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**EFFECTS OF EXPERIMENTAL DROUGHT ON HYDRAULIC  
PROPERTIES AND LEAF TRAITS OF UPPER CANOPY AND  
UNDERSTORY TREE SPECIES IN A PERHUMID TROPICAL  
FOREST IN CENTRAL SULAWESI, INDONESIA**

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## SUMMARY

The remaining tropical moist forests may be threatened in future by more frequent and more severe droughts that come along with the predicted climate change in South-East Asia and South America, though ecosystem consequences of strong drought events are hardly predictable. Therefore, manipulative field experiments are needed to identify gradual ecosystem responses and threshold values of ecosystem functions under a changing climate. Tropical drought experiments have so far only been conducted in seasonal dry forests in East Amazonia, where the biota most likely possess specific adaptations to regular dry spells. Experiments on the drought response of perhumid tropical forests with continuously high soil moistures and air humidity do not yet exist.

Both observational studies on natural drought events and the Amazonian throughfall displacement experiments showed that under prolonged drought especially large and tall canopy trees experienced higher mortalities than trees with smaller size.

We carried out a replicated throughfall displacement experiment in a perhumid premontane old-growth forest stand in Central Sulawesi, Indonesia, with annual precipitation rates of more than 2500 mm and constantly high relative air humidity close to saturation. We assumed that tree species of this forest do not possess adaptations to severe drought (e.g. deep-reaching roots) compared to the Amazonian experiments.

The purpose of this study was twofold. First, we aimed at explaining why tall tropical trees may possess higher mortalities after extended droughts than smaller ones. Secondly, we analyzed the morphological and physiological responses of an abundant tall-growing upper canopy tree species to 24 months of throughfall displacement, which resulted in a reduction of soil moisture content in the upper soil layers below the conventional wilting point.

Three hypotheses were formulated that concerned tree physiological and morphological adaptations to large tree size, and the response of trees from tropical moist forests to soil water shortage. The study aims were to test whether (i) the environmental control of sap flux density is directly related to tree height, (ii) tropical trees adapt their hydraulic architecture when growing tall to counteract the effect of growing hydraulic resistance with increasing flow path length, and (iii) tall trees of the premontane forest in Central Sulawesi are adapted to the prevailing perhumid conditions and thus are more vulnerable to prolonged soil water deficits than species from tropical humid or semihumid forests.

To achieve these goals, a wide range of ecophysiological, morphological and anatomical traits were investigated in mature trees. Key parameters measured were several hydraulic properties of the xylem of twigs and trunks, wood anatomy, leaf morphology and foliar nutrient contents, stable isotope ratios of C, N and O, sap flux density, litter fall and stand microclimatic variables.

We found evidence that co-occurring tropical tree species differ strongly in measured xylem sap flux densities in the trunk, which is largely dependent on the canopy position within the forest stand. Despite the perhumid climate, vapor pressure deficit (VPD) was the most important environmental factor controlling sap flow. Mean VPD increased linearly with height in the canopy. The close relation between sap flux density and tree height in this perhumid forest, irrespective of systematic position, may be interpreted as convergent pattern in the water use of tropical trees.

We found several important changes in the hydraulic architecture with tree height in the eight studied species. Vessels were tapering acropetally from the stem base towards the upper canopy in a tall-growing tree species, and the smallest vessels were found in all species in the distal twigs. Tall trees generally possessed the largest vessels along the whole flow path. The vessel diameter showed an optimum curve with maximal diameters found in the trunk and not in the roots. Leaf-specific and sapwood-area specific conductivity increased with tree height; both conductivities were linked closely to the increase in vessel diameter.

The most abundant upper canopy tree species of this forest (*C. acuminatissima*) did not show signs of critical damage after 24 months of soil desiccation, despite the fact, that the hydraulic conductivity of twigs and trunks decreased due to smaller vessel diameters in the most recent xylem, the number of leaves on distal twigs was lowered, and stem diameter growth was reduced (non-significant tendency) in the trees exposed to soil desiccation. We assume that the prevailing low evaporative demand throughout the experiment in this perhumid climate prevented critical damage to occur, despite soil desiccation beyond the conventional wilting point. Nevertheless, the reduction in sap flux densities in the desiccation period was more pronounced in taller trees than in smaller ones, indicating that drought-induced physiological effects should appear earlier in tall than in smaller trees. Stem diameter growths, the diameter growth of xylem vessels, and leaf bud formation were found to be particularly sensitive growth processes in *C. acuminatissima*, while pre-senescent leaf shedding or canopy dieback were not observed.

We conclude that tall trees in this forest stand possess a number of morphological and physiological traits that distinguish them clearly from trees in the lower strata. We assume that (a) the exposure to a higher evaporative demand in the upper canopy, (b) the inevitable increase in hydraulic resistance in a longer flow path, and (c) the wider vessels at the base of the trunk, that result from the longer flow path, are the most important causes of the reported higher mortality rates of tall tropical trees after prolonged drought.

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*The fact that trees are large and not easy to handle increases the difficulties of measuring the water requirements of trees, but they should not be insurmountable; for no really satisfactory results can be expected until more data are obtained on forest trees and stands under natural conditions, supplemented by laboratory work on a scale comparable with the size of the problem involved.*

*Oran Raber (1937)*



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# **1 FIRST CHAPTER**

## **INTRODUCTION**

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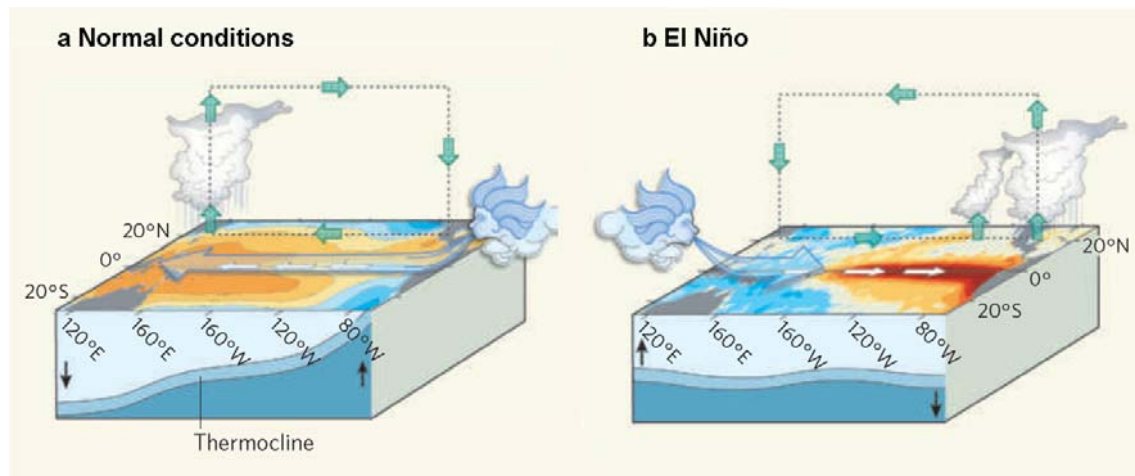
## 1.1 IMPACT OF CLIMATE CHANGE ON TROPICAL RAINFORESTS

Trees, either from tropical or temperate ecosystems, are exceptional organisms that have evolved over approximately 385 million years (Stein *et al.* 2007) and nearly since then have suppressed and dominated other plants in the competition for light (Niklas 1997, Falster and Westoby 2003). Solar radiation has for millions of years been the greatest limitation for terrestrial plant growth after plants were able to produce leaves that could house photosynthetic cells in an aquatic medium (Brodribb 2009). However, this advantage comes with a cost: trees must transport water all the way up to their crowns and inherent physical limitations make them vulnerable to water deficits.

