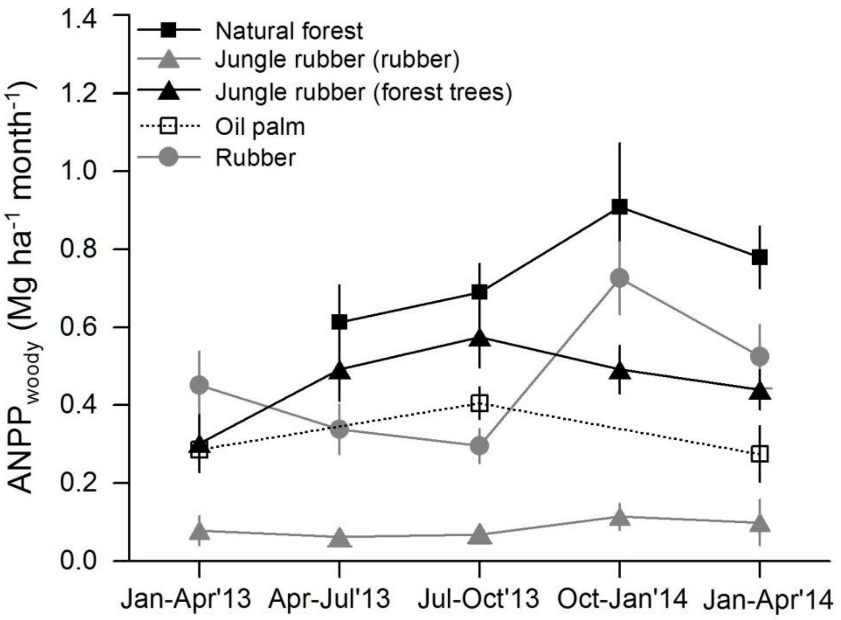

Figure 3.4: Seasonal patterns of aboveground woody net primary production (Mg ha^{-1} month^{-1}) in natural forest, 'jungle rubber' forest trees, 'jungle rubber' rubber trees, rubber monoculture trees and oil palms. Given are means ± SE (n = 8).

ANPP$_{woody}$ correlated across all systems only with canopy cover, while total litter mass was negatively correlated with SLA, total litter N:P ratio and NUE for nitrogen, phosphorus and potassium (Table 3.7). Additionally, there were significant positive relationships between NUE, N:P ratio and canopy cover as well as between all NUE values.

Table 3.7: Pearson correlation coefficients for relations between structural parameters, ANPP$_{woody}$ and litter nutrient traits (n = 32). Highly significant correlations are shown in bold ($p < 0.001$), non-significant correlations ($p > 0.05$) are n.s.

	Litterfall (Mg ha^{-1} yr^{-1})	ANPP$_{woody}$ (Mg ha^{-1} yr^{-1})	Canopycover (%)	SLA (g cm^{-2})	N:P ratio	C:N ratio	NUE$_N$	NUE$_P$	NUE$_{Ca}$
ANPP$_{woody}$	n.s								
Canopycover	-0.67	0.59							
SLA	**-0.88**	n.s	n.s						
N:P ratio	**-0.75**	n.s	**0.72**	n.s					
C:N ratio	**0.93**	n.s	**-0.77**	**-0.84**	**-0.70**				
NUE$_N$	**-0.71**	n.s	0.68	0.66	**0.70**	**-0.70**			
NUE$_P$	**-0.74**	n.s	**0.72**	0.58	**0.96**	-0.68	**0.84**		
NUE$_{Ca}$	n.s	n.s	0.62	n.s	0.61	n.s	0.58	0.64	
NUE$_K$	**-0.78**	n.s	**0.74**	0.64	**0.79**	**-0.75**	**0.81**	**0.83**	0.61

3.4 Discussion

Aboveground litterfall dynamics

In forest ecosystems, aboveground litter production has been found to depend on climatic factors such as light and water availability, nutrient supply, species composition and the successional stage of the forest community (van Schaik et al., 1993, Sundarapandian & Swamy, 1999, Borchert et al., 2002, Lawrence, 2005, Scherer-Lorenzen et al., 2007). Among the four investigated land use types, we found mean annual aboveground litterfall to be highest in the natural forest stands with 9.0 Mg ha^{-1} yr^{-1}. This figure is similar to values found in other lowland rainforests in Southeast Asia (8.8 – 12 Mg ha^{-1} yr^{-1}, (Proctor et al., 1983, Paoli & Curran, 2007) and in South America (8.6 Mg ha^{-1} yr^{-1}, (Chave et al., 2010), but it is lower than figures reported for undisturbed lowland dipterocarp forests in Borneo (9.8 – 15.8 Mg ha^{-1} yr^{-1} (Saner et al., 2012, Kho et al., 2013). Aboveground litterfall was not significantly different between natural forest and rubber agroforest (jungle rubber), which has been reported similarly for sites in primary and secondary rainforests as well as agroforests (Martius et al., 2004, Tang et al., 2010, Leuschner et al., 2013). In contrast, the monoculture plantations of rubber and oil palm produced lower amounts of aboveground litter which has been attributed to the less diverse species composition and canopy structure (Lisanework & Michelsen, 1994, Barlow et al., 2007, Tang et al., 2010). The only principle difference in soil characteristics between the two study regions in Jambi was a somewhat higher sand content in the oil palm and jungle rubber plots of the Harapan region. Despite this variability and in agreement with Chave et al. (2010), we did not find a significant influence of soil type on annual litterfall.

Despite considerable differences among the forest plots in annual litter mass (7.0 - 13.8 Mg ha^{-1} yr^{-1}), which may reflect differences in tree species composition and/or stand structure, seasonal litterfall variation as indicated by the coefficient of variance (CV) was generally smaller in the natural forests than in the jungle rubber system and the species-poor plantations. A similar observation was also made by Barlow et al. (2007) in a comparison of primary, secondary and plantation forests in the Amazon. While litterfall seasonality in tropical dry or temperate deciduous forests shows clear dependence on precipitation and/or temperature patterns (Zhang et al., 2014), tropical moist forests, which experience more or less constant temperatures and precipitation exceeding evapotranspiration throughout the year, should exhibit only weak seasonal variability in aboveground litterfall. In agreement, we found total litterfall in the natural forests and jungle rubber systems decoupled from rainfall patterns with low seasonal variation in the trees' leaf litterfall. However, leaf litterfall tended to be lower in the natural forest during the months with reduced precipitation, while the pattern was reversed in the jungle rubber systems. Studies in moist tropical forests with a more pronounced dry season reported a litterfall seasonality that either was positively related to rainfall seasonality with leaf shedding in the dry season (van Schaik et al., 1993, Rice et al., 2004, Barlow et al., 2007, Chave et al., 2010), or alternatively showed a litterfall peak in the rainy season (Proctor et al., 1983, Parsons et al., 2014). In contrast, no direct correlation between leaf phenology and the timing of rainfall was found in certain Brazilian rainforest stands (Doughty & Goulden, 2008, Vasconcelos et al., 2008). Contrary to our forest sites, the rubber plantations showed a clear seasonality of leaf litterfall and of flowering and fruiting with a main peak of leaf shedding in the drier season from June to September 2013. Flowering and fruit production followed in the subsequent rainy season together with a minor litterfall peak in February and March 2014, when monthly precipitation dropped below 100 mm in the region. The rubber trees in the jungle rubber plantations revealed a similar seasonal pattern. However, the seasonal response of a monoculture is not necessarily comparable to a diverse forest as physiological pattern may define how plants operate. Nonetheless it is important to note that while temporal leaf shedding is indicated as characteristic for *H. brasiliensis*, it occurs with varying intensities in different regions of the tropics and is reported to increase with growing drought intensity (Elliott et al., 2006, Yeang 2007). Rubber trees in monsoonal India are reported to suffer from a bi-annual loss of leaves with a corresponding negative effect on photosynthetic carbon gain and carbohydrate reserves available for new growth after defoliation (Devakumar et al., 1999). In the Amazon, the rhythm of leaf enfolding and leaf shedding seems to be triggered by changes in solar radiation intensity which achieves higher flux rates in the dry months, thus promoting leaf flushing while leaves are abscised during the rainy season with high cloudiness and less radiation input (Myneni et al., 2007, Kim et al., 2012). Furthermore, *H. brasiliensis* is reported to deplete subsurface water resources (Guardiola-Claramonte et al., 2010) as much water is consumed during leaf flushing (Rao et al., 1998). On the one hand, consequently less water is available for latex production which consists of 60-70 % water (Ranasinghe & Milburn 1995). On the other hand, large-scale monocultures are expected to promote the exhaustion of water reserves needed to buffer trees against prolonged drought events (Elliott et al., 2006) such as are predicted to increase in Southeast Asia (Feng et al., 2013). A reduction of species diversity, crown structure and consequently leaf area in monocultures might also lead to reduced overall transpiration and propagation of rainfall as the high diversity of angiosperms is reported to promote propagation of high rainfall environments (Boyce et al., 2010).

Compared to the rubber plantations, the leaf and fruit production in the oil palm monocultures revealed a relatively low seasonality which likely is a consequence of the intensive management regime with frequent pruning and harvesting events. Furthermore, drought stress effects were found to manifest with some delay and they may not be clearly visible in oil palm because the fronds to not wilt due to the high sclerenchyma content, a thick hypodermis and well-developed cuticle (Rees, 1961). Due to the lag in response, the consequences of reduced water availability can be detected months after a drought event in form of decreased fruit yield due to a high proportion of aborted inflorescences (Legros et al., 2009) or hampered development and growth of the palms (Corley & Tinker, 2003, Carr, 2011). It is thus remarkable that we observed increased oil palm fruit production at the end of the drier season in October 2013. This may be a consequence of higher pollination success due to less frequent heavy rainfall events (Corley & Tinker, 2003).

Nutrient and carbon return through aboveground litter

The flux of carbon and nutrients with litterfall to the soil determines important heterotrophic processes in the ecosystem such as decomposition and mineralization. The flux rate is controlled by the amount of litter and the element concentrations in the litter (Vitousek & Sanford, 1986, Kaspari et al., 2008).

In our plots, the return of C, N, Fe and S to the soil with aboveground litter was higher in the natural forests than in the rubber systems and oil palm plantations, while the Ca, Mg and Mn litter input peaked in the jungle rubber plantations. Overall, the nutrient return was lowest in the rubber monocultures due to the relatively low annual litter production. The P and K return with litterfall was highest in the oil palm plantations, even when excluding possible inputs with fruit production that are removed from the system as crop yield; this contradicts our first hypothesis. With a nitrogen input to the soil through aboveground litterfall of 113, 84, and 89 kg ha^{-1} yr^{-1} in natural forest, jungle rubber and oil palm plantation in our study region, we recorded higher return rates than measured by Proctor et al. (1983) in dipterocarp-rich Southeast Asian lowland rainforests, but lower values than observed in other neo- and paleotropical forests (Vitousek, 1982, Vitousek, 1984, Haase, 1999, Zheng et al., 2006, Yuan & Chen, 2009, Posada & Schuur, 2011). The P, K and Ca fluxes with litterfall in the Sumatran lowland forests (and the jungle rubber stands and rubber plantations) were lower than in many other tropical forest ecosystems, e.g. in Malaysia (Dent et al., 2006), Brazil (Haase, 1999, Wood et al., 2005), Australia (Brasell et al., 1980), tropical montane forests (Tanner et al., 1998), and in tropical secondary forest and rubber agroforest in China (Tang et al., 2010). The low nutrient fluxes in Sumatra can be explained by generally nutrient-poor soils and low foliar nutrient concentrations in particular in the natural forest and jungle rubber plots with P and K concentrations around 0.3 and 1.9 mg g^{-1}, respectively. Rainforest trees on alluvial soils or sandstone in Malaysia had twice as high foliar nutrient concentrations (Dent et al., 2006).

In support of our assumption of predominant P limitation at our sites, we found high N:P ratios in aboveground biomass in all systems except oil palm plantations. When applying critical N:P ratios developed for indicating either N or P limitation of upland ecosystems (Koerselman & Meuleman, 1996, Tessier & Raynal, 2003, Güsewell, 2004), all investigated land-use systems except the fertilized oil palm plantations were characterized by high N:P ratios far beyond 14 which indicates P limitation. The N:P ratios for natural forest and jungle rubber aboveground litter were much higher than reported from other non-tropical ecosystems and even 50 % larger than average ratios found in tropical rainforests ranging between 26 to 29 (Wood et al., 2005, Yuan & Chen 2009). Our findings indicate strong P limitation and a tight efficient nutrient coupling at the sites. In the long term decreased nutrient return with litterfall can only be counterbalanced by heavy fertilization of the plantations that is expected to cause increased soil acidification, aluminum toxicity and overall decreased soil fertility in this region (Allen et al., 2015).

Nutrient use efficiency of the systems

As hypothesized, we found oil palm plantations as the most intensively managed and fertilized system to show the lowest nutrient use efficiency (NUE) for all investigated nutrient elements. NUE is assumed to be generally higher in communities on poor soils where plants typically have more long-lived leaves and adaptations to reduce nutrient losses (Aerts & Chapin, 1999). We expected NUE to be highest in the natural forest systems, as they consist mainly of slower-growing, shade-tolerant tree species compared to jungle rubber stands with commonly higher frequency of fast-growing, pioneer species that require more resources during the rapid construction of foliar and wood tissue (Poorter et al., 2010, Baribault et al., 2012). Contrary to expectation, we did not find significant differences in NUE between natural forest, jungle rubber and rubber plantations for the investigated elements except Ca. On the highly weathered soils of the East Sumatra lowlands, it is likely that growth limitation by shortage of P and N and possibly also other elements affects all vegetation types, if not fertilized. The particularly high efficiency of nutrient use in the unfertilized jungle rubber stands may perhaps be related to the relatively high stem density in this system in comparison to the natural forest which could increase root competition and thus nutrient shortage. Similar nitrogen NUE values were found for cacao plantations under forest cover in Sulawesi, where monoculture cacao also showed lower NUE than cacao agroforests (Triadiati et al., 2007). Even though not significant, we measured for all elements a lower NUE in the Bukit Duabelas region than in the Harapan region except for oil palm plantations; this could be related to the somewhat higher clay content and therefore better soil nutrient availability status on clay Acrisols in Bukit Duabelas. Compared to other tropical forests in Malaysia, Brazil and China (Smith et al., 1998, Dent et al., 2006, Tang et al., 2010), the nutrient use efficiencies for N and P in our tree-dominated systems were relatively high indicating that tree growth most likely was under severe P and N limitation in our study region. However, it is important to note that the nutrient concentrations in oil palm leaves are probably not directly comparable to the foliar element concentrations measured in the three non-palm systems because palm fronds are pruned while still green. Even though we analyzed the oldest fronds on the plants, the process of nutrient re-translocation will not have been as complete as in the shed tree leaves of the other systems. Further, no post-mortem nutrient leaching during the presence in litter traps can occur. Thus, leaf N, P and K concentrations must be higher in the palms than in the other systems particularly in the case of highly mobile K (Epstein 1972). NPK fertilization in the oil palm plantations is another factor that has contributed to the observed relatively high N, P and K contents in pruned oil palm leaf tissue (Sun et al., 2011).

Carbon flux to the soil through root litter production

While studies on annual litterfall and also fine root production as estimated with the ingrowth core technique are quite well represented in tropical ecosystems (Hertel et al., 2009b; Chave et al., 2010; Malhi et al., 2011), data on fine root mortality and hence belowground litter production are much rarer (Sanford & Cuevas 1996). Our estimates of annual C flux to the soil through fine root litter production indicate for the upper 30 cm of the soil a decrease in the sequence oil palm plantation > jungle rubber > natural forest > rubber plantation. Similar to observations by Röderstein et al. (2005) in Ecuadorian tropical montane forests and by Hertel et al. (2009a) in tropical lowland forests with different disturbance levels and cacao agroforests in Sulawesi, we found leaf litter quantitatively much more important than root litter in all systems. Our fine root-derived C fluxes are generally in the lower range of data determined in these two studies and those reported from tropical montane forests in Costa Rica (Sanford & Cuevas 1996) and forests and tree plantations in subtropical China (Yang et al., 2004) that ranged between 1.14 – 8.63 Mg C ha^{-1} yr^{-1}. However, the divergence may partly be due to different calculation methods, as root mortality is difficult to be directly measured in the field and the various existing approaches may differ in their results by an order of magnitude (Vogt et al., 1998; Hertel & Leuschner 2002).

The ratio between root- and leaf-borne C fluxes to the soil was highest in the rubber monocultures and decreased over the jungle rubber and oil palm plantations to the natural forest. In principal support of our fourth hypothesis, there was a general trend toward an increase in the root:leaf ratio of litter C input with decreasing canopy cover and increasing management intensity confirming findings of Hertel et al. (2009a) along a disturbance gradient in tropical forests.

Seasonal variation of ANPP$_{\text{woody}}$ *and fine root litter production*

Aboveground woody net primary production (ANNP$_{\text{woody}}$) was seasonally much more variable in the rubber trees, in particular in the jungle rubber systems, than in the natural forest. In general, the production of aboveground tree components in tropical trees is closely associated with seasonal patterns of rainfall and soil water content (Brando et al., 2008, Rowland et al., 2014b) and, as a consequence, ANPP$_{\text{woody}}$ was found to be the most sensitive component of net primary production in long-term rainfall reduction experiments (Brando et al., 2008). Similar to our results, a study on rubber trees in India found most of the stem growth to occur at the beginning of the rainy season and no growth was observed during the dry summer (Devakumar et al., 1999). According to Lodge et al. (1994) and McGrath et al. (2000), the peak in rubber tree growth at the beginning of the rainy season may follow the litter shedding in the dry season which results in increased nutrient availability upon rewetting. The natural forest trees of our study sites exhibited the same seasonal growth pattern as the rubber trees with highest $\text{ANPP}_{\text{woody}}$ at the beginning of the rainy season, whereas the accompanying forest trees in the jungle rubber systems apparently grew best in the drier months, probably due to increased light availability after rubber tree leaf shedding. Oil palm aboveground growth was measured in coarser time intervals which did not allow direct comparison with the dicotyledonous trees. *E. guineensis* is reported to show a delayed response to drought events even when they are severe, because their phytomers require longer development periods (Legros et al., 2009, Carr, 2011).

While stem growth showed the strongest seasonality in rubber trees, fine root litter production peaked most distinctively in the oil palm plantations during the drier season. Oil palm root mortality was significantly higher during periods of low precipitation and soil moisture. It is possible that the apparent root sensitivity to water shortage is a consequence of the missing organic layer in the oil palm plantations, as a litter layer may reduce topsoil desiccation in the tree-dominated systems (Luskin & Potts, 2011). Similar observations have been reported from tropical dry forests, where fine root growth peaked at the beginning of the rain season and root mortality increased during the dry season (Singh & Singh, 1981, Kummerow et al., 1990, Yang et al., 2004). More detailed studies on the seasonality of fine root litter production in oil palm plantations are missing so far.

We found fine root litter production generally not to be synchronized with leaf litterfall in the four studied systems, as was also observed by Röderstein et al. (2005). These authors found a distinct seasonality in fine root biomass and necromass only in stands at 3000 m a.s.l. in the Ecuadorian Andes. Remarkably, we found in natural forest and the rubber systems a reversed pattern to the oil palm plantations with highest root litter production at the end of the rainy season. Roy and Singh (1995) also found increased root mortality immediately after the highest rainfall in the rainy season in subtropical deciduous forests in India, which they explained by lowered N-mineralization rates. Soil water saturation in the rainy season may hamper decomposition through oxygen limitation, thereby reducing nutrient availability and favoring the accumulation of fine root necromass (Schuur & Matson, 2001). However, it remains unclear whether partial anoxia after heavy rainfall, or other factors, increased fine root mortality in the moistest period in our tree-dominated systems in an untypical way. It must be kept in mind that fine roots are not only dying due to external stressors but will be shed irregularly throughout the year and necromass can be decomposed quickly (Yavitt & Wright, 2001), in particular in tropical environments. This renders the investigation of fine root turnover and fine root litter dynamics difficult.

3.5 Conclusion

Vast areas of the lowlands of Sumatra and other regions of tropical Southeast Asia are affected by large-scale forest conversion with far-reaching consequences for the carbon, water and nutrient cycles. Our study in two regions with a large number of plots in four prevalent land-use types shows that forest conversion to oil palm and rubber monocultures decreases carbon and nutrient return with litterfall significantly, while the seasonality of net primary production is increased. Together with severely reduced biomass carbon storage (Kotowska et al., 2015) the consequences of monoculture-dominated areas in tropical regions will not only affect species richness and associated diversity in tree functional types, but also change the biogeochemical cycles in agricultural systems in the long term, making smallholders more dependent on fertilizer use as the plantation soils become acidified and less fertile (Allen et al., 2015). Furthermore, the ecosystems resilience may be altered by a stronger seasonal productivity response of intensively managed plantations where inter-annual climate fluctuation and predicted climate change will have a more directly influence than in species-rich forests.

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3.6 Appendix

Table A 3.1: Element input (kg ha^{-1} month^{-1} or g ha^{-1} month^{-1}) with aboveground litterfall and the relative fraction of the element in the respective plant tissue (%) in the rainy and drier season for the four transformation systems. Given are means ± SE (n = 8).

Element input	Natural forest	Jungle rubber	Rubber	Oil palm
C (kg ha^{-1} month^{-1})				
Leaf				
Rainy season	291.2 ± 19.9 (49.7 %)	229.1 ± 18.5 (47.8 %)		204.5 ± 31.3 (46.7 %)
Drier season	304.6 ± 23.5 (49.7 %)	224.8 ± 17.3 (48.6 %)		293.9 ± 47.6 (45.7 %)
Rubber leaf				
Rainy season		11.5 ± 2.2 (50.2 %)	54.5 ± 5.5 (50.9 %)	
Drier season		41.7 ± 9.5 (52.5 %)	232.5 ± 8.4 (50.4 %)	
Branch				
Rainy season	58.1 ± 12.5 (50.0 %)	36.5 ± 3.3 (47.9 %)	19.7 ± 5.5 (49.2 %)	
Drier season	67.9 ± 10.4 (49.6 %)	43.4 ± 12.8 (48.9 %)	16.3 ± 3.6 (46.8 %)	
Fruit				
Rainy season	15.3 ± 4.1 (49.4 %)	3.3 ± 2.2 (49.3 %)		882.0 ± 59.0 (60.1 %*)
Drier season	11.3 ± 2.5 (49.0 %)	1.2 ± 0.3 (49.5 %)		900.1 ± 108.7 (60.1 %*)
Rubber fruit				
Rainy season		3.3 ± 2.2 (52.6 %)	15.8 ± 4.4 (52.6 %)	
Drier season		1.2 ± 0.3 (48.1 %)	5.6 ± 1.9 (48.1 %)	
Flower				
Rainy season	5.0 ± 1.0 (49.8 %)	9.4 ± 2.8 (48.4 %)	1.1 ± 0.3 (51.9 %)	
Drier season	10.3 ± 3.4 (50.4 %)	5.9 ± 1.7 (48.9 %)	2.0 ± 0.6 (49.4 %)	
N (kg ha^{-1} month^{-1})				
Leaf				
Rainy season	7.73 ± 0.43 (1.34 %)	5.56 ± 0.48 (1.16 %)		7.12 ± 1.10 (1.59 %)
Drier season	7.69 ± 0.63 (1.25 %)	5.14 ± 0.40 (1.11 %)		8.29 ± 1.33 (1.29 %)
Rubber leaf				
Rainy season		0.38 ± 0.08 (1.69 %)	1.61 ± 0.17 (1.52 %)	
Drier season		1.04 ± 0.24 (1.31 %)	6.03 ± 0.24 (1.31 %)	
Branch				
Rainy season	0.93 ± 0.19 (0.80 %)	0.59 ± 0.09 (0.77 %)	0.44 ± 0.13 (1.04 %)	
Drier season	1.14 ± 0.15 (0.83 %)	0.75 ± 0.22 (0.87 %)	0.37 ± 0.08 (0.97 %)	
Fruit				
Rainy season	0.53 ± 0.17 (1.50 %)	0.16 ± 0.02 (1.14 %)		10.12 ± 0.68 (0.68 %*)
Drier season	0.39 ± 0.13 (1.50 %)	0.28 ± 0.18 (0.95 %)		10.32 ± 1.25 (0.68 %*)
Rubber fruit				
Rainy season		0.07 ± 0.05 (1.16 %)	0.39 ± 0.16 (1.16 %)	
Drier season		0.01 ± 0.001 (0.47 %)	0.05 ± 0.02 (0.47 %)	
Flower				
Rainy season	0.15 ± 0.04 (1.53 %)	0.27 ± 0.08 (1.49 %)	0.03 ± 0.01 (1.55 %)	
Drier season	0.32 ± 0.11 (1.58 %)	0.19 ± 0.07 (1.49 %)	0.06 ± 0.02 (1.50 %)	

Element input	Natural forest	Jungle rubber	Rubber	Oil palm
P (g ha^{-1} month^{-1})				
Leaf				
Rainy season	176.7 ± 26.7 (0.3 ‰)	112.3 ± 14.1 (0.2 ‰)		416.4 ± 65.5 (0.9 ‰)
Drier season	187.0 ± 28.8 (0.3 ‰)	124.2 ± 16.5 (0.3 ‰)		472.7 ± 84.1 (0.7 ‰)
Rubber leaf				
Rainy season		9.1 ± 2.5 (0.4 ‰)	50.0 ± 9.8 (0.5 ‰)	
Drier season		20.3 ± 4.5 (0.2 ‰)	140.4 ± 10.4 (0.3 ‰)	
Branch				
Rainy season	19.1 ± 5.1 (0.2 ‰)	21.8 ± 9.3 (0.3 ‰)	6.1 ± 1.5 (0.2 ‰)	
Drier season	24.9 ± 4.3 (0.2 ‰)	27.2 ± 16.5 (0.2 ‰)	17.6 ± 8.7 (0.5 ‰)	
Fruit				
Rainy season	25.4 ± 8.7 (0.7 ‰)	6.0 ± 1.5 (0.3 ‰)		944.6 ± 151.6 (0.6 ‰)
Drier season	25.0 ± 10.8 (0.9 ‰)	12.0 ± 8.1 (0.5 ‰)		1026.2 ± 254.0 (0.6 ‰)
Rubber fruit				
Rainy season		6.7 ± 4.5 (1.1 ‰)	36.8 ± 14.5 (1.0 ‰)	
Drier season		0.8 ± 0.2 (0.3 ‰)	3.0 ± 1.2 (0.3 ‰)	
Flower				
Rainy season	5.5 ± 1.6 (0.5 ‰)	8.2 ± 2.5 (0.4 ‰)	0.7 ± 0.2 (0.3 ‰)	
Drier season	11.8 ± 3.8 (0.6 ‰)	7.6 ± 2.5 (0.6 ‰)	1.4 ± 0.4 (0.3 ‰)	
K (g ha^{-1} month^{-1})				
Leaf				
Rainy season	1056.9 ± 189.7 (1.9 ‰)	822.0 ± 98.4 (1.7 ‰)		1546.8 ± 269.0 (3.6 ‰)
Drier season	1170.3 ± 88.2 (1.9 ‰)	942.4 ± 173.2 (2.0 ‰)		1585.3 ± 217.1 (2.7 ‰)
Rubber leaf				
Rainy season		42.6 ± 9.2 (1.9 ‰)	286.5 ± 35.3 (2.7 ‰)	
Drier season		132.2 ± 40.6 (1.8 ‰)	852.4 ± 112.8 (1.9 ‰)	
Branch				
Rainy season	193.2 ± 79.3 (1.7 ‰)	115.3 ± 32.8 (1.5 ‰)	49.3 ± 9.2 (1.4 ‰)	
Drier season	161.9 ± 32 (1.2 ‰)	165.5 ± 104.6 (1.3 ‰)	111.2 ± 67 (3.0 ‰)	
Fruit				
Rainy season	142.3 ± 38.8 (4.5 ‰)	65.5 ± 18.4 (3.4 ‰)		10665.1 ± 713.3 (7.3 ‰)
Drier season	143.0 ± 74.9 (4.9 ‰)	105.8 ± 83.0 (3.0 ‰)		10884.5 ± 1314.5 (7.3 ‰)
Rubber fruit				
Rainy season		13.6 ± 9.1 (2.2 ‰)	73.2 ± 25.6 (1.9 ‰)	
Drier season		7.2 ± 2.1 (2.9 ‰)	39.4 ± 19.6 (2.9 ‰)	
Flower				
Rainy season	20.7 ± 4.1 (2.5 ‰)	71.5 ± 22.7 (3.6 ‰)	9.0 ± 2.5 (5.2 ‰)	
Drier season	52.4 ± 17.1 (2.6 ‰)	64.6 ± 24.2 (4.7 ‰)	18.9 ± 6.0 (4.9 ‰)	
Ca (g ha^{-1} month^{-1})				
Leaf				
Rainy season	3342.8 ± 481 (5.9 ‰)	3664.2 ± 761.5 (7.4 ‰)		3285.8 ± 645 (7.2 ‰)
Drier season	3653.0 ± 708.8 (6.0 ‰)	4746.5 ± 963.3 (10.0 ‰)		4566.3 ± 992.5 (6.8 ‰)
Rubber leaf				
Rainy season		197.9 ± 33.2 (8.8 ‰)	1010.6 ± 188.2 (9.0 ‰)	
Drier season		791.2 ± 192.4 (10.3 ‰)	5410.3 ± 540 (11.7 ‰)	
Branch				
Rainy season	652.5 ± 197.6 (5.5 ‰)	508.8 ± 87.7 (6.4 ‰)	484.7 ± 178.7 (11.2 ‰)	
Drier season	793.6 ± 148.4 (6.0 ‰)	570.4 ± 210.4 (6.1 ‰)	504.4 ± 174.2 (13.1 ‰)	
Fruit				
Rainy season	77.2 ± 18 (2.7 ‰)	115.4 ± 27.4 (7.1 ‰)		4378.4 ± 292.8 (3.0 ‰)
Drier season	107 ± 40.4 (3.6 ‰)	66.5 ± 26 (4.5 ‰)		4468.5 ± 539.6 (3.0 ‰)
Rubber fruit				
Rainy season		23.1 ± 15.5 (3.7 ‰)	72.7 ± 33.6 (4.8 ‰)	
Drier season		2.9 ± 0.8 (1.2 ‰)	14.5 ± 5.3 (1.2 ‰)	
Flower				
Rainy season	51.2 ± 10.2 (6.1 ‰)	114.1 ± 30.7 (6.2 ‰)	10.3 ± 3.2 (4.9 ‰)	
Drier season	96.3 ± 37.1 (4.6 ‰)	54.3 ± 12.2 (5.2 ‰)	19.1 ± 6.1 (4.9 ‰)	

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CHAPTER

4

Transformation of lowland rainforest into oil palm plantations results in changes of leaf litter production and decomposition in Sumatra, Indonesia

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Abstract

Leaf litter plays an important role for nutrient availability in ecosystems. Conversion of tropical rainforest into different land-use systems can largely alter nutrient cycling via changes in litter production and decomposition. In Indonesia, particularly on Sumatra and Kalimantan, large areas of natural lowland forest were replaced by oil palm plantations. However, the impact of the lowland rainforest transformation to oil palm plantation in Sumatra on soil nutrient status is yet unknown. Here we investigated the aboveground litter production, decomposition rate constants, and seasonal litterfall patterns in oil palm plantation (OP) and natural forest (NF) in Bukit Duabelas National Park Jambi, Sumatra using litter traps and the litter bag method. The annual litter production was higher in OP than in NF. However, oil palm fruits as the dominant component of litter production (79.6 % of total litterfall) are removed from the system causing nutrient loss. Litterfall production was influenced by climatic factors, mainly by rainfall and humidity. Furthermore, litterfall production increased with increasing rainfall and decreasing humidity in NF, while on the contrary, litterfall production in OP increased with decreasing rainfall and increasing humidity. Leaf litter nitrogen content and C/N ratio were the main factors influencing litter decomposition. Our data showed that decomposition rate constants of leaf litter were significantly higher in NF than in OP, meaning that nutrient turn-over via leaf litter in oil palm plantations was slower than that in natural forests.

Keywords: Annual litterfall, Bukit Duabelas National Park, land-use change, nutrient release, nutrient turnover

4.1 Introduction

Indonesia recently became the country with the highest deforestation rate among tropical countries (Hansen et al., 2013; Margono et al., 2014). Oil palm expansion hereby is one of the major drivers of current land-use change (Abood et al., 2014). In Sumatra, this rapid conversion to oil palm plantation occurred in most lowland forest regions (e.g. provinces of Jambi, Riau, South Sumatra) with increasing pressure on forest remnants, driving secondary forest and older agroforestry systems transformation to oil palm monocultures (Villamor et al., 2014). This large scale land-use change from structurally diverse forest to monoculture plantations not only has negative impacts on biodiversity (Sodhi et al., 2004; Fitzherbert et al., 2008; Wilcove et al., 2013), but also changes ecosystem functions (Sangha et al., 2006) like leaf litter production and decomposition process as a key biogeochemical process (Hättenschwiler et al., 2005; Hertel et al., 2009) and the major contributor to total net primary productivity (NPP) in tropical rainforests (Clark et al., 2001). These changes most likely will alter the plant-derived nutrient input to the soil and could influence ecosystem functioning (Triadiati et al., 2011). Despite their key role in the global carbon cycle and ecosystem functions, these changes are not well studied (Dixon et al., 1994; Houghton 2005; Del Grosso et al., 2008; Pan et al., 2011).

Several studies showed that tropical natural forests maintain higher annual leaf litter production compared to plantations, like monoculture plantations of *Cunninghamia lanceolata* (Wang et al., 2008), fast growing monoculture plantations of teak (*Tectona grandis* Lim.) (Ojo et al., 2010), and cacao agroforestry (Hertel et al., 2009; Triadiati et al., 2011). Differences in leaf litter production occurred due to varying environmental condition (Pausas, 1997) and plant species in the ecosystem (Kaye et al., 2000).

Leaf litter decomposition is the main path of nutrients recycling and nutrients turnover in the forest ecosystem, including N (Sariyildiz, 2003; Odiwe & Moughalu, 2003). It has been shown, that the patterns of leaf litter decomposition is different between plantation and natural forest ecosystems (Taylor et al., 1989). According to Triadiati et al. (2011), natural forest showed the most rapid decomposition rate constants, while cacao agroforestry systems with shade tree system have lowest decomposition rate constants. Besides ecosystem, the quantity and quality of litter also impacts the decomposition process (Hättenschwiler et al., 2011). Quality of leaf litter, such as N concentration and the C/N ratio are strongly correlated with decomposition rate constants (Taylor et al., 1989), and the introduction of shade trees in plantations can support the crop nutrient availability through decomposition process (Triadiati et al., 2011). Kang et al. (1999) stated that litter can help supply of the agricultural N, reduce the use of N fertilizer, and prevent the loss of N. To understand the dynamics of N in the plantation or in the forest ecosystem, it is important to analyze the quantity and quality of leaf litter, including leaf litter decomposition rate constants. However, studies on leaf litter production and decomposition particularly in oil palm plantations as compared to natural forests have not been done so far. Knowledge of production and decomposition rate constants of leaf litter as a fundamental role in the biogeochemical cycle of organic matter needs to be extended, especially to estimates nutrient turnover, C and N fluxes and changes of energy flow in transformation systems. The overall objective of our study was to investigate the impact of transformation systems to production and decomposition of leaf litter in oil palm plantation and natural forest in the Sarolangun district in Jambi (Sumatra). We tested the hypotheses (i) that leaf litter production is lower in oil palm plantations than in the natural forests, and (ii) that leaf litter decomposition and related nutrient return to the soil is lower in oil palm plantations compared to natural forests.

4.2 Materials and Methods

Study site

The study was conducted from September 2012 to September 2013 in Sarolangun district, Jambi province. The Bukit 12 National Park (TNBD) is a relatively small national park that covers 605 km^2 in Jambi (Indonesia), which represent the lowland tropical rain forests in Jambi province. Only the northern part of this park consists of primary rainforest, while the rest is old-growth forest with selective logging activities in a close to natural state. In the past, the forest area functioned as a permanent production forest, limited production forest, and other forest land uses which were later merged to a National Park.

The study was conducted in 2 location: natural forest (NF in three sites at TNBD, Sarolangun district) and oil palm plantation (OP (8-12 old) in three sites in Sarolangun district), the coordinate are: S 01°59’42.5’’ E 102°45’08.1’’ (NF1), S 01°56’33.9’’ E 102°34’52.7’’ (NF2), S 01°56’31.9’ E 102°34’50.3’’ (NF3), S 02°04’32.0’’ E 102°47’30.7’’ (OP1), S 02°04’15.2’’ E 102°47’30.6’’ (OP2), S 02°04’15.2’’ E 102°47’30.6’’ (OP3). Plot size was 50 m x 50 m. The monthly rainfall was 217.47 mm with the highest precipitation in December 2012 (529 mm) and the lowest in June 2013 (33 mm), respectively. The average daily temperature ranged from 26.6 °C to 28 °C. The daily air humidity and solar radiation ranged between 77-90 % and 45-62 %, respectively. Climate data were acquired from Climatology Station of Jambi.

Litter production

Aboveground litter production in NF was measured by collecting the litterfall using litter traps. Litter traps were made of nylon gauze with a mesh size of 3 mm with PVC-tubed frames with the trap surface size of 0.75 m x 0.75 m. The traps were set up at about 50 cm above soil surface, with 16 traps for each plot. In OP, data were acquired from pruned oil palm fronds at every harvesting time, as well as the harvested fruits every month. The collected litter was separated into following components: leaves, twigs (≤ 2 cm diameter), and reproductive parts. The litter was then dried in the oven at 80 °C until constant weight. Annual leaf litter production was assumed to equal annual leaf litterfall.

Leaf litter decomposition

The quantification of leaf litter decomposition was determined using the litter bag methods. The fresh leaf litter was placed in nylon bags (30 cm x 30 cm and mesh size of 0.5 mm). For every plot, we placed 24 litter bags during 12 month period of observation time. The litter bags were placed randomly on the forest floor surface and tied on a nail plugged to the ground to prevent displacement or site exchange. Two bags were retrieved once a month. The leaf litters were oven dried at 80°C until constant weight. The dried leaf litter was placed in plastic bags until N and C analysis were conducted. Nitrogen and organic carbon content in leaf litter were determined using the Kjeldahl and the Walkley and Black method, respectively.

The litter decomposition rate constants were calculated based on the equation given by Olson (1963):

$$\ln (Xt / Xo) = -kt$$

Where Xt is the weight of litter after t time, t is time (months), Xo is the fresh litter weight, and k is the decomposition rate constant.

Periodic curve fitting

Periodic curve fitting can be used for periodic data as the observations are equally spaced a complete cycle (daily, weekly, monthly, or yearly cycles). Periodic curve appoint to as a harmonics (Little and Hills, 1977). In this study, periodic curve was applied for monthly data of litterfall production and climates (rainfall, temperature, air humidity, and solar radiation).

Data analysis

Data on leaf litter production and decomposition, N and C release were analyzed using Independence sample t-test. In order to investigate relationship among parameters linear regressions and Pearson’s correlation analysis were performed. The standard level of significant was $p < 0.05$. All analyses were done using SPSS 17 software.

4.3 Results and discussions

Litterfall production

We found different patterns of litter production between NF and OP (Fig. 4.1). The annual forest litterfall production reached values up to 1.4 kg m^{-2} y^{-1} (Tab. 4.1), whereas values in oil palm litterfall production were 2.4 kg m^{-2} y^{-1}.

Table 4.1: Annual litterfall in natural forests (NF) and oil palm plantations (OP). Values are mean ± SD.

Site	Annual litterfall (kg m^{-2} year^{-1})
NF	1.4 ± 1.6
OP	2.3 ± 1.1

Similar annual litterfall production rates of tropical rainforests in Central Sulawesi were found by Triadiati et al. (2011). On the other hand, according to Lowman (1988) annual litterfall production of tropical rain forest in Australia reach only 0.7 kg m^{-2} y^{-1}. The difference of annual litterfall production can be explained by the influence of plant diversity and climate factors (Lowman, 1988).