Recent environmental changes are much more rapid than those experienced during normal glacial cycles (Hartmann 2010), as human activities have for centuries altered the shape of the natural landscape, causing a decreasing albedo of the earth's surface due to land-use changes. Secondly, greenhouse gas emissions have strongly increased since the beginning of the industrial revolution (Houghton 1994, Crowley 2000). Atmospheric CO<sub>2</sub> concentration ranged between 180 and 220 ppm during glacial periods, rose to 280 ppm before the industrial period, and is currently approaching 390 ppm in the modern atmosphere (Ward *et al.* 2005). These two factors increasing greenhouse gases in the atmosphere and decreased albedo are causing an imbalance between incoming solar radiation and outgoing infrared radiation (Forster *et al.* 2007). Hence, the earth has heated up by 0.74 °C during the last century (IPCC 2007), and temperatures are assumed to increase further in large parts of the tropics by 1.5 °C to 2.5 °C (Cox *et al.* 2000), globally even by up to 5.8 °C (Houghton *et al.* 2001). As a result, global and regional climate patterns are changing, putting forest health in jeopardy.

The major threat due to these changes for South-East Asia is the more frequent occurrence of the periodic El Niño Southern Oscillation (ENSO) phenomenon (Timmermann *et al.* 1999). Under normal conditions, warm surface water and air are pushed to the west by prevailing winds in the tropical Pacific (Fig. 1.1a) over the area 20° N to 20° S and 80° W to 120° E. A consequence is upwelling of cold water on the eastern side, and a shallow subsurface boundary that marks a sharp contrast between warm upper and colder deeper waters. Opposite oceanographic conditions prevail on the western side. In the atmosphere, the west is warmer and wetter. On the other hand, when the easterly winds weaken, an El Niño event is produced (Fig. 1.1b). This condition is categorized by warmer than normal sea surface temperatures in the east of the ocean, and is associated with alterations in the thermocline and in the

atmospheric circulation that make the east (e.g. Peru) wetter and the west (e.g. Indonesia) drier (Ashok and Yamagata 2009).



**Fig. 1.1:** Normal (a) and anomalous (b) conditions in the tropical Pacific (modified from Ashok and Yamagata 2009).

An El Niño event occurs every 3-8 years and is associated with anomalous atmospheric circulation patterns known as the Southern Oscillation. In Indonesia, droughts observed between 1830 and 1953 were 93 % associated with the ENSO phenomenon (Quinn *et al.* 1978). These ENSO events are causing plant-available soil moisture to stay below a critical threshold level for a prolonged period. Additionally, climate change prediction models anticipate that the tropical regions of South-East Asia could experience a shift in precipitation patterns leading to more frequent and/or more severe droughts in the future (Cox *et al.* 2004, Christensen *et al.* 2007, Newbery and Lingenfelder 2008, Sheffield and Wood 2008). These global change driven consequences might in the longer term alter tropical species distributions, community composition and diversity patterns (Engelbrecht *et al.* 2007) due to higher rates of tree mortality and increased forest fires (Slik *et al.* 2004, Van Nieuwstadt and Sheil 2005, Nepstad *et al.* 2007, Arago *et al.* 2008, Phillips *et al.* 2009, Costa *et al.* 2010). For instance, during the severe 1997/1998 ENSO event, approximately 11.6 Mio ha were affected by forest fires in Indonesia, emitting large amounts of CO<sub>2</sub> (Siegert *et al.* 2001, Page *et al.* 2002).

Nevertheless, rate and distribution of precipitation regionally strongly depend on a variety of parameters, e.g. topography and particularly vegetation structure and land-use systems. Since 1980, 288 Mio ha (21 %) of tropical rainforests worldwide have been deforested (Bawah *et al.* 2004). South-East Asia, which in 2005 had a forest cover of 203.9 Mio ha (46.8 % of land cover), faces an annual reduction by 2.8 Mio ha (1.3 %), where Indonesian forests are particularly degraded rapidly, annually by more than 1.9 Mio ha (FAO 2007). This rapid

conversion of primary forests, which function as water reservoir, and their rainfall regulating, soil and groundwater protecting properties and their C-sequestration potential, are additionally causing an intensification of the impacts of climate change on a regional scale. Hence, resilience to drought may become increasingly important in these regions, particularly in the tropical perhumid aseasonal old growth rainforests, where the present plant species are not assumed to possess drought-avoiding adaptations. Detailed assessments of the ecological consequences of droughts on these ecosystems are scarce and knowledge whether and how they are adapted to severe droughts is limited. Measuring how these forests respond to perturbations could lead to valuable models how changes in drought frequency and intensity affect their future (Newbery and Lingenfelder 2008).

## 1.2 INFLUENCE OF DROUGHT ON TREES

Water plays an essential role in several vital processes of plants. For every gram of plant organic matter produced, a plant needs to take up approximately 500 g of water (Taiz and Zeiger 2006). As climate change scenarios predict more frequent extreme drought events, trees, in particular, will increasingly need to cope with drought stress (Hartmann 2010). However, our understanding of the hydraulic physiology of plants is far from complete (Brodribb 2009). Therefore, several tree physiological attributes might determine their drought sensibility or resilience.

### 1.2.1 Carbon starvation hypothesis

Carbon depletion has been proposed as one of the underlying mechanism of drought-induced tree mortality (Breda *et al.* 2006). Based hereon, McDowell *et al.* (2008) formulated the carbon-starvation hypothesis to explain tree mortality due to long-term drought. It predicts an eventual depletion of tree carbon stores as a result of stomatal closure and insufficient carbon assimilation to meet carbon demands for tissue maintenance. This implies that species with a large safety margin, which close their stomata at a relatively well-hydrated state, develop a negative carbon balance relatively early during drought and may therefore be forced earlier to rely on carbon reserves (Hartmann 2010). Therefore, drought might not always be immediately lethal, but could occur years to decades after the actual drought event (Bigler *et al.* 2007, Phillips *et al.* 2010). However, the carbon starvation hypothesis is under scrutiny (Sala 2009) since starch and other non-structural carbohydrates in woody plants have been shown to increase rather than decrease in response to decreases in water availability (Latt *et al.* 2001, Würth *et al.* 2005, Sala and Hoch 2009). This is assumed to be caused by fairly large

competing carbon demands (Sala 2009) during drought, since trees store sufficient mobile carbon (Körner 2003). However, since carbon pools may not be fully depleted even after severe water stress leading to tree mortality (Breda *et al.* 2006), it has been suggested that water stress might limit the conversion of stored carbon pools into mobile forms of carbon, their respective mobilization to sites of phloem loading, or their long-distance transport. Sala *et al.* 2010 furthermore highlight that the mechanisms of drought-induced mortality in trees are far from being resolved. Nevertheless, hydraulic failure due to catastrophic xylem dysfunction as a major trigger is broadly accepted, whether it directly causes carbon starvation due to stomata closure after prolonged drought in the first, or not before carbon stocks are depleted or can not be mobilised.

### 1.2.2 Xylem embolism

The continuity of water columns from soil pores throughout the plant to leaf cells, linked to the evaporative flux, is known as the soil-plant-atmosphere continuum. The driving force behind this tension that pulls the water through the xylem to the crown is generated by transpiration and described by the broadly accepted cohesion-tension theory (Dixon and Joly 1894), which during the last century has withstood vigorous experimental scrutiny (Pittermann 2010). Maintenance of this ‘hydraulic robe’ is needed to ensure a continuous water supply to the leaves (Maseda and Fernandez 2006), which is essential for carbon fixation (Cai and Tyree 2010). Among the environmental factors that may influence tree hydraulics, water stress can safely be expected as a major one (Nardini and Salleo 2005).