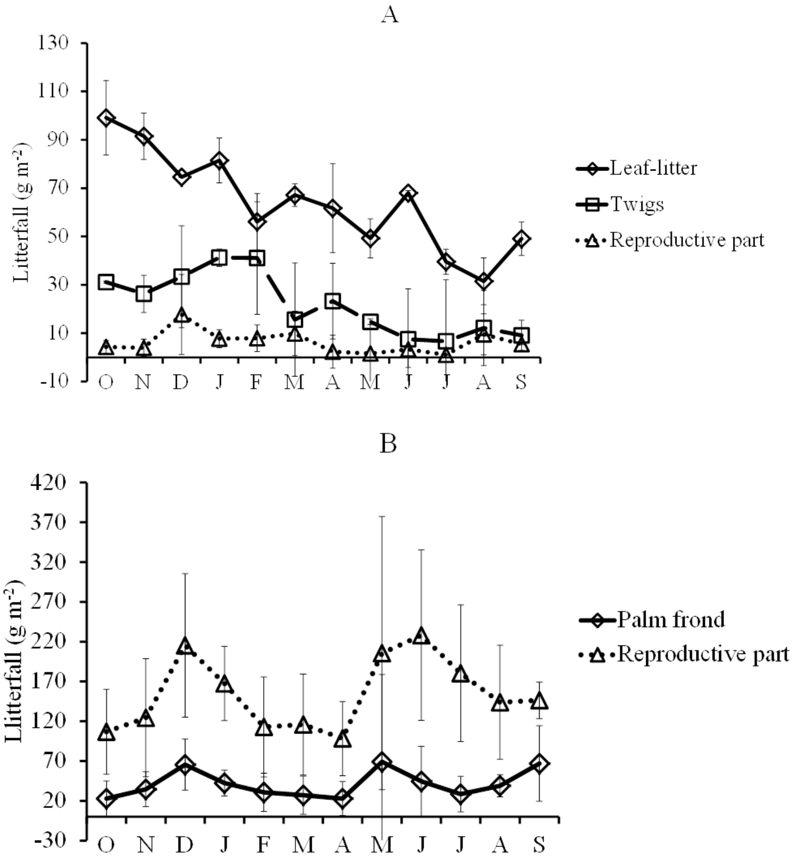

Figure 4.1: Components of litterfall in natural forest (NF) (A) and oil palm plantation (OP) (B) from October 2012 to September 2013. Error bars indicate ± SD.

Leaf litter was the most dominant litter components that contributed to litter production of NF, followed by twigs and reproductive parts (Fig. 4.1.A). Smith et al. (1998) found that the highest litterfall component in both natural forests and three plantation types of *Pinus caribae*, *Carapa guianensis,* and *Euxylophora paraensis* comprises leaf litter, and is generally followed by stem, branches, and reproductive parts. Meanwhile, reproductive parts were the largest litter components of OP litterfall that contributed 79.6 % to the litterfall production (Fig. 4.1.B). However, these parts were not returned to the ecosystem, resulting in high nutrients loss to the system and disturbance of nutrient recycling. On the contrary, all litterfall in NF was returned to the soil, and become a source of nutrients for plants and completing the nutrient cycles.

The highest litterfall production in NF occurred in April 2013, while in OP most leaf litter was produced in December 2012, May and June 2013 (Fig. 4.2). We found significant differences in December 2012 and September 2012 and divergent patterns of litterfall production between both ecosystems.

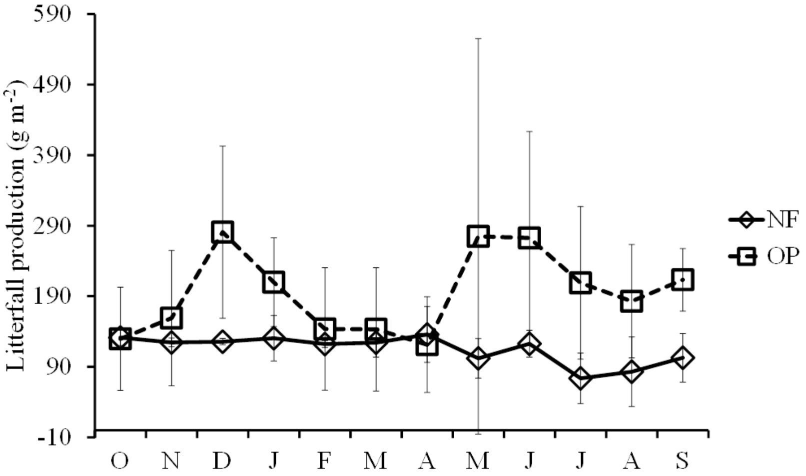

Figure 4.2: Litterfall production in natural forest (NF) and oil palm plantation (OP) from October 2012 to September 2013. Error bars indicate ± SD.

Leaf litter from the forest sites was rich in nutrient elements and had great effect in improving the soil humus productivity. The level of litterfall effectiveness in improving the soil humus depends on the plant species, environmental factors, and the type of soil, climate, accumulation of organic matter, and microbial activity (Sharma and Sharma, 2004). Element concentrations (including N and C) in forest tree contribute to the soil nutrient stocks by means of the decomposition process and becoming soil humus in ecosystem (Vitousek and Sandford, 1987). Our result showed that there were differences in N and C production of fine litterfall between two type ecosystems. Leaf litter in NF contained the highest N and C values, followed by twigs and reproductive parts (Fig. 4.3). According to Oladoye et al. (2010), leaf litter contributed more nutrients, especially N, than other fine litterfall components. On the other hand, the highest N and C contribution in OP was found in reproductive parts (68.1% and 77.8%, respectively), which was significant more than in leaf litter (Fig. 4.3).

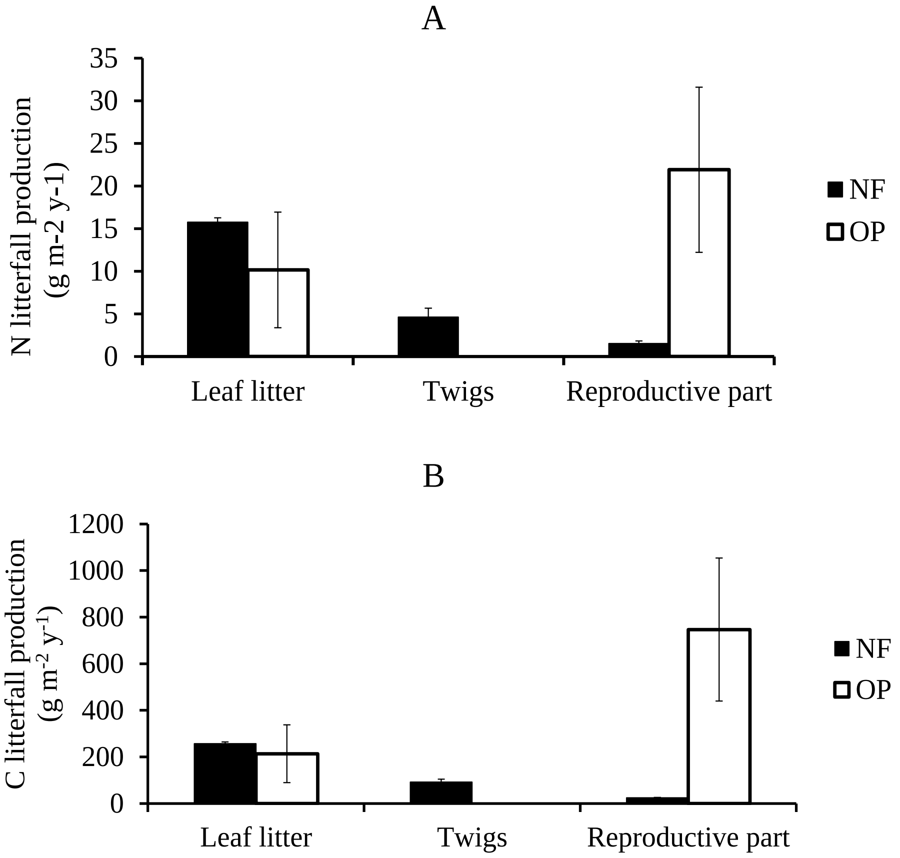

Figure 4.3: Nitrogen and carbon content of fine litterfall in natural forest (NF) compared to oil palm plantation (OP). A = nitrogen litterfall production and B = carbon litterfall production. Error bars indicated ± SD.

However, these reproductive parts were not return to the systems and nutrients were lost from the system. High litter production in monoculture oil palm was driven by intensive fertilization to counterbalance nutrient loss due to harvesting and soil erosion (Witt et al., 2005; Danyo, 2013).

The periodic curve of monthly litterfall and climatic factors (rainfall, temperature, humidity, and solar radiation) are shown in Figure 4.4. Based on the periodic curve we concluded that high litterfall production in NF occurred during the period of high rainfall, high temperature, low humidity and low radiation (Fig. 4.4 A).

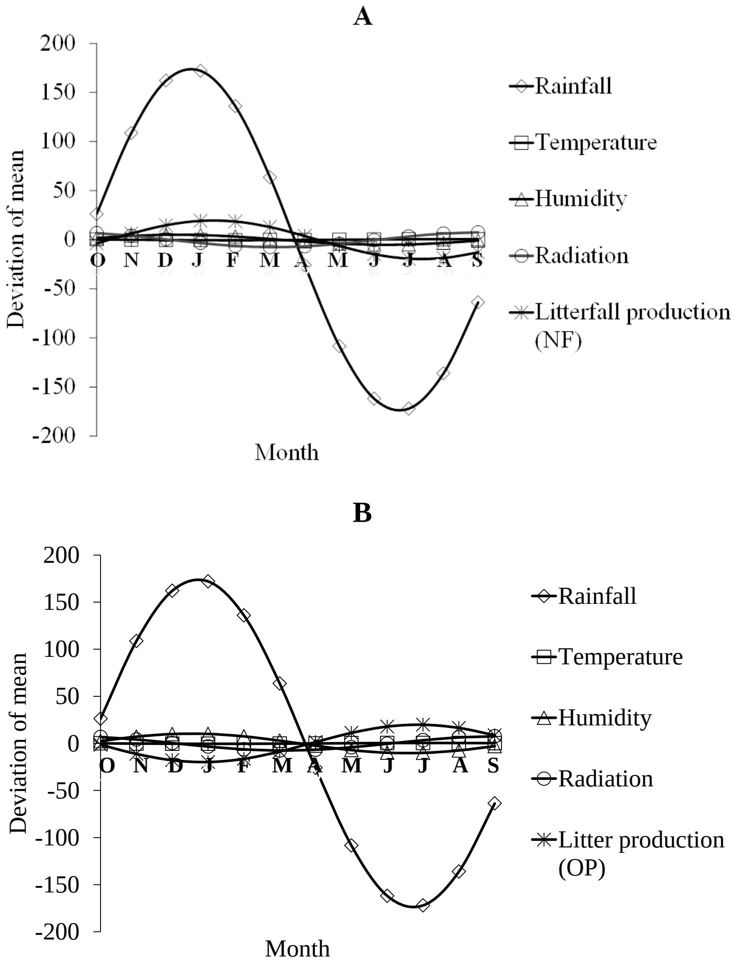

Figure 4.4: Periodic curve of litterfall in October 2012 to September 2013 in natural forest (A) and oil palm (B), and several climatic factors (rainfall, air temperature, air humidity, and solar radiation). NF = positive correlation to rainfall and temperature, and negative correlation to humidity and solar radiation; OP = negative correlation to rainfall and temperature, and positive correlation to humidity and solar radiation.

According to Zheng et al. (2005) and Triadiati et al. (2011), leaf litter production is influenced by climatic factors especially; rainfall, temperature, and humidity. In contrast to NF, high litterfall production in OP occurred during the period of low rainfall, low temperature, high humidity and high radiation. Zhu et al. (2008) stated that oil palm tree grows and production is optimal in hot, wet tropical lowland climates with high radiation, temperature ranging from 24-27 °C and the annual rainfall distribution of 2000-3000 mm. However, different ecosystems are influenced by different climatic variable (Yuan and Chen, 2010). The litterfall in OP was artificially influenced by the harvesting done by farmers, as well as by environmental factors. Cutting of oil palm fronds during the harvesting process, cleaning of the yellow senescent fronds, and exposure to pesticide spraying, caused the higher production of litter in the oil palm plantation. In certain conditions, the farmers did not cut the fronds trees of the palm trees while harvesting of oil palm fruits, thus decreased the litter production and increasing the variability of litterfall for statistics analysis (Fig. 4.1 and 4.2). Regarding the life cycle of palm frond, in oil palm plantation it takes over 4 years to the leaves senescent, whereas NF plants usually remain a much shorter time on the tree. Therefore, the fronds obtained as litters in OP in this study were not senescent leaves, but the leaves that are pruned by farmers. In some conditions, the farmers did prune on a large scale e.g. if there were too many fronds yellowing, as it happened in September 2013 in the study (Fig. 4.1). Here the palm fruit production was low, while the fronds production increased. Hence, we can conclude that not only climatic factor but many other factors such as human treatment and fertilization that influenced the different pattern of litterfall production in NF and OP.

Leaf litter decomposition

Initial element content (N, C, C/N ratio) of leaf litter before decomposition is shown in Table 4.2. The N content was higher in natural forest than that in oil palms, whereas the C content and C/N ratio was higher in OP than that in NF (Tab. 4.2).

Table 4.2: Initial N and C content of leaf-litter in forest (NF) and oil palm (OP). Values are mean ± SD.

Site	Plant parts	Initial N, C content and ratio C/N		
		C (%)	N (%)	C:N
NF	Leaf litter	40.2 ± 1.0	1.66 ± 0.3	24.22 ± 4.6
OP	Palm frond	41.1 ± 0.7	1.47 ± 0.1	27.81 ± 5.9

Dry weight decreased with increasing incubation time in NF and OP (Fig. 4.5). The reduction of remaining mass was more rapid in NF than that of in OP. In the first month of observation, dry weight in NF decreased drastically reaching 28.8 %, while in OP only 6.7 % were reached. The faster decrease could be caused by water-soluble material at the beginning of incubation and slowed down over time as the recalcitrant substances became more abundant in the leaf litter (Berg & McClaugherty, 2008). Physical and chemical processes occurred during this period. Physical process generally dominated the early state of decay in decomposition process. The microorganisms decompose leaf litter in order to gain carbon, nutrients and energy for growth and reproduction (McClaugherty, 2001). This process is through physical fragmentation by wet–dry, shrink-swell, hot-cold, and other cycles. Leaching and transport water is another important physical mechanism (Berg and McClaugherty, 2008). Chemical transformation included oxidation and condensation of leaf litter (Berg and McClaugherty, 2008).

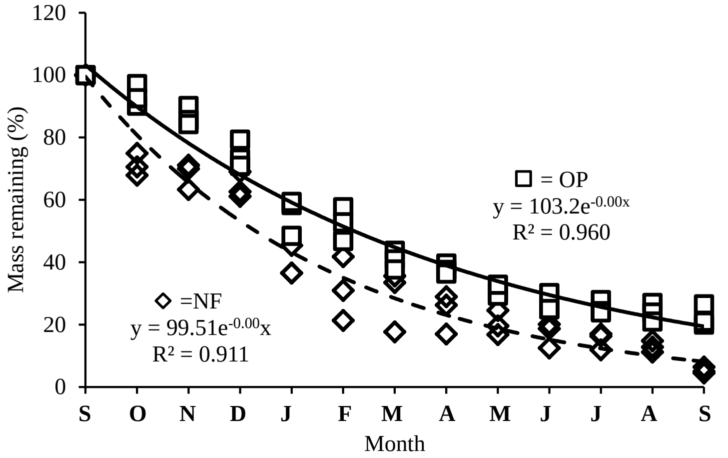

Figure 4.5: Exponential curve of remaining mass (%) in the decomposition process during 12 months of incubation from September 2012 to September 2013 in natural forest (NF) and oil palm (OP). y = leaf-litter mass remaining and x = time (month).

Generally, the most rapid weight loss occurred in the water-soluble component (Andren and Paustian, 1987), such as soluble sugars, phenolics, hydrocarbons, and glycerides (Berg and McClaugherty, 2008). At the end of the incubation, the percentage of mass remaining of leaf litter in NF was lower (5.27 %) than that of in OP (22.48 %) (Fig.4.5). According to Haron and Anderson (2000), the percentage mass remaining in decomposition of oil palm leaves ranged between 5-20 % during the 12 months of incubation. The decomposition rate constants increased with the increasing time incubation. Decomposition rate constant of leaf litter during 12 month incubation in NF was higher than that of in OP. It reached 2.95 and 1.5, respectively (Fig. 4.6). According to Berg and McClaugherty (2008) decomposition rate constants becomes one of indicator of nutrient return in ecosystem. We concluded that the nutrient turnover derived from leaf-litter in OP was much slower than that of NF.

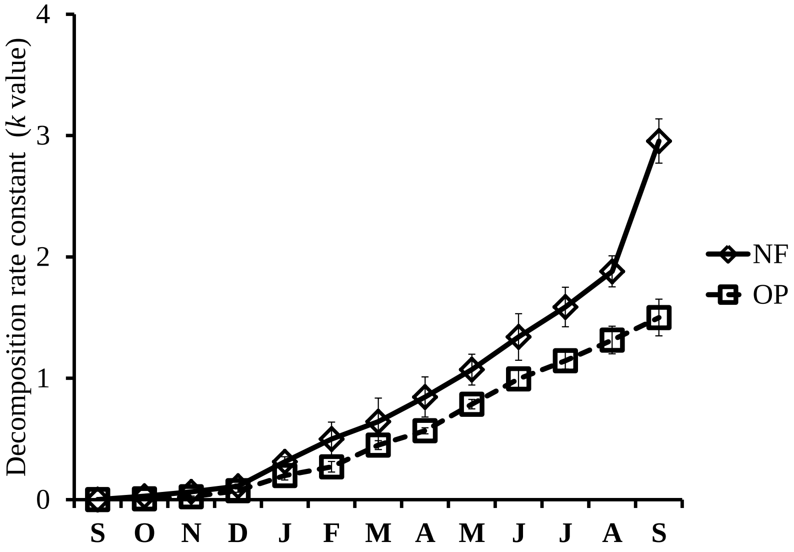

Figure 4.6: Decomposition rate constants (*k* value) in natural forest (NF) and oil palm plantation (OP). Error bars indicates ± SD.

The leaf litter decomposition rate constants was positively correlated with initial N content and negatively correlated with initial C/N ratio of leaf litter (Tab. 4.3). Leaf litter quality was the major factor for leaf litter decomposition in forest ecosystems (Vitousek, 1982). Our results showed that the dry weight loss was faster in NF than that of in OP. This might be caused by different nutrient content of the leaf litter from both ecosystems (Vitousek, 1982) as we found higher N content in NF leaf litter, and lower C content and C/N ratios than that of in OP litter (Tab. 4.3).

Table 4.3: Correlations between nitrogen content and C/N ratio and decomposition rate constants (*k*) (Pearson's). ** indicating significant difference at $p < 0.01$.

Parameter	Source	Correlation	
		r (Pearson's)	*p*
Decomposition rate constants (*k* value)	N content (%)	0.77**	0.00
	C content (%)	-0.32	0.31
	C/N ratio	-0.79**	0.00

These results were supported by correlation between N and C/N ratio to decomposition rate constants. Decomposition rate constants increased with the increased of N content, and decreased with the increased C/N ratio. Similar result showed by other researchers who reported that that decomposition rate constants increased with the increased of N and decreased with the increased of C/N ratio (Semwal et al., 2003; Sing et al., 2003; Scherer-Lorenzen et al., 2007; Zhang et al., 2008). Wenyau et al., (2000) and Xu and Hirata (2005), states that N and lignin content or ratio of lignin/N in plants had a greater influence on the decomposition process compared to the other quality parameters. In addition, Taylor et al. (1989) said that as lignin/N ratio, C/N ratio was the prominent parameter of leaf litter quality in determined decomposition rate constants (Bosire et al., 2005).

Oil palm plantations produce a number of agricultural by-products such as fronds and empty fruit bunches. These by-products usually support nutrients turnover in oil palm plantations through the decomposition process. Salétes et al. (2004) studied the nutrient loss in empty fruit bunches of oil palm during the storage period, and found that the empty fruit bunches yield mineral nutrients quickly, especially the elements of potassium, magnesium, and boron. According to Haron et al. (2000), the efficient management of oil palm residues can improve palm nutrients and hence their uptake, growth and production. However in this study plots, the farmers did not apply the empty fruit bunches of oil palm to the plantation area, so that many nutrients were lost.

4.4 Conclusions

Transformation of natural forest to oil palm plantations influenced the litterfall production and decomposition processes in tropical lowlands. There were different seasonal patterns of litter production between NF and OP. Total litter production was found to be higher in OP than that of in NF. Leaf litter was the largest component of litterfall in NF, while reproductive parts were the major component of litterfall in OP that contributed 79.6 % of litterfall production. The reproductive parts (fruits), however, were removed from the ecosystem and were not returned to the soil. Therefore, many nutrients were lost in oil palm plantations. Climatic factors influencing litterfall production were mainly rainfall and humidity. We found that the decomposition rate constants of litter were significantly higher in NF than in OP. This indicated that nutrient turnover in NF was faster than in OP. The initial N content and C/N ratio of leaf litter affected decomposition rate constants, which implicated slower nutrient turnover.

Acknowledgments

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CHAPTER

5

Patterns in hydraulic architecture from roots to branches in six tropical tree species from cacao agroforestry and their relation to wood density and stem growth

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Abstract

For decades it has been assumed that the largest vessels are generally found in roots and that vessel size and corresponding sapwood area-specific hydraulic conductivity are acropetally decreasing towards the distal twigs. However, recent studies from the perhumid tropics revealed a hump-shaped vessel size distribution. Worldwide tropical perhumid forests are extensively replaced by agroforestry systems often using introduced species of various biogeographical and climatic origins. Nonetheless, it is unknown so far what kind of hydraulic architectural patterns are developed in those agroforestry tree species and which impact this exerts regarding important tree functional traits, such as stem growth, hydraulic efficiency and wood density. We investigated wood anatomical and hydraulic properties of the root, stem and branch wood in *Theobroma cacao* and five common shade tree species in agroforestry systems on Sulawesi (Indonesia); three of these were strictly perhumid tree species, and the other three tree species are tolerating seasonal drought. The overall goal of our study was to relate these properties to stem growth and other tree functional traits such as foliar nitrogen content and sapwood to leaf area ratio. Our results confirmed a hump-shaped vessel size distribution in nearly all species. Drought-adapted species showed divergent patterns of hydraulic conductivity, vessel density and relative vessel lumen area between root, stem and branch wood compared to wet forest species. Confirming findings from natural old-growth forests in the same region, wood density showed no relationship to specific conductivity. Overall, aboveground growth performance was better predicted by specific hydraulic conductivity than by foliar traits and wood density. Our study results suggest that future research on conceptual trade-offs of tree hydraulic architecture should consider biogeographical patterns underlining the importance of anatomical adaptation mechanisms to environment.

Keywords: Shade tree, hydraulic conductivity, wood density, aboveground productivity, foliar nitrogen, perhumid climate, vessel diameter

5.1 Introduction

The water transport pattern in trees is mainly determined by the plant hydraulic architecture, i.e. the spatial distribution of various xylem properties from roots to branches of a tree individual (McCulloh et al., 2010). The hydraulic efficiency of different compartments along the root-to-leaf flow path can be described by the sapwood area-specific hydraulic conductivity (K_S), which is directly related to the hydraulic resistance of a given position (Tyree and Ewers, 1991; McElrone et al., 2004). According to the Hagen-Poiseuille law, even a small increase in mean vessel diameter causes an exponential increase of K_S. This anatomical pattern represents the most economical way for a woody plant to enhance the path-length hydraulic conductivity. Independently of the efficiency of the hydraulic system water is transported in a metastable state below its vapor pressure in vascular plants, which makes them vulnerable to the formation of gas embolism. This can impair the transport of water from the soil to the leaves. Particularly wide vessels are not only most conductive but also most prone to the risk of hydraulic failure in form of xylem embolisms (Maherali et al., 2006; Awad et al., 2010; Cai et al., 2010; Hajek et al., 2014), resulting in a trade-off between hydraulic efficiency and cavitation resistance. As one of the basic organizing principles of tree hydraulic architecture it has been postulated that the mean vessel diameter in the xylem tissue generally decreases acropetally from roots to branches ('vessel tapering': Baas, 1982; Tyree and Zimmermann, 2002; Anfodillo et al. 2013). This principle has stimulated several conceptual models on plant hydraulic architecture during the past 15 years. They state that whole-plant hydraulic conductance dependent on distance to ground in support of the model by West, Brown and Enquist (1999) and Murray’s law (McCulloh et al., 2003). Consistent with these predictions it has indeed commonly been observed that the largest vessels along the water flow path are found in roots of trees from temperate or Mediterranean environments (Martinez-Vilalta et al., 2002; Pratt et al., 2007; Domec et al., 2009). However, recent studies in tropical forests in South America (Machado et al., 2007; Fortunel et al., 2013) and Indonesia (Schuldt et al., 2013) have produced contradictory results regarding the paradigm of continuous vessel tapering. Schuldt et al. (2013) supposed that mechanisms reducing cavitation risk may not have been evolved in these moist or perhumid environments where drought stress is normally not apparent.

Forested perhumid regions particularly in the tropics are underrepresented in studies so far and are moreover converted rapidly. Worldwide approximately 27.2 million ha of humid tropical forests have been cleared between 2000 and 2005 (Hansen et al., 2008) mainly for agricultural land use (Achard et al., 2002; FAO and JRC, 2012). In Southeast Asia, a common driver of deforestation is the conversion of natural forests into cacao (*Theobroma cacao*) agroforestry systems. Cacao is native to tropical South America (Motamayor et al., 2008) and represents one of the commercially most important perennial cash crops worldwide. Traditionally cacao trees are planted under selectively thinned primary or older secondary forest in Indonesia, but nowadays cultivation is shifting to non-shaded monocultures or agroforests with introduced fast-growing legume tree species such as *Gliricidia sepium* to increase short-term income (Rice and Greenberg, 2000). Shade trees in cacao plantations enhance functional biodiversity, carbon sequestration, soil fertility and drought resistance and provide microclimatic benefits such as increased humidity and buffering temperature extremes (Schroth and Harvey, 2007; Tscharntke et al., 2011).

Considering the ecological relevance of the anatomical hydraulic properties described above, it is important to note that systematic studies on the ecological wood anatomy and hydraulic architecture of cacao and shade tree species are lacking so far. This is all the more unsatisfying since tropical agroforestry crop and shade tree species often originate from different biomes and possess distinct drought adaptations, but it is unknown so far if this implies differences in the hydraulic strategy of those crop and shade tree species. It is therefore unknown whether cacao and shade tree species in the agroforestry systems with different biogeographical origin have developed similar hydraulic properties as the tree species of the natural forest replaced by those.

A high aboveground biomass production (incl. high crop yield) has been related to several plant functional traits like high stem hydraulic efficiency, high foliar nitrogen content, or low stem wood density (Brodribb et al., 2002; Tyree, 2003; Zhang and Cao, 2009; Hoeber et al., 2014). Thereby low wood density implying lower hydraulic safety is found to be associated with fast tree growth (Enquist et al., 1999; King et al., 2005; Poorter et al., 2010), while species with dense wood are considered to be more resistant to xylem cavitation due to the commonly assumed relation between wood density and conduit size and thus xylem wall thickness and resistance to cell wall implosion under negative pressure (Jacobsen et al., 2005). Consequently, species with dense wood should show higher hydraulic safety at the cost of lower productivity (Meinzer et al., 2003; Bucci et al., 2004). Nevertheless, several studies, particularly from tropical environments, found wood density decoupled of hydraulic efficiency traits and growth performance (Zhang and Cao, 2009; Russo et al., 2010; Fan et al., 2012; Schuldt et al., 2013). It would therefore be interesting to assess whether hydraulic properties and wood density are related to the aboveground performance of crop and shade tree species in cacao agroforests.

In this study we examined the inter-relationship between sapwood area-specific hydraulic conductivity of the root, stem and branch xylem tissue with wood anatomical traits along the water flow path across six common cacao agroforestry tree species with different biogeographical origins from either seasonally dry or perhumid tropical environments growing in cacao agroforests in Central Sulawesi (Indonesia). We moreover wanted to relate aboveground growth performance to hydraulic efficiency, stem wood density, foliar nitrogen content and foliar $\delta^{13}C$ of these species. We hypothesized (i) that – in contrast to temperate tree species – the largest vessels along the water flow path are found in the stem xylem and not in the roots, (ii) that stem xylem hydraulic properties are unrelated to stem wood density, and (iii) that aboveground productivity across species is positively related to vessel size and hydraulic conductivity.

5.2 Material and methods

Study site, species and sampling

The study was carried out in a cacao agroforestry located in the Kulawi Valley, Bolabapu District, Central Sulawesi, Indonesia (S 01°55.9’ E 120°02.2’, elevation 571 m a.s.l.) in May 2012. The climate of the study region is perhumid without a distinct dry season. Mean annual temperature recorded for the study area by Moser et al. (2010) is 25.5 °C and mean annual precipitation is 2092 mm between 2002 and 2006. For the study, a cacao agroforestry plot with multi-species shade tree layer was selected from a larger number of preselected cacao agroforestry plots of a different investigation that were found to be representative in terms of management, aboveground structure and topographical patterns for this region. Caution was taken during the selection process that the plot was far enough above the groundwater table to guarantee that the trees had no direct access to this water source. All trees in the agroforest were planted simultaneously around 25 years ago.

Theobroma cacao L. (Malvaceae) originating from rainforests of lowland northern South America and five common shade tree species were studied: *Leucaena leucocephala* (Lam.) de Wit and *Gliricidia sepium* (Jacq.) Steud. (both Fabaceae), which are introduced species from seasonal dry forest areas of Central America. The three other species represent native origins: *Gnetum gnemon* L. (Gnetaceae), the short-term drought-tolerating *Erythrina subumbrans* (Hassk.) Merill (Fabaceae) and the strictly perhumid species *Durio zibethinus*. Murr. (Malvaceae). In the following we have grouped the species according to their drought tolerance as perhumid (*T. cacao, D. zibethinus, G. gnemon*) and seasonal (*G. sepium, L. leucocephala, E. subumbrans*). All species have diffuse-porous wood with *G. gnemon* being a gymnosperm bearing vessels structurally similar to angiosperms (Carlquist, 1994; Fisher and Ewers, 1995). We chose six tree replicates of each species with a diameter and height representative for the whole agroforestry.

For each tree three sun-exposed upper-crown branches and three topsoil root segments (diameter 6-14 mm; length 25-35 cm) were collected as well as one stem core of 5 cm length per tree taken with an increment corer (Haglöf, Långsele, Sweden) at 130 cm stem height. To ensure species identity the roots were traced back to the tree stem. In order to avoid microbial growth in the extracted tree organs, samples were stored in polyethylene tubes filled with water containing a sodium-silver chloride complex (Micropur Katadyn, Wallisellen, Switzerland). The samples were kept cool at 4 °C and the conductivity measurements took place not more than 7 days after collection.

Wood density, aboveground biomass and productivity

Wood density, defined as oven-dry weight over wet volume, was measured for each stem core. The fresh volume of each sample was determined by Archimedes' principle. Samples were then oven dried for 48 h at 105 °C and dry mass recorded.

Aboveground biomass of the trees was calculated using the allometric equation of Chave et al. (2005) for tropical wet stands as: $\mathrm{AGB} = \exp\ (-2.187 + 0.916 \times \ln\ (\mathrm{WD} \times \mathrm{DBH}^2 \times \mathrm{H}))$, where AGB is the estimated aboveground biomass (kg), DBH the trunk diameter at 130 cm height (cm), H the total tree height (m), and WD the stem wood density ($\mathrm{g\ cm^{-3}}$). Since we obtained proper data on tree height only at the beginning of the study, we used stem basal area increment (BAI, $\mathrm{cm^2\ yr^{-1}}$) determined over a period of 12 month using dendrometer tapes (UMS GmbH, München, Germany) as indicator for aboveground productivity. However, it has been shown that aboveground biomass increment and basal area increment are very closely related in tropical trees (Hoeber et al., 2014). For *T. cacao, G. sepium and D. zibethinus* six tree replicates were monitored, whereas data from just three *G. gnemon*, two *L. leucocephala* and one of *E. subumbrans* were available for BAI.

Leaf morphological and chemical properties

From each branch segment harvested for the hydraulic and anatomical measurements, all distal leaves were stripped off and oven-dried at 70 °C for 48h to determine leaf dry weight. Specific leaf area (SLA, $\mathrm{cm^2\ g^{-1}}$) values were determined using data from nine additional branches per species where leaf surface areas were measured with the WinFolia software (Régent Instruments, Quebec, Canada). Total leaf area per branch segment (A_L, $\mathrm{m^2}$) was calculated by dividing dry weight through species-specific SLA values. Subsequently, leaf samples were grounded and analyzed for their foliar concentrations of C and N and for their foliar signatures of $\delta\ ^{13}\mathrm{C}$ in the leaf bulk tissue with a Delta plus isotope mass spectrometer (Finnigan MAT, Bremen, Germany), a Conflo III interface (Thermo Electron Cooperation, Bremen, Germany) and a NA2500 elemental analyzer (CE-Instruments, Rodano, Milano, Italy) using standard δ notion: $\delta = (R_\mathrm{sample} / R_\mathrm{standard} - 1) \times 1000$ (‰) in the laboratory for stable isotope measurements (KOSI) at the University of Göttingen.

Empirical conductivity measurements

Hydraulic conductivity of one to three root and branch segments per tree was empirically measured using the method described by Sperry et al. (1988). In total, 44 root and 39 branch segments were analyzed (mean root segment length ± SE: 291 ± 7.0 mm and diameter: 7.87 ± 0.25 mm; mean branch segment length: 308 ± 4.3 mm and diameter: 9.12 ± 0.29 mm). All segments were recut under water with a razor blade, small lateral roots and branches cut-off and sealed with quick-drying superglue (Loctite 431, Henkel, Düsseldorf, Germany) and activator (Loctite 7452 Aktivator, Henkel, Düsseldorf, Germany) that function on wet materials. Afterwards, segments were attached under water to the tubing system of the conductivity apparatus, where the pressure difference of 6 kPa was generated by a 60 cm high water column. De-ionized water with a sodium-silver chloride complex (16 µg L^{-1} Ag, 8 mg L^{-1} NaCl, Micropur katadyn, Wallisellen, Switzerland) was used as measuring solution in order to avoid microbial growth in the tubing system, a common problem in tropical environments. While comparing our data with conductivities determined by other solutions, it has to be considered that different perfusion solutions can affect hydraulic conductivity (Espino and Schenk, 2011). The solution was passed through a 0.2 µm membrane filter (Maxi Capsule, Pall Corp., USA) and each sample measured three times in row and flushed with the measuring solution for 5 min at 120 kPa in between each measurement to remove potential emboli. The hydraulic conductivity (K_h^{emp}, kg m s^{-1} MPa^{-1}) was calculated as $K_h = (\Delta V/\Delta t) \times (l/\Delta P)$ where l is the length of the segment (m), ΔP the pressure difference applied to the segment (MPa), ΔV the amount of water flowing out of the segment (kg), and Δt the time interval of measurement (s).

Segments of the branches and roots used for conductivity measurements were planed with a sliding microtome (G.S.L.1, WSL, Birmensdorf, Switzerland) to obtain high-quality top view images with a stereo-microscope (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) and total cross-sectional (A_{cross}, mm^2) and xylem cross-sectional area (A_{xylem}, mm^2) analyzed with ImageJ (v1.44p, http://rsb.info.nih.gov/ij). Subsequently, for each species a regression analysis between A_{cross} and A_{xylem} was carried out (Table A 5.1). Empirical sapwood area-specific hydraulic conductivity (K_S^{emp}, kg m^{-1} MPa^{-1} s^{-1}) was calculated by dividing K_h^{emp} by the calculated mean xylem cross-sectional area without pith and bark by applying the species-specific regression coefficients, and empirical leaf area-specific hydraulic conductivity (K_L^{emp}, kg m^{-1} MPa^{-1} s^{-1}) by dividing K_h by the total supported leaf area (A_L).

Vascular anatomy

For the cross-sectional xylem anatomical analysis, 3 cm of the basipetal end of each root or branch segment used for empirical conductivity measurements was stained with safranin (1% in 50% ethanol, Merck, Darmstadt, Germany) and 10-20 µm semi-thin discs cut with a sliding microtome (G.S.L.1, WSL, Birmensdorf, Switzerland). For stem wood anatomy the outermost 4 cm of the increment core were used. Photographs of the cross-sectional cuts were taken with a stereo-microscope with an automatic stage equipped with a digital camera (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) at 100x magnification. Per sample, 32 up to 107 single images were stitched together to obtain the whole cross-sectional area. Image processing was done with Adobe Photoshop CS6 (version 13.0.1, Adobe Systems Incorporated, USA) and ImageJ (version 1.47, http://rsb.info.nih.gov/ij) using the particle analysis-function for estimating vessel density (VD, n mm^{-1}), the idealized vessels diameter (d) from major (a) and minor (b) vessel radii using the equation given by White (1991) as $d = ((32 \times (a \times b)^3) / (a^2 + b^2))^{¼}$, and cumulative vessels lumen area (A_{lumen}, m^2). Single vessel diameters (d) were used to calculate the hydraulically weighted vessel diameter (d_{h}) according to Sperry et al. (1994) as $d_{\mathrm{h}} = \Delta d^4 / \Delta d^5$. For these measurements all vessels of a cross section were analyzed, yielding 110 to 3,600 measured vessel per species and organ. The theoretical hydraulic conductivity ($K_{\mathrm{h}}^{\mathrm{theo}}$) of a segment can be calculated based on Hagen-Poiseuille's law as $K_{\mathrm{h}}^{\mathrm{theo}} = (\pi \times \Sigma r^4) / 8\ \eta) \times \rho$, where r is the vessel radius, η the viscosity ($1.002{\times}10^{-3}$ Pa s) and ρ the density of water (998.2 kg m^{-3}), both at 20 °C. Theoretical sapwood area-specific hydraulic conductivity ($K_{\mathrm{S}}^{\mathrm{theo}}$, kg m^{-1} MPa^{-1} s^{-1}) was obtained from $K_{\mathrm{h}}^{\mathrm{theo}}$ by dividing through the microscopically determined xylem cross-sectional area without bark and pit, and theoretical leaf area-specific hydraulic conductivity ($K_{\mathrm{L}}^{\mathrm{theo}}$, kg m^{-1} MPa^{-1} s^{-1}) by division of $K_{\mathrm{h}}^{\mathrm{theo}}$ by the total supported leaf area (A_{L}).

Statistical analyses

A principal-component analysis (PCA) was done to evaluate how aboveground growth performance, wood anatomical and leaf traits are associated among each other using the package CANOCO, version 4.5 (Biometris, Wageningen, the Netherlands). The matrix species factors were lumen area (A_{lumen}), vessel density (VD), hydraulically weighted vessel diameter (d_{h}), stem basal increment (BAI), empirical ($K_{\mathrm{S}}^{\mathrm{emp}}$) as well as theoretical hydraulic conductivity ($K_{\mathrm{S}}^{\mathrm{theo}}$). All other statistical calculations were done with the R software package, version 3.1.0 (R Development Core Team, 2014). Pearson correlations were calculated for all pairwise combinations of wood anatomical properties, wood density and hydraulic traits. In case of non-linear relationships where the data are presented on a log-linear scale, the data were log10 transformed to achieve normal distribution before further statistical analyses were conducted. Comparisons of hydraulic and leaf traits among organs were conducted using mixed linear models (lme, package: 'nlme' and lm package: 'stats') with species as random factor to account for pseudo-replication. Predicted random effects and residuals of the models were checked for normal distribution and homoscedasticity using diagnosis plots and dependent variables were log-transformed and/or variance functions (varIdent or varExp) were used (Pinheiro and Bates, 2000) when necessary. Subsequently, multiple comparison tests between group means were tested post-hoc with Tukey HSD tests (glht package: ‘multcomp’). In case of heteroscedasticity an adjusted statistical framework for simultaneous inference and robust covariance estimators (Herberich et al., 2010) was used to account for different variances between groups. To test the best predictor for aboveground growth performance we applied stepwise backward model selection (step.AIC, package: ‘MASS’) to identify the most parsimonious model, defined as the model with the lowest AIC (Akaike information criterion) score (Burnham and Anderson, 2002) including K_S^{theo}, WD, N_{leaf}, $\delta\ ^{13}C$ as well as species affiliation (whether it is perhumid or seasonal) and their interactions as explanatory variables.