During drought, when the evaporative demand increases and at the same time the soil-moisture-content decreases, high negative xylem tensions in the xylem sap will trigger stomatal closure, decreased photosynthesis, and as last ‘hydraulic fuse’ cause leaf shedding (Tyree *et al.* 1993, Nepstad *et al.* 2002, Farooq *et al.* 2009). However, water stress is well known to impair the conductive efficiency of the plant vascular system through xylem embolism (Tyree and Sperry 1989). One of the first consequences of these high negative xylem tensions is the occurrence of cavitations, which are causing embolisms (displacement of water through air) in the water conducting conduits and hence a direct loss of hydraulic conductivity (Ewers *et al.* 2007). Xylem embolism can be viewed as a control mechanism which, in connection with stomatal activity, regulates the amount of water extracted by the plant (Salleo *et al.* 2000, Chaves *et al.* 2003). Consistently, the ability to refill embolized conduits after rewetting despite the presence of tension in the xylem seems to be widespread, but how this occurs is so far not known. Weighing different possibilities, Zwieniecki and

Holbrook (2009) concluded that low-molecular weight sugars might be the principle osmoticum for refilling, especially since the amount of starch stored within stems corresponds well to what would be needed for refilling. Their conclusions are further supported by Sala and Hoch (2009) who found significantly higher contents of non-structural carbohydrates in trees from a dry site compared to a moist site within the same species. If this implies that low wood density species are better capable of refilling due to a higher amount of parenchymatic tissue, it is so far unknown.

However, xylem embolism is correlated with drought tolerance (Pockmann and Sperry 2000, Tyree *et al.* 2003) and species distribution, since cavitation resistance increases across species with decreasing mean annual precipitation (Maherali *et al.* 2004) and is associated with the range of water potentials experienced in the field (Hacke *et al.* 2000, Pockmann and Sperry 2000, Sperry 2000). Plants differ widely in their vulnerability to drought-induced cavitation and the responses to drought are species-specific and depend on the tree's hydraulic strategy (Breda *et al.* 2006). Consistently, severe embolisms are the main primary cause of death in drought-stressed rainforest trees. By investigating 14 different tree species from a moist forest in Brunei, Tyree *et al.* (1998) found that each tree species was highly susceptible to drought-stress induced xylem embolism. Their vulnerability was higher than in trees from sites with higher drought frequencies, which can be assumed to possess an adjusted hydraulic system to the frequent occurrence of drought periods. The ability to control or tolerate embolism, and the capability of refilling embolized vessels, are key attributes of drought-adaptation in tropical rainforest trees.

During drought plants might increase their axial hydraulic conductance to facilitate water uptake despite low soil water potentials, which automatically would cause high negative xylem tensions (Mencuccini 2003, Maseda and Fernandez 2006). These species can be classified as 'drought-tolerant' or 'anisohydric' since they exhibit simultaneous decreases in stomatal conductance and water potential due to lower stomatal sensitivity. These species thereby dehydrate strongly during seasonal drought, although they are displaying structural and functional adaptive traits (Picon *et al.* 1996, Martinez-Ferri *et al.* 2000). Otherwise, plants might decrease their hydraulic conductance to particularly avoid cavitations (Hacke *et al.* 2001). These species can be classified as 'drought-avoiding' or 'isohydric' due to maintenance of a nearly constant leaf water potential during drought (Hartmann 2010) by early stomatal closure before any damage e.g. catastrophic xylem dysfunction occurs. These species-specific drought-avoiding or drought-tolerance strategies depend on several

parameters, e.g. stomatal sensitivity, leaf-specific hydraulic conductivity and the hydraulic architecture, e.g. rooting depth, xylem path length and shape and distribution of the conduits.

### 1.2.3 Conduit anatomy and cavitation risk

According to the Hagen-Poiseuille Equation, lumen conductivity to water should increase with the 4<sup>th</sup> power of diameter, hence a doubling of diameter will result in a hydraulic conductivity that increases by 16-fold on per-conduit basis and by fourfold on cross-sectional basis (Tyree and Zimmermann 2002). Additionally, conduit length seems to depend on conduit diameter (Ewers *et al.* 1990, Cai *et al.* 2010). Therefore, stems with large and long conduits are much more efficient and conductive, but at the same time more prone to cavitation. Hence, there is a trade-off between stem hydraulic efficiency and stem safety against cavitation. Accordingly, conduit diameter (e.g. Carlquist 1977, Machado *et al.* 2007, Psaras and Sofroniou 1999) as well as tree ring width (e.g. Sass and Eckstein 1995, Körner *et al.* 2005, Eilmann *et al.* 2006) correlate positively with overall annual precipitation rates within and among species, and also with the resistance to cavitation expressed as the xylem tension at which 50 % of hydraulic conductivity is lost (Maherali *et al.* 2004). It has further and repeatedly been corroborated in the last two decades that there is a direct relation between increasing conduit diameter and increasing empirically determined cavitation risk. These findings, whether based on the acoustic method (Salleo and LoGullo 1989), the anatomical method of counting open vessels after colouring (Hargrave *et al.* 1994) or the current most common method of establishing vulnerability curves ( $\Psi_{50}$ , Davis *et al.* 1999, Pockman and Sperry 2000, Martinez-Vilalta 2002, Pittermann and Sperry 2003, Wheeler *et al.* 2005, Willson and Jackson 2006, Hacke *et al.* 2009b, Awad *et al.* 2010, Cai and Tyree 2010, Zhu and Cao 2010). Hacke *et al.* (2009a) argue that there should be no direct causal linkage between conduit diameter and assumed mechanism of cavitation due to water stress (air seeding hypothesis), since the relationship between these traits rather should be caused by changes of the pit pore structure (pit area hypothesis). Accordingly, greater conduit numbers could increase conductivity with no effect on safety, as long as the total pit area per conduit remains constant. This is based on the assumption that increasing total area of the pit membrane should automatically lead to a higher risk of at least one pore on a pit membrane allowing air to enter at a particular pressure potential gradient, the ‘rare pit hypothesis’ (Hacke *et al.* 2006, Choat and Pittermann 2009, Christman *et al.* 2009). Assuredly, conduits possessing pit membranes with smaller pores are less vulnerable to embolism, but also have a lower hydraulic conductivity, since pit membranes may account for up to 50 % of overall

xylem resistance to flow (averaged across a wide range of species, Choat *et al.* 2008). Furthermore, what would be the evolutionary advantage for a plant having larger conduits, if not automatically their hydraulic conductivity increases? Accordingly, Martinez-Vilalta *et al.* (2002) confirmed that increasing conduit diameter is directly linked to an increase in total pit area, thus leading to a higher vulnerability to embolism. Similar results were found by Jarbeau *et al.* (1995) through a comparison of two chaparral shrub species. Even though they suggested that the size of pores in pit membranes may be a factor in determining both xylem efficiency and vulnerability to embolism, the species with narrower conduits had smaller pores, and on the other hand the species with wider conduits also wider pores, indicating a greater total pit area of the latter. Altogether, it seems that a universal relation between conduit size and total pit pore area might exist, which would be in support of the ‘air seeding hypothesis’ and additionally the ‘rare pit hypothesis’. Additionally, Wheeler *et al.* (2005) confirmed a relationship between pit area per vessel and vulnerability to cavitation ( $r^2 = 0.75$ ), which conforms with the relationship between conduit diameter and vulnerability to cavitation mentioned at the beginning of this paragraph. Recent studies by Hacke *et al.* (2009b) found a significant negative correlation between stem conduit diameter and cavitation resistance among 22 arid-land shrub species with conduit diameters ranging from 17.7  $\mu\text{m}$  to 57.8  $\mu\text{m}$ , confirming previous findings.