Table 5.1: List of major variables with definition and units employed.

Symbol	Unit	Definition
H	cm	Tree height
DBH	cm	Diameter at breast height
AGB	kg	Aboveground biomass
BAI	$cm^2\ yr^{-1}$	Basal area increment
WD	$g\ cm^{-3}$	Wood density
d	µm	Vessel diameter
d_h	µm	Hydraulically weighted vessel diameter
VD	$n\ mm^{-2}$	Vessel density
A_{lumen}	%	Relative vessel lumen area (lumen to sapwood area ratio)
A_{cross}	mm^2	Branch cross sectional area
A_{xylem}	mm^2	Branch sapwood area
K_S^{emp}	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Empirical sapwood area-specific hydraulic conductivity
K_S^{theo}	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Theoretical sapwood area-specific hydraulic conductivity
K_L^{emp}	$10^{-4}\ kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Empirical leaf area-specific hydraulic conductivity
K_L^{theo}	$10^{-4}\ kg\ m^{-1}\ MPa^{-1}\ s^{-1}$	Theoretical leaf area-specific hydraulic conductivity
N_{leaf}	$g\ kg^{-1}$	Foliar mass-specific nitrogen content
SLA	$cm^2\ g^{-1}$	Specific leaf area
HV	$10^{-4}\ m^2\ m^{-2}$	Sapwood to leaf area ratio (Huber value)
$\delta^{13}C$	‰	Carbon isotope signature

5.3 Results

Tree size and aboveground growth performance

The variability in mean aboveground biomass (AGB) between the studied species was high, ranging between 16.9 kg in *T. cacao* and 888.2 kg in *L. leucocephala* reflecting marked differences in height and diameter between the pruned *T. cacao* and *G. sepium*, and the other four shade tree species (Table 5.2).

Table 5.2: Tree height (H), diameter at breast height (DBH), wood density (WD), aboveground biomass (AGB) and basal area increment (BAI) of the six tree species in cocoa agroforests. Shown values are means ± SE and the number of investigated tree individuals. * For BAI, however, only three tree individuals of *Gnetum gnemon*, two of *Leucaena leucocephala*, and one of *Erythrina subumbrans* were available (see Material and Methods section).

Species	Code	n	H (m)	DBH (cm)	WD (g cm^{-3})	AGB (kg)	BAI (cm^2 yr^{-1})
Perhumid							
Theobroma cacao	Th_ca	6	5.83 ± 0.37	11.36 ± 0.45	0.398 ± 0.007	16.89 ± 2.14	6.51 ± 1.92
Durio zibethinus	Du_zi	6	14.10 ± 1.44	25.56 ± 4.03	0.430 ± 0.019	230.65 ± 72.72	67.99 ± 20.03
Gnetum gnemon	Gn_gn	6	12.40 ± 0.30	18.73 ± 1.63	0.591 ± 0.013	131.80 ± 20.71	28.34 ± 9.71
Seasonal							
Gliricidia sepium	Gl_se	6	10.90 ± 0.56	11.68 ± 0.51	0.601 ± 0.029	45.75 ± 3.67	19.02 ± 4.83
Leucaena leucocephala	Le_le	6	13.75 ± 2.07	36.30 ± 8.61	0.609 ± 0.010	888.20 ± 320.79	87.61 ± 28.87
Erythrina subumbrans	Er_su	6	10.06 ± 0.58	33.05 ± 2.29	0.273 ± 0.008	162.03 ± 20.88	10.18*

L. leucocephala was on average more than two times higher and larger compared to *T. cacao*; the other four species ranged between these two extremes even though all trees were planted at the same time. Stem wood density (WD) varied by a factor of two across the six tree species with *E. subumbrans* showing the lowest WD and *G. sepium* and *L. leucocephala* showing the highest WD values. BAI numbers were thus very different across the six tree species and ranged from 6.5 and 10.2 cm^2 yr^{-1} in *T. cacao* and *E. subumbrans*, respectively, to 68 and 88 cm^2 yr^{-1} in *D. zibethinus* and *L. leucocephala*, respectively. AGB was found to be a very good predictor for the annual basal area increment (BAI) amongst all species (Figure 5.1).

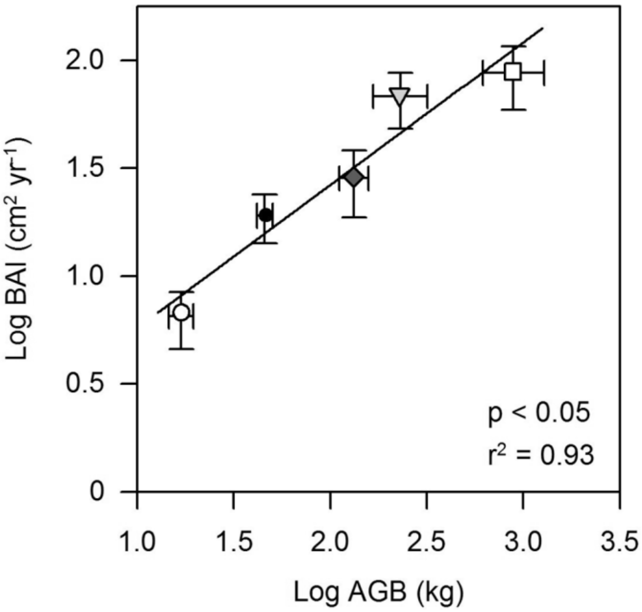

Figure 5.1: Relationship between stem basal area increment (BAI) of cacao and four shade tree species and aboveground biomass (AGB). Each symbol represents mean values for each tree species (○ Th_ca; ▽ Du_zi; ◆ Gl_se; □ Le_le; ● Gn_gn). Error bars indicate ± SE.

Changes in hydraulic conductivity along the water flow path

The empirically determined sapwood area-specific hydraulic conductivity (K_S^{emp}) of root segments differed by a factor of 100 across species with *E. subumbrans* showing the highest values by far, whereas the smallest values were observed in roots of *T. cacao* (Figure 5.2, Table A 5.2).

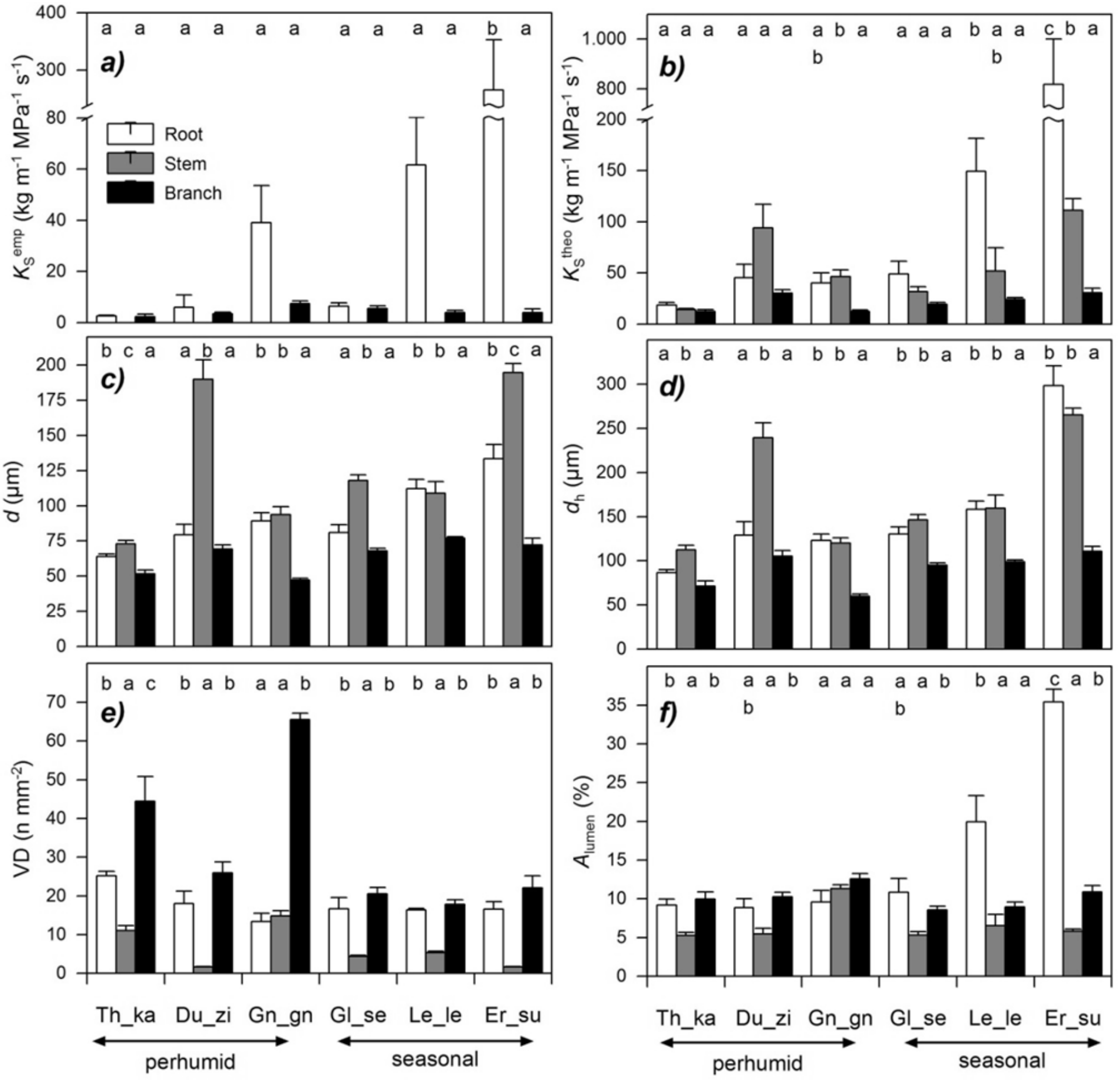

Figure 5.2: Hydraulic characteristics – a) empirical sapwood area-specific hydraulic conductivity (K_S^{emp}), b) theoretically calculated sapwood area-specific hydraulic conductivity (K_S^{theo}), c) vessel diameter (d), d) hydraulically weighted vessel diameter (d_h), e) vessel density (VD), and f) lumen area (A_{lumen}) - of six cacao agroforestry species (Th_ca; Du_zi; Gn_gn; Gl_se; Le_le; Er_su) among root (white bars), stem (grey bars) and branch xylem (black bars). Error bars indicate ± SE.

The differences in K_S^{emp} of branches across species were much less pronounced (2.3 to 7.4 kg m^{-1} MPa^{-1} s^{-1}) with *G. gnemon* showing the highest and *T. cacao* the lowest numbers. Overall, root segments always showed higher hydraulic conductivities than branches (‘lme’; $p < 0.001$). Furthermore, K_S^{emp} values (in both root and branch segments) were always smaller than the theoretically calculated hydraulic conductivity

(K_S^{theo}) as derived from vessel diameters by Hagen-Poiseuille's law. Even though branch and root segments around 30 cm lengths were used, probably open-cut vessels could not be avoided particularly for root segments of *E. subumbrans*. However, mean K_S^{emp} values reached 9-45% of respective K_S^{theo} values indicating that open-cut vessels were negligible for most species, except for *G. gnemon* where 50-81% of respective K_S^{theo} values were measured (Figure 5.2). Empirically measured and calculated specific conductivity in root segments showed a positive linear relationship ('lme'; $p < 0.001$), but not for branch segments ('lme'; $p = 0.71$).

Anatomical differences across species in root, stem, and branch wood properties

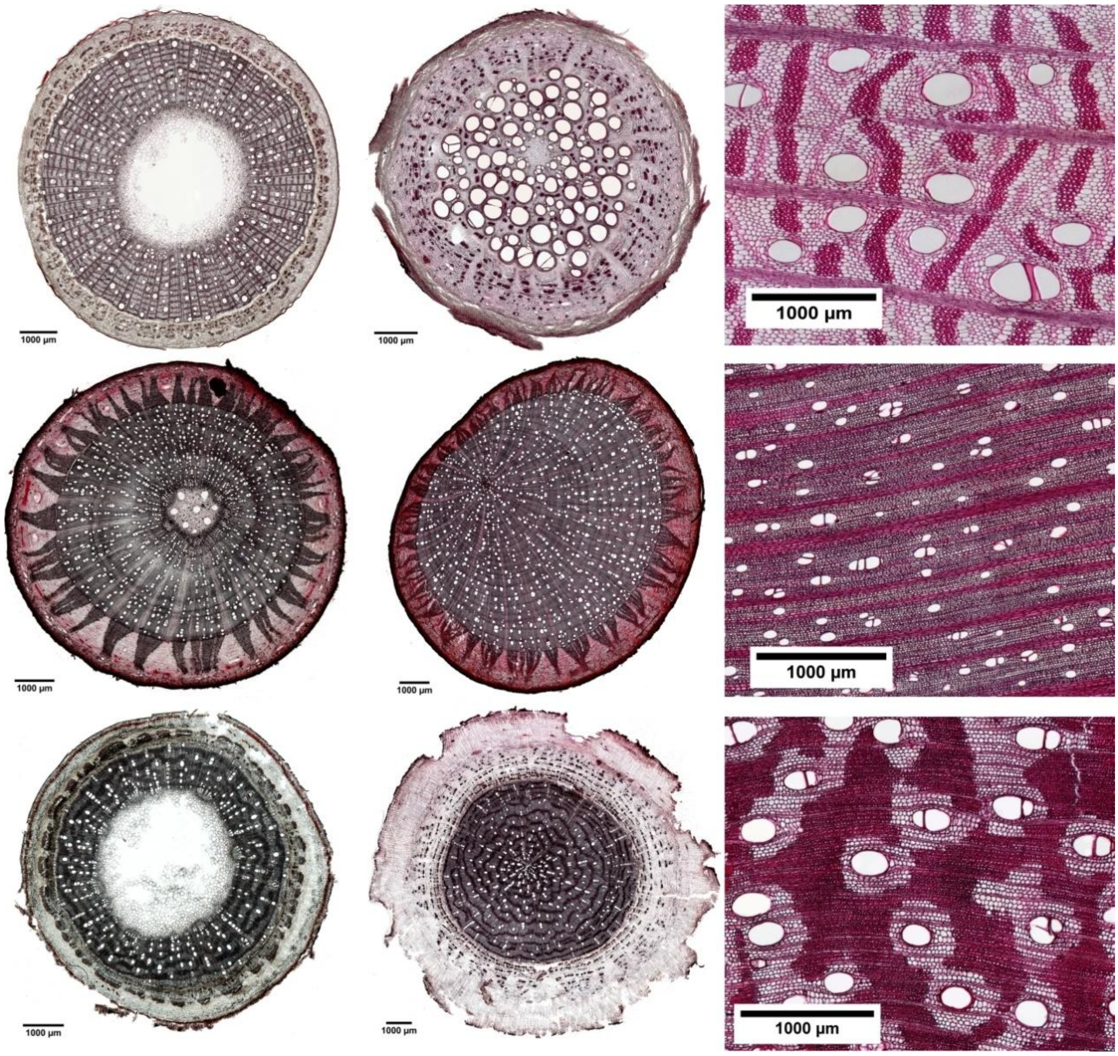

Figure 5.3: Cross-sections of different tree parts along the flow path: branch (left row), roots (middle row) and stems (right row) for three common tree species from cocoa agroforests in Sulawesi, Indonesia. *Erythrina subumbrans* (upper line), *Theobroma cacao* (middle line) and *Gliricidia sepium* (lower line). The scale bars are presented in the figures and black bars represent 1000 µm.

We found considerable variation in wood anatomical and derived hydraulic traits along the flow path from root, to stem and branch wood for all six species. Exemplary pictures for this variation from three of the species are given in Figure 5.3. In four of the six species average vessel diameter (*d*) was significantly largest in the stem and not in the root wood; in the remaining two species *d* was comparable between root and stem wood (Figure 5.2). Along the flow path smallest vessels were always observed in the branch wood of all species with the exception of *D. zibethinus* (Figure 5.2). The same pattern was observed for the hydraulically weighted vessel diameter (d_h) for branch wood, while the differences in d_h between root and stem wood were only significant in *T. cacao* and *D. zibethinus*. In general, several wood anatomical and derived hydraulic traits allowed a grouping between the three perhumid tree species originating from strictly wet tropical environments, and the three seasonal tree species reported to tolerate moderate droughts. As mentioned above, d_h was not significantly higher in stem than in root wood for the three seasonal tree species, and vessel density (VD) was comparable between root and branch wood and did not differ significantly. On the other hand, highest vessel densities were observed in the branch wood of all perhumid tree species, although differences were only significant in two of the three species. However, when comparing the two groups (perhumid vs. seasonal) significant differences were found (‘lme’; $p < 0.001$). In general, VD varied considerably between the organs and species as well and was found to decrease in the order branch – root – stem across all six species (Figure 5.2). Variation in VD numbers was lowest (factor < 2) in the root xylem and highest (factor > 10) in the stem xylem. VD decreased exponentially with increasing vessels diameter; we therefore concentrate on changes in *d* along the flow path in the following (Figure 5.4).

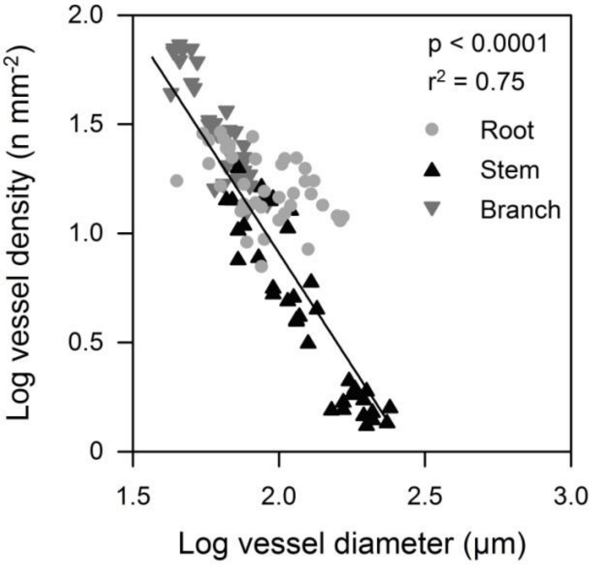

Figure 5.4: Mean vessel diameter in relation to vessel density in tree organs (roots, stems and branches) along the flow path for the six tree species.

Relative vessel lumen area (A_{lumen}), i.e. the ratio of lumen to sapwood area, was lowest in the stem wood in all species except of *G. gnemon* (Figure 5.2). Root and branch wood showed therefore higher A_{lumen} values that tended to show similar dimensions with the exception of the seasonal tree species that showed significantly higher A_{lumen} values in the root segments.

When concentrating on hydraulic properties we found a similar pattern in K_S^{theo}, where hydraulic conductivity was highest in roots of seasonal tree species ('lme'; $p < 0.001$), while there is no overall significant difference between the root and stem wood in the perhumid species ($p > 0.05$).