However, large trees were found to have higher daily water uses (DWU) compared with smaller ones (Granier *et al.* 1996, Wullschleger *et al.* 1998, Oren *et al.* 1999, Meinzer *et al.* 2004, Fisher *et al.* 2007), and can therefore be assumed to possess corresponding higher hydraulic conductivities. If this automatically implies a higher cavitation risk due to larger conduits, it is so far unknown.

#### 1.2.4 Wood density

Besides the shape and distribution of the conduits, wood density seems to be a second important controlling variable of drought resistance and water flux patterns in trees. 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). Lighter wood can store more water due to a higher amount of parenchymatic tissue (Holbrook 1995) or larger tracheids surrounding the vessels, where water storage is primarily located (Borchert and Pockman 2005). Wood density is typically inversely correlated with the growth rate of trees. Fast growing tree species usually have lower wood density and higher hydraulic conductivities compared with slow growing species, but cannot withstand as



negative xylem tensions, which might lead to cell implosion and, like embolized conduits, cause a loss of conductivity. Therefore, tree species with high wood density are assumed to be less vulnerable to cavitation (Tyree *et al.* 1994, Hacke *et al.* 2001, Bucci *et al.* 2004). Although this relation has not been investigated in tropical trees, tree species from Borneo (van Nieuwstadt and Sheil 2005) and from the Amazon (Phillips *et al.* 2010) with higher wood density were found to be more drought resistant. This would imply that wood density is controlling a trade-off between rapid growth and drought resistance. However, trees of tropical semi-deciduous forests with a severe dry season ranged from ‘drought-avoiding’ stem-succulent species with low wood density ( $\rho < 0.5 \text{ g cm}^{-3}$ ), which maintain high stem water potentials ( $\Psi > -0.7 \text{ MPa}$ ) throughout the year, to ‘drought-tolerant’ deciduous hardwood species ( $\rho > 0.75 \text{ g cm}^{-3}$ ), which dehydrate strongly during seasonal drought ( $\Psi < -6 \text{ MPa}$ , Borchert and Pockmann 2005). Accordingly, it is not fully understood so far, if wood density in perhumid environments determines drought sensitivity, or only characterizes different drought avoiding adaptations.

### 1.2.5 Rooting depth

Root distribution and maximal rooting depth are further key traits in tree drought response, since deep-rooting species may temporarily be able to withstand moderate drought periods and maintain high transpiration rates through access to soil water stored in deeper horizons (Jipp *et al.* 1998, Klinge *et al.* 2001, Sommer *et al.* 2003). Additionally, deep-rooting species might be capable of performing a ‘hydraulic lift’, a passive transport of water from deeper wet soil layers to drier top soil layers and thereby support the majority of their fine roots and additional tree individuals or the understory with a certain amount of water (Burgess *et al.* 1998, Olivera *et al.* 2005, Scott *et al.* 2008, Hao *et al.* 2010).

Zotz *et al.* (1994) classified evergreen tropical trees into ‘drought evaders’ and ‘drought tolerators’, according to the classification used by Borchert and Pockmann (2005) to describe drought-avoiding adaptations based on their wood density. The former are deep-rooting and have a highly conductive hydraulic system to avoid potential drops and the risk of cavitation (typically with low wood density), the latter are more shallow-rooting and tolerate very negative xylem pressure potentials (high wood density). Accordingly, Condit *et al.* (1995) did not find evidence that tropical trees with shallow root systems suffered more from drought than deep-rooting canopy trees. On the other hand, aseasonal perhumid tropical forests typically have more shallow root systems (Schenk and Jackson 2002), since rooting depth decreases with increasing overall precipitation. This includes upper canopy tree species

despite their tree height and brings up the question of whether larger trees in the perhumid tropics are more vulnerable to desiccation than smaller trees (Williamson *et al.* 2000). During the severe 1997/1998 ENSO event in Borneo, particularly large and tall tropical canopy species showed a higher mortality compared to the understory (Slik *et al.* 2004, Van Nieuwstadt and Sheil 2005), raising the question of whether these canopy tree species possessed deep root systems. Otherwise, even deep root systems might be insufficient due to water shortage of the deeper soil layers under prolonged and severe drought periods. In this case other factors, e.g. conduit anatomy or wood density, might determine tree mortality. However, recently published data from a throughfall exclusion experiment in the Amazon indicates that the capacity for deep root uptake of water is limited by changing soil-to-root resistance under severe drought, which may in part result from the high matric potential of water retention in high-clay soils (Markewitz *et al.* 2010). Even other processes of hydraulic flow such as capillary rise or hydraulic redistribution may not move large volumes of water in these tropical seasonal dry ecosystems with deep roots. Based hereon it can be assumed that perhumid aseasonal ecosystems with a shallower root system are even more dependent on the water uptake from the upper soil layers.

#### 1.2.6 Tree size

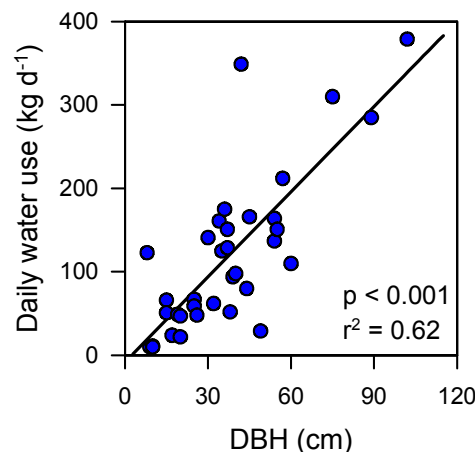
Tall trees experience increased risk of xylem embolism from air-seeding (Domec *et al.* 2008), since the vertical water movement through the vascular system from the soil to the distal leaves encounters resistance to flow due to path-length effects and gravity. Based on this physical law, water transport within trees has been hypothesized as a limiting factor to height growth in tall trees due to insufficient water supply to the leaves (Ryan and Yoder 1997, Koch *et al.* 2004), as the hydraulic resistance of a tube is proportional to its length (Hagen-Poiseuille Equation, Tyree and Ewers 1991). Even sufficient soil moisture contents might provoke hydraulic limitation in tall trees (McDowell *et al.* 2005), since these are operating close to the edge of hydraulic dysfunction and more cavitation occurs at increasing tree height (McDowell *et al.* 2002). However, the xylem structure of tall trees is adjusted to satisfy the conflicting requirements for water transport and water column safety despite path-length dependent increase in resistance. For instance, the model of West, Brown and Enquist (1999) predicts that vessel diameter of conducting tubes must taper with growing tree height to minimize the increasing risk of xylem dysfunction. Their model has since then been confirmed among several angiosperm and gymnosperm species (Anfodillo *et al.* 2006, Weitz *et al.* 2006, Coomes *et al.* 2007, Petit 2007), implying its validation as universal rule. Besides

the shape of the conduits, Domec *et al.* 2008 found the pit aperture diameter of tracheids in a conifer to steadily decrease with height. Even though it is not recommended to compare adjustments between angiosperms and gymnosperms, tall trees are tailored to satisfy the conflicting requirements. Despite that, the avoidance of runaway embolism imposes increasing constraints on water transport efficiency. Therefore, large trees are more vulnerable to drought-induced cavitation than small trees and must fine-tune transpiration rates more tightly.

Otherwise, as trees grow taller, allocation is predicted to shift from foliage to transport tissue, most notably to fine roots, resulting in a larger size of the root system (Magnani *et al.* 2000). This is further supported by the pipe model theory by Shinozaki *et al.* (1964a, b). Based on their higher rooted soil volume, tall trees might have access to deep soil water storage, but according to Schenk and Jackson (2002) this is not assumable in a perhumid tropical environment. Here, the larger root system size should rather spread out horizontally to guarantee a sufficient nutrient uptake.