Leaf morphological, chemical and hydrological properties

Specific leaf area (SLA) of sun-exposed leaves was higher by roughly a factor of two in *E. subumbrans*, *G. sepium* and *L. leucocephala* than in *D. zibethinus*, *T. cacao*, and *G. gnemon* (Table 5.3). The sapwood to leaf area ratio ('Huber value', HV) of the sun-lit branch samples was lowest in *G. sepium* and *T. cacao*, and highest in *E. subumbrans*. Empirical leaf area-specific hydraulic conductivity (K_L^{emp}) in these branch samples showed a large variation across species ranging from 1.2 10^{-4} kg m^{-1} MPa^{-1} s^{-1} in *T. cacao* over 4.3-4.8 10^{-4} kg m^{-1} MPa^{-1} s^{-1} in *D. zibethinus*, *G. sepium*, *E. subumbrans*, and *L. leucocephala* to 14.2 10^{-4} kg m^{-1} MPa^{-1} s^{-1} in *G. gnemon*. The variation in theoretical leaf area-specific hydraulic conductivity (K_L^{theo}) derived from the wood anatomical properties was less pronounced. Lowest values were found in *T. cacao*, followed by *G. sepium*, while the other four tree species had ca. 2-5 times higher K_L^{theo} values (Table 5.3).

Table 5.3: Leaf morphological, hydraulic, and chemical properties of the six investigated tree species. Values are means ± SE; the number of investigated trees and measured samples (in parentheses) is also given. Different small letters indicate differences between species. See Table 5.1 for definition of abbreviations.

Species	**SLA** **(cm^2 g^{-1})**	**HV** **(m^2 m^{-2})**	**$K_L^{\mathrm{emp}} \times 10^{-4}$** **(kg m^{-1} MPa^{-1} s^{-1})**	**$K_L^{\mathrm{theo}} \times 10^{-4}$** **(kg m^{-1} MPa^{-1} s^{-1})**	**N_{leaf}** **(g kg^{-1})**	**$\delta^{13}C$** **(‰)**
Perhumid						
T. cacao	125.76 ± 8.38 a 3 (9)	1.34 ± 0.33 a 6	1.23 ± 0.75 a 2	9.90 ± 1.89 a 6	1.87 ± 0.25 a 6 (18)	-29.45 ± 0.39 ab 6 (18)
D. zibethinus	124.74 ± 12.19 a 3 (9)	3.07 ± 0.99 a 6	4.27 ± 0.92 a 6	51.11 ± 13.18 b 6	2.28 ± 0.25 a 6 (18)	-29.87 ± 0.46 a 6 (18)
G. gnemon	146.75 ± 5.35 a 3 (9)	2.90 ± 0.71 a 6	14.23 ± 4.22 b 6	29.81 ± 10.57 ab 6	2.69 ± 0.21 ab 6 (18)	-29.83 ± 0.42 a 6 (18)
Seasonal						
G. sepium	271.48 ± 19.74 b 3 (9)	1.72 ± 0.26 a 6	4.29 ± 1.09 a 6	13.31 ± 1.97 ab 6	3.35 ± 0.17 bc 6 (18)	-29.09 ± 0.19 a 6 (18)
L. leucocephala	293.2 ± 21.3 b 3 (6)	2.07 ± 0.52 a 6	4.79 ± 0.81 a 6	47.16 ± 11.23 ab 6	3.59 ± 0.12 c 6 (18)	-27.93 ± 0.08 c 6 (18)
E. subumbrans	264.38 ± 11.11 b 3 (9)	3.91 ± 1.40 a 6	4.76 ± 1.69 a 6	38.25 ± 14.05 ab 6	3.59 ± 0.14 c 6 (18)	-27.89 ± 0.28 bc 6 (18)

Mass-specific foliar nitrogen concentration (N_{leaf}) was lowest in *T. cacao*, medium high in *D. zibethinus* and *G. gnemon*, and highest in the three seasonal species *G. sepium*, *L. leucocephala* and *E. subumbrans* (Table 5.3). Variation in leaf carbon isotopic composition was rather small. The two species *E. subumbrans* and *L. leucocephala* revealed a ca. 1.0-1.8 higher $\delta\,^{13}$C value than the four other species that did not show significant differences in this variable.

Interrelationships between vascular properties, tree stem growth and hydraulic conductivity

A principal component analysis (PCA) on the inter-relationships between the investigated traits explained a large proportion of the total variance of the data set along the first four axes (Table 5.4).

Table 5.4: Results of a Principal Components Analysis (PCA) on the response of six agroforestry tree species with respect to stem basal area increment, anatomical properties of the coarse root, stem and branch wood as well as hydraulic and leaf traits. Given are the loadings of the selected variables along the four main explanatory axes as well as the cumulative r^2 values (in brackets) for a given variable. Numbers below the four axes indicate the eigenvalues (EV) of the axes. Numbers in bold indicate the variables with the closest relation to the respective axis.

	Axis 1		**Axis 2**		**Axis 3**		**Axis 4**	
	EV 0.46		**EV 0.21**		**EV 0.16**		**EV 0.12**	
AGB	0.31	(0.10)	-0.25	(0.16)	**0.87**	(0.93)	0.06	(0.93)
DBH	**0.81**	(0.65)	0.08	(0.65)	0.54	(0.94)	0.06	(0.94)
BAI	0.17	(0.03)	-0.09	(0.04)	**0.83**	(0.72)	0.52	(1.00)
WD	-0.58	(0.34)	-0.05	(0.34)	**0.75**	(0.90)	-0.11	(0.94)
$A_{\text{lumen root}}$	**0.90**	(0.81)	-0.03	(0.81)	-0.03	(0.81)	-0.42	(0.99)
$A_{\text{lumen stem}}$	-0.29	(0.08)	**0.79**	(0.70)	0.43	(0.88)	-0.32	(0.98)
$A_{\text{lumen branch}}$	-0.12	(0.01)	**0.93**	(0.88)	-0.11	(0.90)	0.21	(0.94)
$d_{\text{h root}}$	**0.92**	(0.84)	0.13	(0.86)	-0.11	(0.87)	-0.36	(1.00)
$d_{\text{h stem}}$	**0.91**	(0.82)	0.11	(0.83)	-0.17	(0.86)	0.32	(0.97)
$d_{\text{h branch}}$	**0.82**	(0.68)	-0.37	(0.81)	0.04	(0.82)	0.27	(0.89)
$K_{\text{S root}}^{\text{theo}}$	**0.88**	(0.77)	0.10	(0.78)	-0.26	(0.84)	-0.39	(1.00)
$K_{\text{S stem}}^{\text{theo}}$	**0.88**	(0.78)	0.36	(0.91)	-0.05	(0.92)	0.27	(0.99)
$K_{\text{S branch}}^{\text{theo}}$	**0.89**	(0.79)	-0.09	(0.80)	0.06	(0.80)	0.39	(0.95)
$K_{\text{S root}}^{\text{emp}}$	**0.85**	(0.72)	0.18	(0.76)	-0.18	(0.79)	-0.45	(0.99)
$K_{\text{S branch}}^{\text{emp}}$	-0.29	(0.08)	**0.66**	(0.52)	0.31	(0.62)	-0.40	(0.78)
$K_{\text{L}}^{\text{emp}}$	-0.21	(0.04)	**0.87**	(0.79)	0.35	(0.92)	-0.27	(0.99)
$K_{\text{L}}^{\text{theo}}$	**0.78**	(0.61)	0.39	(0.76)	0.26	(0.83)	0.41	(1.00)
HV	**0.77**	(0.59)	0.64	(0.51)	-0.02	(0.70)	0.05	(0.98)
N_{leaf}	-0.23	(0.05)	**0.68**	(0.51)	-0.44	(0.70)	0.53	(0.98)
$\delta^{13}C$	**0.71**	(0.50)	-0.41	(0.67)	0.28	(0.74)	-0.49	(0.99)

The first axis was strongly positively associated with all wood anatomical traits (incl. HV and δ ^{13}C), but negatively with WD. Axis 1 was furthermore positively related to DBH. Axis 2 was strongly associated with stem and branch lumen area as well as with the leaf traits (K_L^{emp} and N_{leaf}). In contrast to K_S^{emp} in root segments, branch K_S^{emp} was associated with axis 2 and therefore showed an inter-relationship with K_L^{emp}. BAI showed an only moderate association with the first axis and thus was only weakly correlated with the majority of wood anatomically and tree structural variables. BAI was correlated best with the third axis that was only associated with the variables AGB, DBH and WD (positively), as well as root K_S^{theo} and K_S^{emp} (negatively). A Pearson's coefficient of correlation analysis, however, revealed a strong relationship between BAI and K_S^{theo} on a species level for root, stem, and branch wood tissue (Figure 5.5 a-c).

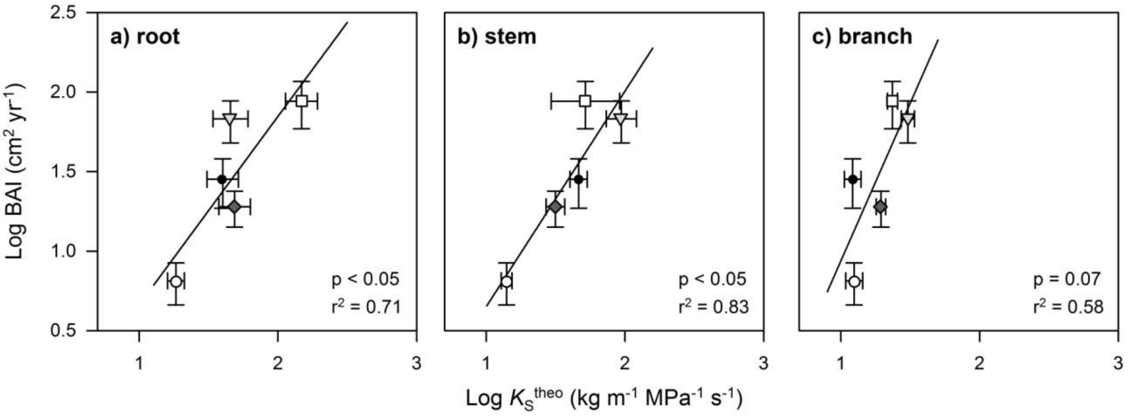

Figure 5.5: Relationship between stem basal area increment (BAI) of cacao and four shade tree species and theoretically calculated cross sectional sapwood area-specific hydraulic conductivity (K_S^{theo}) in the root (a), stem (b) and branch wood (c). Each symbol represents mean values for each tree species (○ Th_ca; ▽ Du_zi; ◆ Gl_se; □ Le_le; ● Gn_gn). Error bars indicate ± SE.

A systematic correlation analysis of pairs of traits confirmed that most of the inter-relationships identified in the PCA on a species level were also valid on a tree individual level (Table 5.5).

Table 5.5: Pearson's coefficients of correlation between pairs of traits (n = 36). Highly significant correlations are shown in bold ($p < 0.001$), non-significant correlations ($p > 0.05$) are n.s. The correlation analysis was based on comparisons on a tree individual level.

	BAI	AGB	DBH	WD	A_{lumen} root	A_{lumen} stem	A_{lumen} branch	$d_{\text{h root}}$	$d_{\text{h stem}}$	$d_{\text{h branch}}$	K_S^{theo} root	K_S^{theo} stem	K_S^{theo} branch	K_S^{emp} branch	K_S^{emp} root	K_L^{emp}	K_L^{theo}	HV	$\delta^{13}C$
AGB	**0.77**																		
DBH	**0.82**	**0.93**																	
WD	*n.s.*	*n.s.*	*n.s.*																
$A_{\text{lumen root}}$	*n.s.*	*n.s.*	0.45	-0.41															
$A_{\text{lumen stem}}$	*n.s.*	0.38	*n.s.*	0.37	*n.s.*														
$A_{\text{lumen branch}}$	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.36													
$d_{\text{h root}}$	*n.s.*	0.34	0.47	-0.38	**0.83**	*n.s.*	*n.s.*												
$d_{\text{h stem}}$	0.63	0.50	**0.64**	-0.52	0.55	*n.s.*	*n.s.*	**0.68**											
$d_{\text{h branch}}$	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.45	*n.s.*	*n.s.*	0.52	**0.80**										
K_S^{theo} root	*n.s.*	0.35	0.49	-0.40	**0.94**	*n.s.*	*n.s.*	**0.97**	**0.64**	0.50									
K_S^{theo} stem	**0.70**	**0.68**	**0.73**	*n.s.*	0.48	0.36	*n.s.*	**0.64**	**0.87**	**0.59**	**0.59**								
K_S^{theo} branch	0.48	*n.s.*	0.35	*n.s.*	0.40	*n.s.*	*n.s.*	0.44	**0.79**	**0.86**	0.44	**0.66**							
K_S^{emp} branch	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*						
K_S^{emp} root	*n.s.*	*n.s.*	0.42	*n.s.*	**0.66**	0.36	*n.s.*	**0.74**	*n.s.*	*n.s.*	**0.75**	0.46	*n.s.*	*n.s.*					
K_L^{emp}	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.43	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	**0.75**	*n.s.*				
K_L^{theo}	*n.s.*	0.44	0.44	*n.s.*	0.35	*n.s.*	*n.s.*	0.42	**0.58**	0.54	0.40	**0.66**	**0.64**	*n.s.*	*n.s.*	*n.s.*			
HV	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.40	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.35	*n.s.*	*n.s.*	*n.s.*	0.43	**0.82**		
$\delta^{13}C$	*n.s.*	*n.s.*	*n.s.*	*n.s.*	**0.58**	*n.s.*	*n.s.*	0.38	*n.s.*	*n.s.*	0.49	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	
N_{leaf}	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.54	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	-0.40

BAI was strongly interrelated with AGB as well as DBH and showed moreover a significant correlation with stem d_h and stem K_S^{theo}. None of these three variables were correlated with WD that generally showed only few and moreover relatively low correlations with other variables in the Pearson correlation analysis. Mixed effect models incorporating the pseudo-replication due to species confirmed that WD does not explain neither K_S^{theo}, d_h nor BAI in our data well ('lme'; $p > 0.05$).

Contrary to significant relationships of stem wood K_S^{theo} with AGB, BAI and DBH, no relationship of K_S^{emp} between any of these traits could be found, except for K_S^{emp} in root segments that were related to DBH.

As expected, all species and organs showed a positive relationship between K_S^{theo} and d_h (Table 5.5). Foliar nitrogen content (N_{leaf}) as well as the carbon isotope signature ($\delta\ ^{13}C$) did not show any relation with neither leaf area-specific hydraulic conductivity (K_L^{theo}), K_S^{emp} nor Huber value (HV), but a strong significant correlation within each other. N_{leaf} was unrelated to BAI among species ($p > 0.1$, $r = 0.05$) also when excluding the three seasonal species. Stepwise model selection confirmed that K_S^{theo} is the best predictor for AGB together with WD and neither N_{leaf}, $\delta\ ^{13}C$ nor K_S^{emp} were explaining the variability in our data significantly.

5.4 Discussion

Patterns in xylem anatomy among species in stem, root and branch wood

Most studies on hydraulic anatomical properties in trees describe vessel sizes to be largest in roots and basipetally taper to the branches (Tyree and Zimmermann, 2002; McElrone et al., 2004; Goncalves et al., 2007; Domec et al., 2009; Lintunen and Kalliokoski, 2010). The first notification of this paradigm even goes back to observations by Nehemiah Grew in the 17th century (Baas, 1982). Generally, variation in conduit diameter is a compromise between hydraulic efficiency, safety and the maximization of conductivity per growth investment due to conduit tapering (Sperry et al., 2008; Sperry et al., 2012). As concluded by Tyree and Zimmermann (2002) the reason for conduit tapering is the control of water distribution, and more importantly to counter increases in flow resistance and gravimetrically forces with tree height to minimize the increasing risk of xylem dysfunction with path length (West et al., 1999; Anfodillo et al., 2006; Sperry et al., 2012). This is additionally mirrored in the meanwhile commonly observed relation between conduit size and vulnerability to cavitation (Wheeler et al., 2005; Maherali et al., 2006; Cai et al., 2010; Domec et al., 2010; Sterck et al., 2012). It is argued that in roots water stress will not be as great as in stems, since water potentials drop in going from root to stem to leaf (Tyree and

Zimmermann, 2002). As long as soil water is still extractable, roots would then be less exposed to drought-induced embolism and might therefore afford larger vessels. Furthermore, with a small need of structural support and embedded in a soil matrix, biomechanical stress is unlikely to affect roots (McElrone et al., 2004; Pratt et al., 2007). Additionally, most plants have developed a mechanism to restore vessel functionality by refilling embolized vessels through living rays and paratracheal parenchyma. The contribution of paratracheal parenchyma was recently shown for grapevine by Brodersen et al. (2010), while the molecular and physiological paths were investigated by Chitarra et al. (2014). As coarse roots are located close to the water source it seems beneficial to restrict hydraulic failure to areas within the complex hydraulic network that are easily refilled. Embolism reversal is thought to occur by active transport of sugars into empty conduits, which are generally accumulated in high amounts within a trees rooting system (Würth et al. 2005).

Our results are in contrast to the common assumption as we found the largest vessels along the flow path in the stem xylem and not in the roots. Supporting our first hypothesis, our results are in accordance with the observations of a hump-shaped vessel size distribution along the flow path found in tropical trees of Indonesia (Schuldt et al., 2013), supported by findings from South America where the largest vessels were observed in the stem wood (Machado et al. 2007) or comparing just root and branch wood both organs showed similar vessel sizes (Fortunel et al., 2013). Our confirmative finding could be a response to permanent water availability and low evaporative demand in this humid region, where trees without severe drought limitation might have developed roots with large relative lumen area and less structural tissue that can achieve sufficiently high axial conductivities in these organs. Thereby they would compensate for the smaller vessel diameters in roots than in the trunk in accordance with the pipe model theory by Shinozaki et al. (1964). Originally, this theory attempted to explain plant architecture in a quantitative way by proposing that photosynthetic organs should be supported by an adequate structure of non-photosynthetic organs in order to guarantee functionality (Chiba, 1998). Nevertheless, one has to keep in mind that the pipe model theory is not a hydraulic model, but should be viewed as a biomass allometry model with no particular implications concerning either hydraulics or biomechanics as proposed by McCulloh and Sperry (2005).

Machado et al. (2007) argued that shallow roots of moist tropical forest species, which is a common rooting pattern in tropical moist forests (Leuschner et al., 2006; Hertel et al., 2009), are subjected to variations in water availability and the narrower vessels in the root wood are a safety trade-off against cavitation. However, the vessel sizes found in coarse roots in the present study as well as in other tropical studies (Machado et al., 2007; Fortunel et al., 2013; Schuldt et al., 2013) are at least 30% larger compared to e.g. temperate forest tree species (Köcher et al., 2012), and therefore might not directly be rated as an increased safety against cavitation compared to the stem or branch wood. It seems rational to assume that not the coarse root xylem, despite large vessel sizes, represents the most drought-sensitive organ, but rather that of fine roots with smaller diameter. In contrast to coarse roots, which are primarily responsible for axial water transport, fine roots represent the highest resistance for water transport within the rooting system due to radial water flow either along the apoplastic or cellular pathway (Steudle, 2000). As the most distal organs they are scarified in response to drought in order to avoid serious harm to coarse and large roots like it has been observed in various temperate and boreal forests (Gaul et al., 2008; Chenlemuge et al., 2013; Hertel et al., 2013). Fine roots might thereby act as a sort of 'hydraulic fuse', which evolved from Zimmermann's segmentation hypothesis (Tyree and Zimmermann, 2002) in analogy to the leaf petiole (Zufferey et al., 2011). At the root level this 'hydraulic segmentation' might additionally protect the below-ground system preventing the reverse water flow from main to lateral roots and back to the dryer soil as discussed for grapevine by Losivolo et al. (2008). Woody plants would accordingly restrict hydraulic failure to redundant organs that are readily replaced (Sperry et al., 2002) although it has been argued that the term 'hydraulic fuse' should be reconsidered since roots are not necessarily an 'expandable' organ (Gonzales-Benecke et al., 2010). The construction costs of fine roots and lignified small-diameter roots in term of carbon and nutrients may not be much smaller than for twigs and leaves, and the loss of roots is directly related to the loss of absorption capacity for nutrients and water. However, comparable data on fine root mortality and percentage loss of conductivity in coarse roots that would empirically support the idea that fine root are sacrificed in order to protect the hydraulic system are to our knowledge not available so far.