Besides path-length effects and root distribution, water storage in plants is an adaptation that might help overcome drought (Holbrook 1995). Tall trees generally have higher water storage due to their greater bole volume. This might allow them to draw on these resources during periods of reduced soil water uptake. Phillips *et al.* (2003) found the proportion of stored water used for transpiration to increase with tree size and thereby potentially compensating for hydraulic limitations. They concluded that water storage plays a significant role in the water and carbon economy of tall trees and old forests. This would imply that tall tree species with low wood density and thus higher water storage would overcome drought rather than tall trees with high wood density, even though low wood density species can not withstand as negative xylem tensions. In addition, by comparing thirteen tropical and two temperate species representing different functional types, Borchert and Pockman (2005) concluded that the rate of water uptake during rehydration and the minima of leaf water potential observed in the field during the dry season were highly correlated with water storage capacitance, indicating that wood anatomy is a major determinant of drought adaptation. On the other hand, Verbeeck *et al.* (2007) found water storage in Scots pine to be strongly related to diameter at breast height (DBH), sapwood area and leaf area, but not to tree height, which might reflect the larger water uptake capacity of their root system. Nevertheless, they could confirm that on days where transpiration was high due to high evaporative demand trees were more dependent on stored water. However, large tropical canopy trees can consume up to approximately  $800 \text{ kg H}_2\text{O d}^{-1}$  (Meinzer *et al.* 2004), much more than temperate and smaller

tropical trees, which typically use 10-200 kg H<sub>2</sub>O d<sup>-1</sup> (Wullschleger *et al.* 1998). Using the dataset on DWU (heat dissipation method, Granier 1987) and DBH provided by Wullschleger *et al.* (1998) from temperate and tropical trees, a linear relationship between water consumption and tree size was revealed (Fig. 1.2). This tree size depending relation is further supported by Granier *et al.* (1996), Oren *et al.* (1999), Meinzer *et al.* (2004) and Fisher *et al.* (2007).



**Fig. 1.2:** Daily water use (DWU) in relation to tree size (DBH, modified from Wullschleger *et al.* 1998).

Although Meinzer *et al.* (2001) found a strong positive correlation between DBH and active sapwood area, a negative correlation was found between DBH and total daily or maximal sap flux density for tropical tree species of an old growth forest in Panama. Nevertheless, the role of stored water as a means of survival during prolonged drought may be questionable (Hartmann 2010) for tall trees consuming such high amounts of water under normal environmental conditions. On the other hand, it might enable tall tropical trees to withstand short moderate drought periods.

Tall tropical rainforest trees were found to have the highest tree mortality after prolonged and severe drought compared to trees of the understory in South-East Asia (Slik *et al.* 2004, Van Nieuwstadt and Sheil 2005), South America (Nepstad *et al.* 2007, Phillips *et al.* 2009, Costa *et al.* 2010, Phillips *et al.* 2010), and the same was reported for temperate trees of North America (Floyd *et al.* 2009). In spite of these findings, the possible physiological causes for the dying of these trees are still uncertain.

### 1.3 TROPICAL THROUGHFALL DISPLACEMENT EXPERIMENTS

The consequences of strong drought events on different ecosystems are hard to predict, but the particular ways in which these ecosystem respond to decreased water availability or

increased occurrence of drought are considered a key issue in climate change scenarios (Wigley *et al.* 1984). Evaluating the reaction of an ecosystem based on a naturally occurring severe drought event would imply that the measurements had been carried out before, during and after its occurrence, which mostly happens accidentally due to long-term measurements. Therefore, large-scale manipulative field experiments were found to provide a powerful tool in the identification of gradual and threshold ecosystem responses that might result from future precipitation changes (Hanson and O'Hara 2003). These field experiments should be of sufficient size and complexity to handle questions of individual plant response, interplant interactions, as well as stand-level carbon, water, and nutrient cycling responses (Hanson 2000). Meanwhile, several large-scale throughfall displacement experiments have been carried out over the last decades, mainly in temperate ecosystems, e.g. the 'Walker Branch Throughfall Displacement Experiment' in Tennessee, USA (Hanson and Wullschleger 2003), the Solling roof experiment in Germany (Bredemeier *et al.* 1998, Borken *et al.* 2003), a throughfall exclusion experiment in a Mediterranean *Quercus ilex* forest (Limousin *et al.* 2008, 2009) and several more. However, so far only two tropical large-scale *in situ* throughfall displacements experiments have been carried out, the 'Tapajós Throughfall Exclusion Experiment' (TTEE, Santarém, Brazil, Nepstad *et al.* 2002) and the 'Caxiuanã Throughfall Exclusion Experiment' (CTEE, Pará, Brazil, Fisher *et al.* 2007, Costa *et al.* 2010). Both were located in the Eastern Amazon in a seasonal dry forest with a strong dry season of several months each year. The implications of these studies are that these investigated ecosystems have adapted appropriate mechanisms of drought tolerance or avoidance. Accordingly, these two experiments had a maximum rooting depth of coarse roots of 10 m and more (TTEE) or 5 m (CTEE) in support of the observation of Schenk and Jackson (2002), that rooting depth should increase with increasing dry season length. Therefore, these forests were at first remarkably resistant. As expected, photosynthesis slowed down to conserve water, and the roots drew water from soil layers up to 13 m down. Trees in the experimental plots slowed their growth, and many of the smaller trees stopped growing entirely (Stockstad 2005).

Even though these two throughfall displacement experiments were geographically proximal, they showed different reactions within the first two years of the treatment. Asner *et al.* (2004) found no change in predawn leaf water potentials over the course of the first two years for the TTEE, suggesting that the treatment did not provoke substantial drought stress in the canopy, even though 1.2 years later the mortality rates had increased enormous. On the other hand, removing 50 % of the rainfall in the CTEE caused a decrease in total sap flow of 41 % with

the most severe drought periods causing an 80 % reduction in sap flow compared with the control (Fisher *et al.* 2007).

One explanation for the different reactions between these two sites might be the differences in their soil properties. The TTEE was located on a clayey soil which is known to be at least 90 m deep. The vertical extent of the root system and the water holding capacity of the soil may therefore have contributed to the increased drought resistance of the TTEE forest compared to the CTEE stand. The CTEE on the other hand, is located on a sandy loam and has a stony laterite layer, which may prevent the development of substantial deep root systems, although roots were found below this layer.

Within these two studies, the nearly identical forest stands, which mainly differ in their soil type, reacted differently over the course of the first two years of experimental desiccation. However, after approximately four years of throughfall displacement during the rain season, both forest stands showed remarkably consistent reaction in relation to tree mortality, wood production and above-ground biomass. The TTEE treatment resulted in 38 % increased mortality rates across all stems > 2 cm DBH. Mortality rates increased 4.5-fold among large trees and twofold among medium-sized trees in response to the treatment, whereas the smallest stems were less responsive. Overall, potential overstory tree species were more vulnerable than midcanopy and understory species. Additionally, lianas proved to be more susceptible to drought-induced mortality than trees or palms (Nepstad *et al.* 2007). Lianas are known to possess very large vessels and a long flow path (Ewers *et al.* 1997), and according to the relation between increasing cavitation risk with increasing conduit diameter, and an increase in hydraulic resistance with path length, this might be an explanation for this observation. After seven years of 50 % throughfall removal, the CTEE resulted in approximately a twice as high tree mortality for the experimental plot compared with the control plot, whereas differences in stem mortality between plots were, likewise with the TTEE, greatest in large trees (3-fold). In addition, wood production in the experimental plot was 30 % lower than in the control plot.

Summarizing the results from both experiments, tropical seasonal dry forest stands proved to be remarkably resistant within the first two years until a certain threshold in soil water content was reached after more than three years. However, to be able to adjust climate change scenarios on a regional and global scale, the two experiments proved that further data on tropical ecosystem responses to reduced rainfall regimes are urgently needed, especially for tropical ecosystems that are not assumed to possess drought-avoiding adaptations.

## 1.4 PROJECT OBJECTIVES

After severe and prolonged drought events in tropical climates, the highest tree mortality rate was reported for tall upper-canopy tree species. This remarkable result was found in seasonally dry forests (Nepstad *et al.* 2007, Costa *et al.* 2010) as well as in perhumid environments with no marked dry seasons (Slik 2004). Universal patterns seem to exist, in which tall tree species differ physiologically and morphologically from smaller-growing ones. The presented work was embedded in the DFG-research unit 552 ‘Stability of rainforest margins in Indonesia’ (STORMA). As part of an interdisciplinary research project, the present study was conducted in the framework of the ‘Sulawesi Throughfall Displacement Experiment’ (STDE) with the overall aim to investigate the effects of extended drought periods on tropical rainforests. In this context, we studied tree-height-related physiological and morphological attributes and attempted to identify attributes that distinguish tall upper-canopy tree species from the understory and that might explain their higher vulnerability to severe water deficits.

One of the tallest and also most frequent tree species of this stand, the Fagaceae *Castanopsis acuminatissima* (Blume) Rheder, was investigated in more detail in its drought response to the experimental two-year desiccation.

The overarching hypotheses of the present study were:

- (i) The environmental control of sap flux density is directly related to tree height
- (ii) Tropical trees show an adaptation of their hydraulic architecture when growing tall for counteracting the effect of increasing hydraulic resistance with increasing flow path length
- (iii) Tall trees of the premontane forest in Central Sulawesi are adapted to the prevailing perhumid conditions and thus are more vulnerable to prolonged soil water deficits than species from humid or semihumid forests

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## **2 SECOND CHAPTER**

### **METHODOLOGY**

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## 2.1 CHARACTERIZATION OF THE STUDY AREA

### 2.1.1 Study site

The study was carried out in a tropical premontane primary rainforest in the remote Pono Valley located on the western boundary of the Lore Lindu National Park of Central Sulawesi, Indonesia, near the village Toro. The Lore Lindu National Park was founded 1992 by The Nature Conservancy in partnership with the Directorate General of Protection and Conservation of Nature (PKA) and is recognized as a UNESCO Man and Biosphere Reserve. The park is composed of a complex of rift valleys and steeply folded mountains stretching across 217,000 ha and contains one of the largest intact forests in Indonesia with 90 % of its canopy cover still intact.

The study site (S 01°29.6' E 120°03.4', elevation 1050 m) is located on a plateau with an inclination of 0-20° in an otherwise rugged and steep landscape. This site was chosen due to its undisturbed condition, well-drained soils and deep water table (> 4 m). The forest has a high tree species diversity with about 130 species ha<sup>-1</sup>, an average stem density of 456 stems ha<sup>-1</sup> (DBH > 10 cm) and a canopy height of about 45 m with a few trees reaching a tree height of 55 m (Culmsee and Pitopang 2009, Culmsee *et al.* 2010).

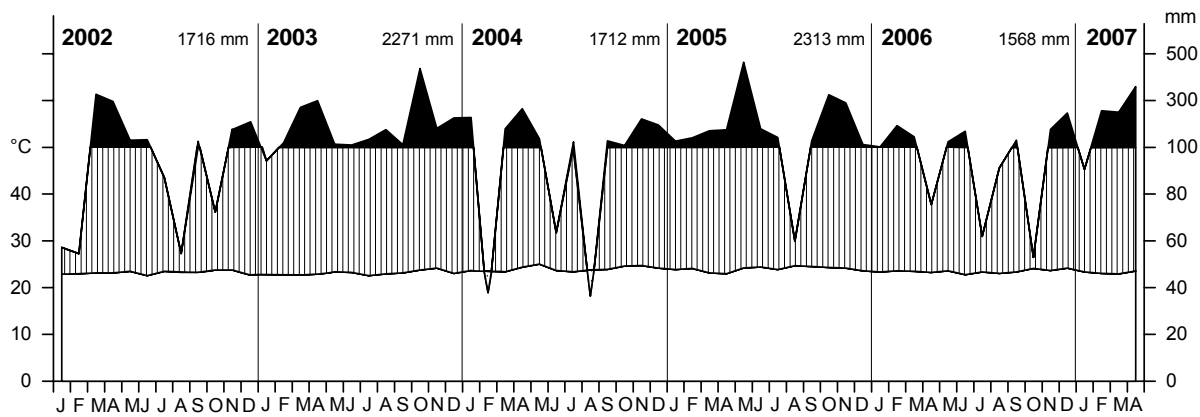
### 2.1.2 Climate

Central Sulawesi is influenced by the Inner-Tropical Convergence zone (ITC) and is therefore characterized by a daytime climate, which is best described with reference to rainfall since the temperature, air humidity and global radiation are relatively constant throughout the year (Tab. 2.1, Fig. 2.1, Fig. 2.2).

**Tab. 2.1:** Maximal and mean temperature, minimal and mean air humidity and maximal and mean global radiation for 2007 until 2009 from the forest site at the Pono valley, derived from monthly means. Measurements started in April 2007 and ended in October 2009.

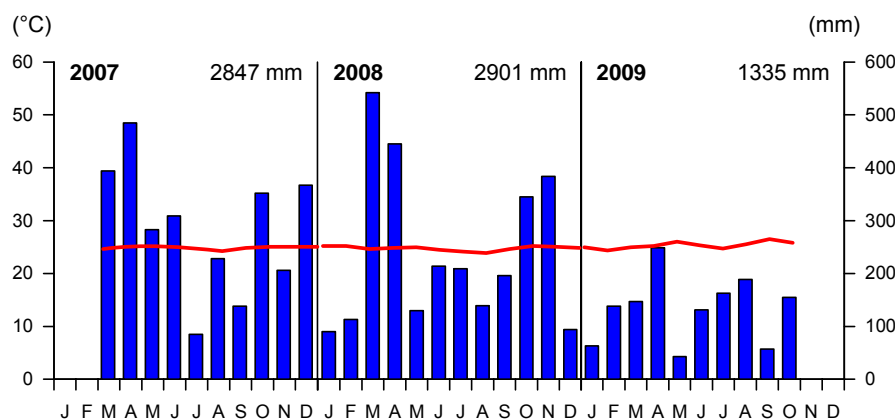
Year	$T_{\max}$ (°C)	$T_{\text{mean}}$ (°C)	$RH_{\min}$ (%)	$RH_{\text{mean}}$ (%)	$GR_{\max}$ (MJ m <sup>-1</sup> d <sup>-1</sup> )	$GR_{\text{mean}}$ (MJ m <sup>-1</sup> d <sup>-1</sup> )
2007	28.7	20.7	47.2	89.3	15.4	10.6
2008	28.6	20.6	48.5	88.7	20.4	14.4
2009	29.7	21.1	44.2	86.3	19.9	15.3

On the other hand, other climatic variables such as wind velocity, evaporation and air humidity can change within even small areas (Whitten *et al.* 1988). Additionally to the ITC, Central Sulawesi is influenced by the Australian-Asian Monsoon.



**Fig. 2.1:** Climate diagram of the climate station located in the village Toro (S 01°30.2' E 120°02.1, elevation 788 m a.s.l.), Central Sulawesi, close to the remote study area for the period January 2002 until April 2007 (Kreilein, Oltchev and Gravenhorst, unpublished data).

The ITC, in combination with the dry air masses from Australia, typically cause a decrease in rainfall from August until September (Fig. 2.1). However, no clear seasonal pattern in precipitation could be observed during the experiment from March 2007 until October 2009 at the forest site in the Pono valley (Fig. 2.2).