Concurrently with decreasing vessel size, conduit frequency is generally reported to increase from the roots to the branches (e.g. Lintunen and Kalliokoski, 2010). This commonly observed trade-off between vessel density and vessel diameter (Preston et al., 2006; Sperry et al., 2008; Zanne et al., 2010) could not be confirmed in our study where the stem wood showed by far the lowest vessel density compared to roots and branches. Since flow in capillary systems is proportional to the fourth power of vessel radius according to Hagen-Poiseuille law, variations in vessel diameter has a much greater effect on K_S^{theo} than variations in vessel density. However, due to the occurrence of a higher relative vessel lumen area and a few large vessels in roots we have observed that specific conductivity in the three seasonal species, i.e. *G. sepium*, *E. subumbrans and L. leucocephala*, was higher in roots than in stems, even though the largest vessels were observed in the stem wood. At least for *E. subumbrans and L. leucocephala* this pattern could additionally be explained by the highest relative vessel lumen area found in roots, i.e. less space was occupied by tracheids or fibers compared to the stem or branch wood. Furthermore, disproportionally high empirical conductance measured in *E. subumbrans* might be attributed to the presence of open-cut vessels, which are highly conductive as water does not have to pass pit membranes, which generally account for more than 50% of the total hydraulic resistance (Choat et al. 2008). However, since tree hydraulic traits have been associated with general habitat preferences of various species (Sperry, 2000; Maherali et al., 2004), this finding could be due to the biogeographic background and could represent genetically determined adaptations to different water availability in the natural habitat of the species. While *T. cacao, D. zibethinus* and *G. gnemon* are known to be strictly wet tropical forest trees rather sensitive to drought and low air humidity (Brown, 1997; Carr and Lockwood, 2011), the other three species are reported to be fast-growing drought-resistant trees (Mrema et al., 1997; Fagbola et al., 2001). While drought resistance is recorded for some *Erythrina* species (da Silva et al., 2010; Manoharan et al., 2010), not many data are available on *E. subumbrans*, which is a species native to Indonesia. In a habitat where water stress is generally modest or absent such as the humid climate in Sulawesi, cavitation-avoiding mechanisms might be less beneficial than hydraulic efficiency and largest vessels can occur in stem xylem, thereby reducing the hydraulic resistance along the flow path. However, it remains speculative why the largest vessels along the flow path are observed in the root xylem only in biomes that frequently experience either drought- or frost stress. The size of a vessel is thought to be caused by the concentration of the plant hormone indole-3-acetic acid (IAA), an endogenous auxin, at the time of cell differentiation (Aloni 1987, Lovisolo et al. 2002), which is also related to the cambial age and related cambial activity as seen by the radial increase in vessel size at the stem base of a tree (Spicer and Gartner 2001). It would thus be of interest to extent the results of the present study to a quantification of IAA concentration in both coarse root and stem cambium in tropical and temperate trees; the latter should show higher concentrations in the root xylem independently of cambial age in agreement with the common paradigm that largest vessels are found in the rooting system.

Relationships between vascular properties, tree stem growth and hydraulic conductivity

Wood density (WD) is an easy to measure functional wood property that has been linked to various ecological and other functional traits. In species showing a relatively large fraction of vessels close to the hydraulically weighted mean vessel diameter (d_{h}), $K_{\mathrm{S}}^{\mathrm{theo}}$ should correlate negatively with WD (Bucci et al., 2004; Meinzer et al., 2008; Gonzalez-Benecke et al., 2010). Similar to observations on tropical forest trees from perhumid tropical environments (Poorter et al., 2010; Schuldt et al., 2013) we expected WD to be unrelated to wood anatomical and hydraulic properties. Even though we found a correlation between WD and d_{h} on tree level, this relationship could not be confirmed accounting for species pseudo-replication in mixed effect models. Also we found no significant relationship of WD to basal stem area increment, contradicting former results on a close relation between WD and growth for tropical trees (King et al., 2006; Poorter et al., 2010; Hietz et al., 2013). Several other studies report WD to be partially decoupled from hydraulic conductivity due to variation of frequency and size of fibers in angiosperms (Preston et al., 2006; Martinez-Cabrera et al., 2009; Zanne et al., 2010). Results on the relationship between WD and vascular properties as well as tree growth are thus partly conflicting; while some studies confirm that WD varies inversely with vessel size (Preston et al., 2006; Jacobsen et al., 2007; Thomas et al., 2007; McCulloh et al., 2011; Gleason et al., 2012), others did not support this finding (Martinez-Cabrera et al., 2009; Poorter et al., 2010; Russo et al., 2010; Zanne et al., 2010; Fan et al., 2012). These contradicting results are indicating that the relation between WD and growth or vessel traits is not necessarily interrelated and should be viewed separately. We further suspect that the relation between wood properties and tree hydraulics may depend as well on biogeographical origin and drought-adaptation strategy of the species investigated since convergent environmental factors such as water availability are known to lead to adaptations in functional wood anatomical properties (Swenson and Enquist, 2007; Gleason et al., 2013; Richardson et al., 2013).

We found wood anatomical and derived hydraulic properties to be a much better predictor for tree stem growth performance than WD as K_S^{theo} of the all tree organs studied were strongly positively correlated with stem basal area increment on a species level. This is in accordance with a growing body of studies showing strong links between growth rate and wood anatomical traits (Zhang and Cao, 2009; Poorter et al., 2010; Russo et al., 2010; Fan et al., 2012). In contrast, neither empirically measured branch and root K_S^{emp}, nor foliar $\delta\ ^{13}C$ or foliar nitrogen content were good predictors for aboveground growth performance.

We expected to find close correlations between functional leaf traits assumed to be associated with high aboveground productivity, i.e. high foliar N content and more negative foliar $\delta\ ^{13}C$, and stem increment in our samples. However, no such correlation was found. This is most likely explained by the fact that our sampled species contained several N-fixing legume species, our relatively low species number as well as due to the fact that our study was conducted in a perhumid region were drought stress is not to be expected.

5.5 Conclusions

Our study results suggest that even though vessel traits, growth performance and wood density relations follow distinct conceptually determined trade-offs, some of these long-established paradigms might not be uniformly applicable to tree species from all biogeographic regions presumably due to their varying drought adaptation strategies. In moist tropical environments we could not confirm the paradigm of continuous conduit tapering from roots to branches although some traits (vessel density, relative vessel lumen area and theoretical sapwood area-specific conductivity) enabled a clear separation between the three strictly wet tropical species and the three seasonal tree species. We therefore expect patterns in vessel traits along the flow path from roots to branches to be dependent on the long-term precipitation regime at the biogeographic origin of the investigated tree species. Furthermore and contrary to common knowledge, the investigated tree species did neither show a relationship between aboveground growth performance and wood density nor foliar nitrogen content, nor between wood density and vessel size. Instead, we found growth rate to be closely linked with wood anatomical and derived hydraulic traits. Future research should thus include a systematic approach to different biogeographic regions and cover a wider range of ecosystem types particularly underrepresented biomes.

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Appendix

Table A 5.1: Results from linear regression analyses between branch and root cross-sectional area (A_{cross}, mm^2) and corresponding xylem cross-sectional area (A_{xylem}, mm^2) without pith and bark for the eight tree species, and averaged across species for branches and roots. Given are sample number, intercept of the x- and y-axis, slope, p-value, coefficient of determination and the xylem to cross-sectional area ratio (A_{xylem} / A_{cross}, mean ± SE).

Species	**Organ**	**n**	**$A_{xylem} = a + b \times A_{cross}$**					
			y(0)	**a**	**b**	**p**	**r^2**	**A_{xylem} / A_{cross}**
Th_ka	branch	6	4.03	-2.0914	0.5196	<0.001	0.98	0.48 ± 0.01
Er_su	branch	6	12.61	-7.4852	0.5936	0.021	0.68	0.45 ± 0.04
Du_zi	branch	6	27.53	-18.8424	0.6844	0.001	0.94	0.49 ± 0.02
Gl_se	branch	6	7.42	-4.7291	0.6375	0.002	0.92	0.56 ± 0.04
Le_le	branch	6	-0.67	0.4622	0.6875	<0.001	0.99	0.70 ± 0.01
Gn_gn	branch	6	-2.54	1.6189	0.6378	0.001	0.96	0.66 ± 0.01
All	*branch*	*36*	*-0.91*	*0.5033*	*0.5507*	*<0.001*	*0.76*	*0.56 ± 0.02*
Th_ka	root	6	0.14	-0.0863	0.6161	<0.001	0.99	0.61 ± 0.01
Er_su	root	8	5.82	-2.6486	0.4547	<0.001	0.89	0.40 ± 0.02
Du_zi	root	8	3.25	-2.2785	0.7020	<0.001	0.96	0.64 ± 0.01
Gl_se	root	5	23.40	-13.1864	0.5636	0.016	0.72	0.42 ± 0.05
Le_le	root	6	-13.21	4.6253	0.3501	0.006	0.84	0.43 ± 0.02
Gn_gn	root	6	519.48	58.8047	-0.1132	0.225	0.15	0.25 ± 0.05
All 1)	*root*	*33*	*-0.84*	*0.4062*	*0.4830*	*<0.001*	*0.68*	*0.51 ± 0.02*

1) Gn_gn excluded from regression analysis.

Table A 5.2: Wood anatomical and hydraulic properties of the root, stem and branch wood of the six studied agroforestry tree species. Given are means ± SE and the number of investigated trees and measured samples (in parentheses). Lowercase letters indicate statistically significant differences between species within same organ and letters in parentheses indicate significant differences between organs within a given species.

	K_S^{emp} (kg m^{-1} MPa^{-1} s^{-1})	K_S^{theo} (kg m^{-1} MPa^{-1} s^{-1})	d (µm)	d_h (µm)	VD (n mm^{-2})	A_{lumen} (%)
Perhumid						
Theobroma cacao						
root	2.64 ± 0.3 a (a) 6 (6)	18.4 ± 2.56 a (a) 6 (6)	63.63 ± 2.01 a (b) 6 (6)	86.71 ± 3.22 a (a) 6 (6)	25.19 ± 1.11 b (b) 6 (6)	9.20 ± 0.76 a (b) 6 (6)
stem		14.03 ± 1.26 a (a) 6 (6)	72.88 ± 2.29 a (c) 6 (6)	112.18 ± 5.04 a (b) 6 (6)	11.04 ± 1.23 c (a) 6 (6)	5.29 ± 0.35 a (a) 6 (6)
branch	2.33 ± 0.94 a (a) 2 (4)	12.48 ± 1.74 a (a) 6 (6)	51.43 ± 2.77 a (a) 6 (6)	71.28 ± 5.88 a (a) 6 (6)	44.42 ± 6.39 bc (c) 6 (6)	9.95 ± 0.92 ab (b) 6 (6)
Durio zibethinus						
root	5.99 ± 4.8 a (a) 6 (8)	45.45 ± 12.87 ab (a) 6 (8)	79.13 ± 7.64 ab (a) 6 (8)	129.01 ± 15.35 ab (a) 6 (8)	18.01 ± 3.23 ab (b) 6 (8)	8.88 ± 1.12 a (ab) 6 (8)
stem		94.11 ± 23.14 bc (a) 6 (6)	189.81 ± 13.8 d (b) 6 (6)	239.45 ± 16.86 c (b) 6 (6)	1.66 ± 0.11 a (a) 6 (6)	5.46 ± 0.74 a (a) 6 (6)
branch	3.49 ± 0.61 a (a) 5 (5)	30.39 ± 3.32 b (a) 6 (6)	69.00 ± 2.98 bc (a) 6 (6)	105.19 ± 6.23 b (a) 6 (6)	25.95 ± 2.8 ab (b) 6 (6)	10.26 ± 0.59 ab (b) 6 (6)
Gnetum gnemon						
root	39.14 ± 14.45 a (a) 6 (7)	40.03 ± 10.18 ab (ab) 6 (6)	89.4 ± 5.73 b (b) 6 (6)	122.93 ± 7.39 b (b) 6 (6)	13.41 ± 2.13 a (a) 6 (6)	9.59 ± 1.50 ab (a) 6 (6)
stem		46.39 ± 6.53 b (b) 6 (7)	93.88 ± 5.5 b (b) 6 (7)	119.93 ± 6.14 ab (b) 6 (7)	14.85 ± 1.31 c (a) 6 (7)	11.32 ± 0.50 b (a) 6 (7)
branch	7.44 ± 1.07 a (a) 6 (7)	12.16 ± 1.66 a (a) 6 (6)	46.99 ± 1.42 a (a) 6 (6)	59.75 ± 2.54 a (a) 6 (6)	65.54 ± 1.65 c (b) 6 (6)	12.56 ± 0.70 b (a) 6 (6)
Seasonal						
Gliricidia sepium						
root	6.41 ± 1.29 a (a) 6 (8)	48.79 ± 12.49 ab (a) 6 (6)	81.05 ± 5.67 ab (a) 6 (6)	130.1 ± 8.35 b (b) 6 (6)	16.7 ± 2.84 ab (b) 6 (6)	10.85 ± 1.80 ab (ab) 6 (6)
stem		31.58 ± 4.82 b (a) 6 (6)	118.11 ± 3.85 c (b) 6 (6)	146.64 ± 5.76 b (b) 6 (6)	4.35 ± 0.3 b (a) 6 (6)	5.32 ± 0.42 a (a) 6 (6)
branch	5.54 ± 0.98 a (a) 6 (10)	19.44 ± 1.5 ab (a) 6 (6)	67.75 ± 1.88 b (a) 6 (6)	95.04 ± 2.41 b (a) 6 (6)	20.57 ± 1.65 a (b) 6 (6)	8.55 ± 0.52 a (b) 6 (6)
Leucaena leucocephala						
root	61.72 ± 22.77 a (a) 6 (6)	149.49 ± 32.24 b (b) 6 (6)	112.25 ± 6.54 bc (b) 6 (6)	158.51 ± 9.23 b (b) 6 (6)	16.4 ± 0.4 a (b) 6 (6)	19.93 ± 3.39 b (b) 6 (6)
stem		51.84 ± 22.93 ac (ab) 4 (4)	109.09 ± 8.14 bc (b) 4 (4)	159.85 ± 14.71 ab (b) 4 (4)	5.36 ± 0.4 b (a) 4 (4)	6.54 ± 1.43 ab (a) 4 (4)
branch	3.85 ± 0.97 a (a) 6 (6)	24.05 ± 1.99 b (a) 6 (6)	76.76 ± 1.03 c (a) 6 (6)	98.75 ± 2.24 b (a) 6 (6)	17.87 ± 1.11 a (b) 6 (6)	8.94 ± 0.64 a (a) 6 (6)
Erythrina subumbrans						
root	265.03 ± 87.86 b (b) 6 (8)	818.17 ± 181.89 c (c) 6 (8)	133.33 ± 10.11 c (b) 6 (8)	298.17 ± 22.34 c (b) 6 (8)	16.53 ± 1.97 a (b) 6 (8)	35.40 ± 1.65 c (c) 6 (8)
stem		111.45 ± 11.21 c (b) 6 (9)	194.54 ± 6.44 d (c) 6 (9)	265.14 ± 7.72 c (b) 6 (9)	1.71 ± 0.09 a (a) 6 (9)	5.82 ± 0.29 a (a) 6 (9)
branch	3.96 ± 1.42 a (a) 6 (7)	30.81 ± 4.2 b (a) 6 (6)	71.91 ± 4.99 bc (a) 6 (6)	110.6 ± 5.39 b (a) 6 (6)	22.09 ± 3.1 ab (b) 6 (6)	10.88 ± 0.82 ab (b) 6 (6)

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CHAPTER

6

Synopsis

Synopsis

The following chapter sections integrate the information from our four studies about carbon stocks, litter dynamics, net primary productivity, and wood hydraulic anatomy in Indonesia incorporating them into a wider context of tropical land-use change and consequences of forest conversion. The overall goal of this study was to test the hypotheses that forest conversion into cash-crop land-use systems such as oil palm or rubber plantations alters carbon storage, sequestration and nutrient dynamics in tropical lowlands. With water and nutrients generally being limiting plant growth resources, the present work was furthermore aimed at evaluating whether tree growth performance can be linked to wood hydraulic architecture and if there are differences between native and introduced tree species according to their drought adaptation strategies. Overall, implications for carbon and nutrient budgeting of these transformation systems as scientific basis for modeling approaches should be presented in this chapter as well as a contribution to the development of strategies for sustainable land-use management.

6.1 Changes in above- and belowground biomass and carbon stocks with forest transformation in lowlands of Sumatra

Converting diverse natural rainforests to agricultural systems in the tropics leads to profound changes in the structure as well as species compositions of the ecosystem. Numerous studies have investigated aboveground biomass and carbon stocks in tropical old-growth forests (e.g. Laumonier et al., 2010). However, comparisons of above- as well as belowground components integrating different land-use types and forest reference sites with the same methodological approach are scarce (Berenguer et al., 2014).

As hypothesized, transformation of rainforest in our study area on Sumatra clearly resulted in significantly lower total carbon stocks in all converted land-use types (*chapter 2*). Furthermore, we found structural parameters such as canopy cover, organic litter layer, and total basal area significantly reduced as a consequence of conversion to agricultural use. According to our estimations, natural forests in this region store three times more carbon in the tree biomass (195.2 ± 13.0 Mg C ha^{-1}) than even the extensively utilized jungle rubber system (77.49 ± 3.24 Mg C ha^{-1}). The total carbon pools comprising aboveground tree biomass, dead wood debris as well as coarse and fine roots in rubber and oil palm monocultures (38.32 ± 4.04 and 27.83 ± 2.09 Mg C ha^{-1}, respectively) consist of less than 20 % of the natural forest C stocks they are replacing (Fig. 6.1).

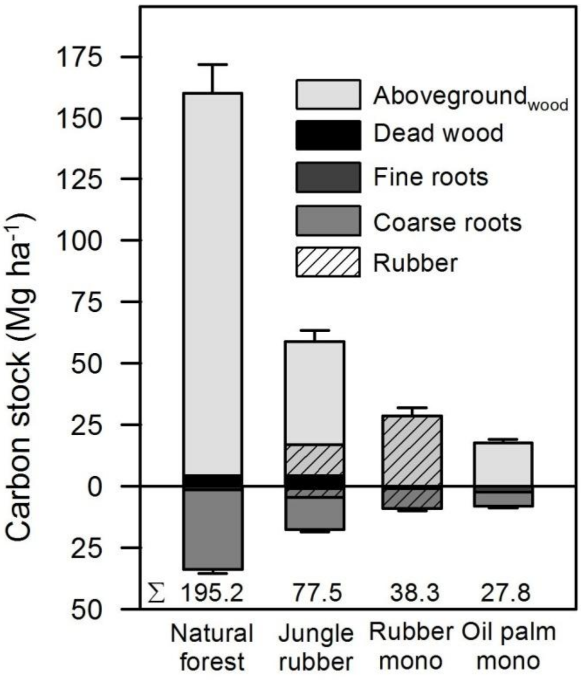

Figure 6.1: Above- and belowground carbon stock (Mg ha^{-1}) of the four land-use systems in Jambi, Sumatra. Shown are means ± SE (n = 8).

Among our investigated sites upper soil chemical parameters such as soil C:N and pH values did not vary distinctly, whereas base cation saturation showed high but non systematical variation. Even notable differences in soil structure composition between the two regions in Jambi Province, where we found higher sand component fractions in Harapan region, did not have influence on biomass and consequentially carbon stock of all systems similar to the other soil chemical variables.

Observed relatively low proportion of large trees in the forest reference sites can be attributed to former selective logging activities implicating even a higher carbon storage potential for undisturbed sites in the region. This might be one of the reasons why our total C stock estimates for forest reference sites (195.2 ± 13.0 Mg C ha^{-1}) were lower compared to other forests in Southeast Asia (Adachi et al., 2011, Katayama et al., 2013). Usually, dipterocarp rich forests native to lowlands in moist tropical Indonesia and Malaysia are reported to have the worldwide highest carbon densities (Slik et al., 2010). We conclude that conversion of natural forest to oil palm or rubber monocultures is reducing the phytomass C stock by up to 170 Mg C ha^{-1} in this lowland area. Thus, compensating for the emitted carbon caused by land-use change even on mineral soils not containing carbon reservoirs fixed as peat may take hundreds of years and may even be irreversible.