**Fig. 2.2:** Monthly mean temperature and total rainfall from March 2007 to October 2009 from the study site in the Pono valley (S 01°29.6' E 120°03.4', elevation 1050 m). Measurements were carried out on a 16 m high tower in a natural gap 50 m away from the plots.

According to Aldrian and Susanto (2003), Central Sulawesi would be the most affected island in Indonesia by an ENSO event after Java, Sumatra and South Kalimantan.

### 2.1.3 Soils and root distribution

The heavily weathered soils of the premontane old-growth forest have a clayey-loamy texture dominated kaolinite and hematite. However, the soil type could not clearly be identified. The established soil physical and chemical parameters indicate, that these soils can be classified as an Acrisol, even though the first 20 cm show properties of a Ferralsol (Word Reference Base

for Soil Resources, Leitner 2010). The soil physical and chemical properties for the upper 250 cm of the soil profile are summarized in Tab. 2.2.

**Tab. 2.2:** Soil physical and chemical properties: texture, bulk density, carbon and nitrogen content, effective cation exchange capacity (CEC) and pH of the 250 cm soil profile of the premontane forest site in the Pono valley. All values are means  $\pm$  SE. For all variables  $n = 3$ , except bulk density  $n = 6$ . Modified from Leitner 2010.

Soil depth (cm)	Bulk density (g cm <sup>-3</sup> )	Soil texture (%)			Carbon (g kg <sup>-1</sup> )	Nitrogen (g kg <sup>-1</sup> )	CEC (cmol kg <sup>-1</sup> )	Soil pH (H <sub>2</sub> O)
		Sand	Silt	Clay				
5	0.73 $\pm$ 0.05	32.3 $\pm$ 2.1	30.3 $\pm$ 2.3	37.6 $\pm$ 2.7	34.1 $\pm$ 7.0	2.8 $\pm$ 0.5	7.2 $\pm$ 0.4	4.3 $\pm$ 0.1
10	0.86 $\pm$ 0.04	27.7 $\pm$ 2.7	31.9 $\pm$ 3.9	40.4 $\pm$ 6.1	28.7 $\pm$ 4.4	2.1 $\pm$ 0.3	5.7 $\pm$ 0.3	4.3 $\pm$ 0.0
20	0.92 $\pm$ 0.04	27.8 $\pm$ 2.2	29.6 $\pm$ 4.2	42.6 $\pm$ 5.0	15.2 $\pm$ 1.8	1.1 $\pm$ 0.1	4.9 $\pm$ 0.2	4.7 $\pm$ 0.1
40	1.08 $\pm$ 0.07	28.7 $\pm$ 2.7	34.5 $\pm$ 5.7	36.8 $\pm$ 4.7	13.9 $\pm$ 1.3	1.0 $\pm$ 0.1	4.5 $\pm$ 0.4	4.6 $\pm$ 0.1
75	1.32 $\pm$ 0.02	31.8 $\pm$ 1.4	39.9 $\pm$ 4.4	28.2 $\pm$ 5.8	6.4 $\pm$ 0.3	0.4 $\pm$ 0.0	5.4 $\pm$ 0.7	4.7 $\pm$ .01
150	1.34 $\pm$ 0.03	36.1 $\pm$ 1.5	49.6 $\pm$ 1.3	14.3 $\pm$ 1.7	3.5 $\pm$ 0.3	0.2 $\pm$ 0.0	6.0 $\pm$ 0.7	5.0 $\pm$ 0.1
250	1.27 $\pm$ 0.08	36.5 $\pm$ 5.9	52.6 $\pm$ 9.0	10.9 $\pm$ 3.1	3.2 $\pm$ 0.5	0.2 $\pm$ 0.0	5.8 $\pm$ 1.2	5.2 $\pm$ 0.0

With soil depth, the silt content increases and hence should result in a better water supply than closer to the soil surface. Probably as a result of the rapid decrease of soil nutrients with soil depth, the majority of both fine (74.3 %) and coarse (91.1 %) roots are concentrated within the top 20 cm of the soil profile (Hertel *et al.* 2009). CO<sub>2</sub> production profiles have a similar depth distribution (van Straaten 2010).

**Tab. 2.3:** Volumetric water content, at which field capacity and permanent wilting point (PWP) are reached at different soil depths (van Straaten, pers. communication).

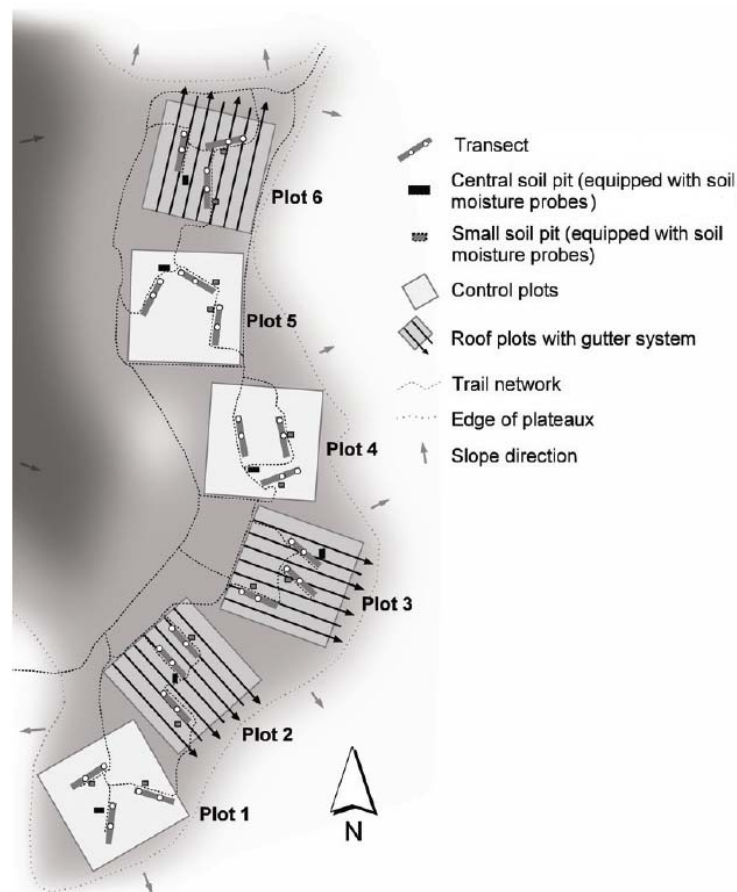
Soil depth (cm)	Field capacity	PWP
5	0.44	0.34
10	0.47	0.35
20	0.49	0.39
40	0.48	0.40
75	0.44	0.37
150	0.43	0.31
250	0.46	0.25

Established pressure plate analyses (van Straaten, pers. communication) show a characteristic pF curve according to the high clay content, indicating the permanent wilting point (PWP) to be situated between 25 and 40 % volumetric water content depending on soil depths (Tab. 2.3).

## 2.2 EXPERIMENTAL DESIGN

The aim of the ‘Sulawesi Throughfall Displacement Experiment’ (STDE) was to simulate a prolonged drought period as they occur during a natural ENSO event. In 2006, six floristically and structurally similar plots of 0.16 ha (40 x 40 m) were established close to each other in a

stratified random design spread out over an area of approximately five hectares for minimizing gradients in stand climate, soil conditions, forest history and structure (Fig. 2.3). While three plots were left as control plots, the remaining three plots were covered by roofs and used to simulate drought conditions. With this experimental design a replicated desiccation experiment was established. The experimental roofs were constructed with light and removable transparent plastic-lined bamboo-frames on a wooden gutter construction. These panels were 5 m long and 0.5 m wide, on average mounted at 1.7 m above ground and overlain at their edges to avoid lateral runoff to the soil surface. Panels of different sizes were used to cover big gaps around large trees or gaps caused by the understory, mainly rattan palms.