6.2 Effects of forest conversion on net primary production and carbon sequestration

Contrary to our hypothesis where the highest net primary production (NPP) was predicted for natural forest, we have measured decreasing total NPP values from oil palm (16.26 ± 0.89 Mg C ha^{-1}) > natural forest (11.62 ± 0.64 Mg C ha^{-1}) > jungle rubber (9.64 ± 0.46 Mg C ha^{-1}) > rubber monoculture (7.73 ± 0.39 Mg C ha^{-1}) (*chapter 2*). However, the main components of oil palm NPP, namely fruit production with 61 % of total carbon in NPP did not contribute to C cycling as the fruit bunches were harvested and removed from the system (Fig. 6.2).

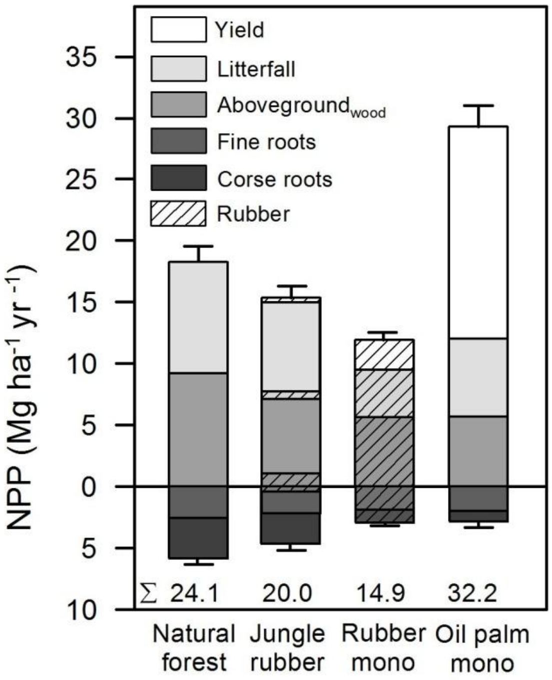

Figure 6.2: Net primary production (Mg ha^{-1} yr^{-1}) of the four land-use systems in Jambi, Sumatra. Shown are means ± SE (n = 8).

Monoculture plantations with rubber and oil palm showed significantly lower leaf litterfall than natural forests and jungle rubber that can be attributed to the less complex canopy structure and lower species diversity (Lisanework & Michelsen, 1994, Barlow et al., 2007, Tang et al., 2010). Nonetheless, aboveground litterfall was the main component of carbon allocation in the investigated systems, followed by wood production and finally fine root production as it was also observed by Malhi et al. (2014). The exception was monoculture rubber that allocated most carbon in stem wood growth, despite the carbon loss due to annual leaf shedding and their replacement. Increasing relative importance of carbon allocation to fine roots was observed for oil palm and rubber monocultures. A similar partitioning could be observed comparing the ratio of annual leaf and fine root litter carbon input to the soil as calculated by the decision matrix (*chapter 3*). Forest transformation has shifted the carbon flux from aboveground leaf litter towards belowground fine root components as also described by Hertel et al. (2009) along a forest disturbance gradient in Sulawesi.

Beside changes in the annual net primary production and its partitioning, land-use intensification with introduced cash-crops is also expected to have influence on seasonal growth responses in moist tropical lowlands even with only moderately dry seasons occurring as it is reported for primary, secondary and plantation forests in the Amazon (Barlow et al., 2007). Since temperature fluctuations throughout the year are minimal, the main variable triggering responses in plant growth in the tropics is generally attributed to precipitation. We found a higher coefficient of variance (CV) following forest transformation for all examined processes namely aboveground litterfall, fine root mortality, and aboveground woody production (*chapter 3*). According to the expectation, we found total aboveground litterfall in the natural forest sites and jungle rubber systems decoupled from precipitation patterns, while leaf litterfall in rubber monocultures peaked markedly during month with low rainfall. A similar sensitivity to low water availability could be observed for stem growth and consequentially aboveground woody production ($ANPP_{woody}$) in rubber trees. Trees in the natural forest sites follow the same pattern as rubber trees showing highest $ANPP_{woody}$ values at the beginning of the rainy season, whereas forest trees in jungle rubber seem to grow best in the drier months, probably due to increased light intensities after rubber tree leaf shedding in this system. The monocotyledonous oil palms do not conduct stem wood production due to its secondary diameter growth pattern; therefore, $ANPP_{woody}$ is determined by height growth only. Since palm growth was measured in coarser time resolution, the observed variation in $ANPP_{woody}$ cannot be clearly attributed to seasonal precipitation patterns. While rubber trees showed the strongest seasonal response in stem growth, root mortality in oil palm plantations was significantly increased during periods of low precipitation and soil moisture. This high fine root mortality may be attributed to a missing organic matter layer and a harsher microclimate that is unable to buffer temperature and moisture extremes (Luskin & Potts, 2011). On the other hand, forest trees as well as rubber monoculture trees showed the highest root litter production at the end of the rainy season. Lowered N-mineralization rates and water saturation causing oxygen limitation and hampered decomposition rates may be some of the reasons as shown by Roy and Singh (1995) in mixed deciduous forests. However, root dynamics as well as seasonal responses of net primary production in moist tropical regions remain mostly unexplored.

In the long term, converting tropical lowland forests or structurally diverse agroforests into rubber or oil palm monocultures reduces not only the biomass carbon stock to a great extent, but also lowers the carbon sequestration potential with biomass production as harvest and removal of oil palm fruits, and rubber latex occurs. Since the built-up of biomass stocks is faster in natural forest and jungle rubber, the establishment of oil palm or rubber plantations on former forest land does not enhance carbon sequestration potential despite the high total net primary production of oil palms. Furthermore, as these monoculture systems show higher seasonal response in litterfall, stem growth and fine root mortality, global climate change associated with increasing mean temperatures and seasonality of precipitation patterns (Malhi & Wright, 2004) are likely to further deplete carbon storage potential in tropical lowlands.

6.3 Nutrient return and nutrient use efficiency along forest transformation intensity

Balanced nutrient in- and outputs are essential for long term sustainability of natural and agricultural systems. The input by plant material is not only dependent on alterations of NPP, but also on the nutrient stoichiometry of the responsive NPP components. In this study we found that element content in the leaves as main component of litterfall increased for nitrogen (N), phosphorus (P) and potassium (K) from forest trees in jungle rubber < natural forest trees < rubber trees < oil palm (*chapter 3*). Similar nutrient concentration ranges were found for leaf litter in tropical forest in Sarawak (Proctor et al., 1983), although nutrient contents except nitrogen in our study were lower compared to other studies in tropical rainforests (Haase, 1999). Consequentially, for the nutrients P, K and Ca, litter inputs in all systems excluding oil palm were lower than in other natural rainforest and rubber agroforests (Brasell et al., 1980, Haase, 1999, Dent et al., 2006, Tang et al., 2010). Comparing the nutrient return among the systems in our sites, we found that the return of nutrients was lowest in rubber monoculture due to the overall low annual litter production in line with our hypothesis. Nutrient return with aboveground litter of N, Fe and S in natural forest exceeded input in rubber systems and oil palm plantations, while Ca, Mg and Mn litter input was highest in jungle rubber plantations. The return of P and K to soil via aboveground litter was highest in oil palm plantations even when excluding fruits that are removed from the system, thus partly contradicting our hypothesis.

On the other hand, we found oil palm plantations to show the lowest canopy nutrient use efficiency (NUE) for all investigated nutrients as the most intensively fertilized system. Between natural forest, jungle rubber and rubber plantations no significant differences in NUE for most nutrients except Ca could be detected. In the unfertilized jungle rubber the occurrence of a smaller number of species with similar nutrient requirements (2004) or the increased competition due to high tree densities may be the cause for the observed high NUE. Due to the annual leaf shedding, rubber trees might have developed efficient nutrient re-translocation mechanisms explaining the rather high NUE values in this system. We found NUE of all elements slightly higher in the

Harapan region than in Bukit 12 area except of oil palm plantations, presumably caused by higher clay contents and accordingly better soil nutrient status on clay Acrisols in Bukit 12.

Looking at element ratios in aboveground litterfall, very high aboveground litter N:P ratios > 35 were detected in all systems except oil palm plantations. For that reason, it that P limitation of plant growth is likely to occurs in our sites as predicted beforehand. Low P availability is a commonly recognized constraint for lowland tropical forests on old, heavily weathered soils (Walker & Syers, 1976, Vitousek et al., 2010). On the other hand, we found C:N rations of leaf litter lowest in oil palm followed by rubber > forest > jungle rubber leaves indicating a higher overall decomposability of the nutrient richer litter in fertilized plantation such as oil palm and rubber. In fact, leaf litter nitrogen and C:N ratio were the main factors that influenced litter decomposition when comparing natural forest and oil palm plantations in Bukit 12 region (*chapter 4*). Decomposition rate constants of leaf litter were significantly higher in natural forest than in oil palm plantations, meaning that nutrient turn-over via leaf litter was slower in oil palm monocultures. Even though, litter quality based on the C:N ratio was lower in natural forest and slowed decomposition rates should be expected (Scherer-Lorenzen et al., 2007), factors such as lower moisture levels in the top soil and different microbial community (Haettenschwiler et al., 2011) may have decelerated leaf decomposition in oil palm plantations.

Overall, nutrient return to the soil via aboveground litterfall was significantly reduced for N, Ca, Fe, Mg, Mn and S in monoculture plantations, particularly in rubber. In order to maintain yield outcome, the demand for fertilization is high. The especially high fertilizer input to oil palm plantations has likely caused the significantly lower NUE for all major nutrients. Under current land-use and climate change in tropical lowlands further increases in seasonality of net primary production as well as potentially increasing drought stress and decreasing nutrient cycling in these initially highly productive and self-contained regions are to expect.

6.4 Growth performance as a function of wood hydraulic architecture

Trees in moist tropical regions are characterized by a high growth and biomass accumulation rate, as in a climate with high precipitation and stable temperatures plant growth is supported throughout the year. To maintain a permanent water supply from roots to leaves, efficient water transportation is essential. For this highly productive systems not only nutrient, but also water supply may thus become a challenge. Adaptation mechanisms in wood anatomy features as well as hydraulic strategies may differ compared to trees from temperate and subtropical regions. However, strategies of tropical trees in hydraulic properties and their adaptations to the non-seasonal wet climate remain mostly unstudied (Zach et al., 2010).

In the study on hydraulic architecture of the root, stem and branch wood in *Theobroma cacao* and five common shade tree species in agroforestry systems on Sulawesi, we found wood anatomical and derived hydraulic properties to be a good predictor for tree stem growth performance (*chapter 5*). Theoretical sapwood area-specific hydraulic conductivity (K_S^{theo}) of all tree organs was strongly positively correlated with stem basal area increment (BAI) on a tree and species level as hypothesized. In contrast, neither wood density (WD), nor empirically measured branch and root hydraulic conductivity, foliar $\delta^{13}C$ or foliar nitrogen content were good predictors for aboveground growth performance. Less negative $\delta^{13}C$ values are expected to be linked to reductions in stomatal aperture, a decreased photosynthetic carbon gain and consequentially slower growth (Ryan & Yoder, 1997), while high foliar nitrogen contents should theoretically be connected with high aboveground productivity (Smith et al., 2002). Hypothetically, K_S^{theo} should correlate negatively with WD (Meinzer et al., 2008) when a relatively large fraction of vessels shows values close to the samples mean vessel diameter. As a relatively easy to measure functional wood property, WD has been linked to various ecological and functional traits. While light wood is associated with fast-growing at low carbon and nutrient cost, high wood density is characteristic for slow-growing trees assuring high biomechanical strength and hydraulic safety e.g. (Hacke et al., 2001). Our results contradict former results on a close relation between WD and growth for tropical trees (King et al., 2006, Poorter et al., 2009, Hietz et al., 2013). Variation of frequency and size of fibers may account for the decoupling of WD from hydraulic conductivity (Zanne et al., 2010). However, our sample size and species number was small, so the relationship might change with increasing sample number. Therefore, we tested the hypothesis also on stem wood of 92 sampled trees in natural forest, jungle rubber and rubber monocultures on Sumatra. A similar relationship was found between BAI and K_S^{theo} (Fig.6.3), while WD did not correlate with growth performance.

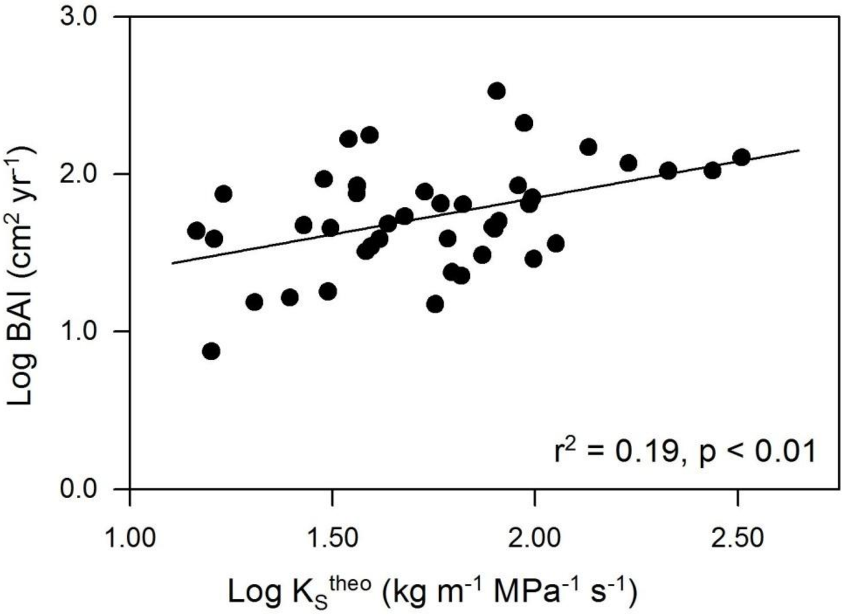

Figure 6. 3 : Relationship between stem basal area increment (BAI) and theoretically calculated hydraulic conductivity (K_S^{theo}) in the stem wood of 92 trees in natural forest, jungle rubber and rubber monocultures. Where several samples per genus were available, mean values per genus were used (n = 42).

Furthermore, our results are in contrast to the common assumption of continuous vessel tapering (Baas, 1982, Tyree & Zimmermann, 2002) as we found the largest vessels along the flow path in the stem xylem and not in the roots. Vessels with larger diameters are likely to embolize fastest, following the commonly observed trade-off between conduit size and vulnerability to cavitation (Wheeler et al., 2005, Cai et al., 2010, Domec et al., 2010) Therefore, at the root level a hydraulic segmentation with roots embolizing fastest might protect the below-ground system and prevent a reverse water flow from main to lateral roots and back to the dryer soil. In contrast, a deviating pattern between species from seasonally dry and more humid regions was observed with larger vessels in stem wood e.g. (Machado et al., 2007). In regions with high precipitation and continuous soil water supply, adaptations to water shortage seem to be less economic. Under conditions of prevailing high atmospheric humidity, it seems more advantageous for trees to develop a high plant hydraulic conductance in the trunk, rather than to minimize the drought-induced risk of xylem embolism as suggested by Schuldt et al. (2013).

In this context, the study in cacao agroforests revealed divergent patterns of hydraulic conductivity, vessel density and relative vessel lumen area between root, stem, and branch wood of drought-adapted species compared to subhumid forest species. We have observed that specific conductivity in the three seasonal species, i.e. *G. sepium, E. subumbrans* and *L. leucocephala,* was higher in roots than in stems, even though the largest vessels were observed in the stem wood. On the other hand, hydraulically weighted vessel diameter (d_h) was not significantly higher in stem than in root wood for the three seasonal tree species i.e. *T. cacao, G. gnemon* and *D. zibethinus*, and vessel density (VD) was comparable between root and branch wood. Apparently due to varying adaptation strategies to periodical water limitation, a separation between the three strictly wet tropical species and the three seasonal tree species was enabled. However, many factors such as tree age, small-scale site specific conditions, and management history may co-influence the relationships among wood anatomy and plant functional traits making them more complex and non-linear. Nonetheless, we expect patterns in vessel traits along the flow path from roots to branches to be dependent on the long-term precipitation regime at the biogeographical origin of the investigated tree species. Therefore, the study results suggest that even though vessel traits, growth performance and wood density relations follow distinct conceptually determined trade-offs, some of these long-established paradigms might not be uniformly applicable to all tree species. Future research on conceptual trade-offs of tree hydraulic architecture should thus include a systematic approach to biogeographic regions and cover principally underrepresented biomes.

6.5 Implications and perspectives on carbon and nutrient fluxes

Indonesian forests are disappearing with increasing speed, replaced by either large-scale oil palm concessions, rubber monocultures or smallholder owned rubber and cacao agroforests. Results from this study have shown that conversion of lowland rainforest on Sumatra leads to significant losses of carbon stocks for rubber agroforests (~ 60 %) and even more for monoculture rubber and oil palm plantations where more than 80 % are lost (*chapter 2*). Carbon stock reductions of similar magnitude have been shown for transformation of forest to cacao agroforests (Steffan-Dewenter et al., 2007). Not only is the carbon released by forest conversion emitted to the atmosphere, but also changed species composition and vegetation cover are likely to decrease the carbon sequestration potential via net primary production in the long-term. Currently half of the global carbon emissions are being absorbed by land ecosystems and the oceans. However, as the absorption is sensitive to climate and to atmospheric CO_2 concentrations, a feedback loop is created (Cao & Woodward, 1998). This carbon-cycle feedback is expected to significantly accelerate climate change and the occurrence of El-Niño over the twenty-first century and may turn the terrestrial biosphere from a carbon sink to source (Cox et al., 2000), as also predicted for the Amazon rainforests (Tian et al., 1998). Increased mean temperatures and seasonality of precipitation patterns are expected for tropical lowlands (Malhi & Wright, 2004) intensified through less dense canopy closure of plantations resulting in higher surface temperature (Ramdani et al., 2014), more harsh microclimate in large-scale monocultures such as oil palm (Luskin & Potts, 2011), and lower transpiration rate as tall trees are reported to have higher daily water use than smaller trees (Zach et al., 2010) contributing less to the recycling of rainfall through evapotranspiration. These changes will likely increase water stress for plant growth and deplete subsurface water resources as reported for rubber plantations (Guardiola-Claramonte et al., 2010).

Other ecosystem services are affected as well. We have shown that nutrient return via litterfall is reduced for rubber systems and oil palm plantations and litter decomposition is slowed in oil palm monocultures compared to natural forest. Extensively used systems such as rubber or cacao agroforests have the potential of sustaining some forest ecosystem functions while additionally providing valuable products and food to local people (Montagnini & Nair, 2004). It is assumed that ecosystems show nonlinear responses to land-use intensification opening management options with low ecological loss and agreeable economic gain. Other studies support the scheme of land sparing in the tropics agreeing it may be more beneficial than land sharing (Baudron & Giller, 2014). High-yield farming may allow more species to persist on spared land (Green et al., 2005) and protecting forests may offer a quick and cost-effective way of reducing carbon emissions (Schrope, 2009) as promoted by the initiative “Reducing Emissions from Deforestation and Forest Degradation” (REDD +). However, the oil palm case suggests that improvements in tropical crop yields will further transfer agricultural production from temperate to tropical regions, leading to more tropical deforestation (Carrasco et al., 2014). In general, the net environmental outcome of shifting agriculture from long-settled and urbanized temperate regions to developing tropical countries with carbon-rich and diverse primary forests is understandably usually negative. And financial opportunity costs of oil palm plantations on mineral soil preceded by logging of forest in Indonesia are substantially high (Koh & Ghazoul, 2010, Irawan et al., 2013). This trend likely will continue, since Indonesia has indicated the potential for a near doubling of oil-palm hectarage and 35 % of Indonesia’s remaining forests are located within industrial concessions (Abood et al., 2014). Rising demand of cash-crops is likely to create further intensification and land-use conflicts if not consistently politically stabilized. Political haggling and inertia, corruption, competing priorities and lack of capacity support further forest clearance (Jepson et al., 2001, Fitzherbert et al., 2008). The role of science is to provide robust scientific evidence to quantify the costs and benefits of land-use change and assess the trade-off via relevant ecological and economical models aiming at the creation of a more heterogeneous agricultural landscape that will foster higher biodiversity and consequentially provide a wider range of ecosystem services and shift land-use towards a more sustainable path.

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