**Fig. 2.3:** Design of the three control and three experimental roof plots of the STDE in the natural forest (modified from van Straaten 2010).

The desiccation period started in May 2007. At the beginning, approximately 70 % of the plot area was covered by the plastic-lined frames to collect the throughfall water and channel the runoff down-slope away from the plots. In early 2008, the roof closure was further increased to approximately 90 % by building custom-sized panels to close gaps around tree stems and odd-sized openings. To avoid lateral topsoil and surface water flow and to disable trees to

take up water from outside the study plots, all plots were trenched along the perimeter to 0.4 m soil depth and lined with plastic foil. Since 74.1 % of the fine root biomass is located in the upper 20 cm of the soil profile (Hertel *et al.* 2009), we assumed this trenching depth to be sufficient. At regular intervals, the litter, which had accumulated on top of the roof construction and collected from the runoff, was transferred back to the soil surface. Air temperature and air humidity under the panel system did not differ significantly from the control plots.

## 2.3 FIELD SETUP, INSTRUMENTATION AND METHODS

### 2.3.1 General components of the field setup

The main component of the field setup was the installation of 190 sap flux sensors after the constant heating method (Granier 1985) and the associated infrastructure. To guarantee sufficient power supply and to enable micrometeorological measurements, a 16 m high wooden tower was erected about 50 m distant to the closest study plot in a natural forest gap and equipped with 30 solar panels. Due to the long distance from the wooden tower to the study plots (> 310 m), a generator was needed every second night to guarantee sufficient power supply.

Microclimatic measurements were carried out with an automated weather station to obtain continuous global radiation ( $R$ ), relative air humidity (RH), air temperature ( $T$ ) and gross precipitation ( $P$ ).

To analyze vertical changes in stand microclimate with forest height, especially the vertical increase of vapor pressure deficit, we installed three parallel sets of microclimate sensors for air temperature and relative humidity measurements (HOBO<sup>®</sup> H8 Pro Series, Onset Computer Corporation, Bourne, MA, USA) at five different forest height positions (5, 10, 15, 20, 25 and 30 m) in June 2009 (days of year 159 - 170). At each height, the microclimate parameters were separately logged every 30 minutes for 12 days. A total of 15.52 mm of rain fell during the measurement period which resembles a low-rainfall period in the study area.

To provide access to different soil layers for continuous measurement of volumetric soil water content ( $\theta$ , m<sup>3</sup> m<sup>-3</sup>), and to detect the vertical soil layering and root distribution patterns, in total 18 soil pits (3 per plot) were excavated until 3 m soil depth. In the beginning of 2007, the soil water monitoring system which consisted of 72 time domain reflectometry (TDR) probes was installed by Michael Köhler.

In addition to the 72 permanently installed TDR probes, manual measurements were carried out every second week with a self-constructed portable TDR system. A TDR probe was connected to a power supply, and the impulse frequency measured with a voltmeter (Votcraft VC260, Conrad Electronic SE, Hirschau, Germany). The probes were inserted from the soil surface vertically to 30 cm depth. For each of the six plots, 25 sampling grid points with a constant distance to each other were permanently marked. Per point, 4 measurements in N/E/S/W direction were conducted and all 100 measurements afterwards averaged over a plot.

### 2.3.2 Summary of the measured parameters

The following parameters were measured in the context of the present PhD thesis. Several of these methods are described in more detail in the following section. Additional methodological information is provided in the corresponding chapters where the obtained results are presented.

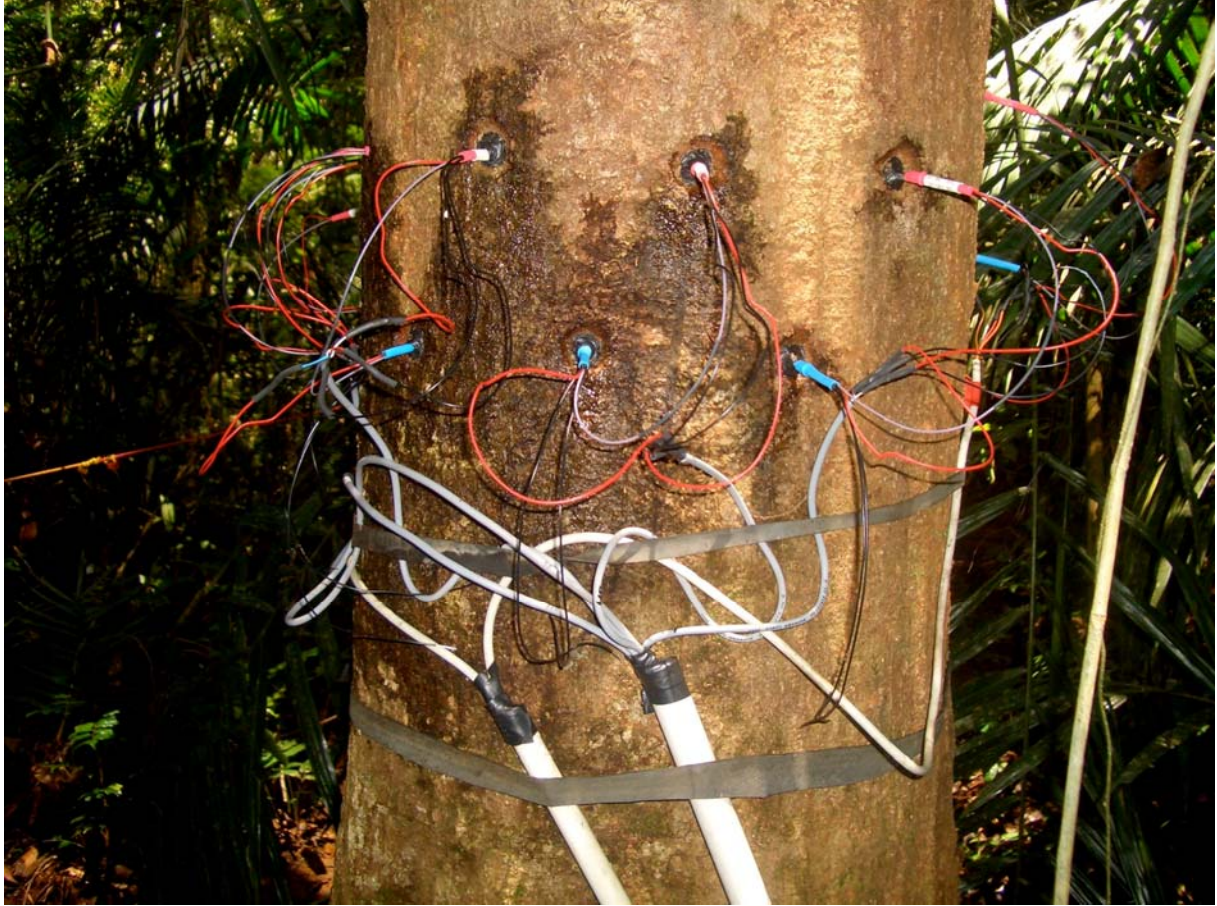
- Continuous measurement of xylem sap flux density in the trunk and microclimatic conditions from March 2007 until October 2009.
- Continuous collection of litter fall every second week from March 2007 until October 2009.
- Manual measurement of volumetric soil water content every second week from April 2007 until September 2009.
- Determination of conductive sapwood area in eight tree species and 57 trees using dyes and investigation of radial sap flow profiles with sap flux sensors inserted in five different depths in the sapwood of five tree species (see Fig. 2.4).
- Extraction of trunk cores for wood anatomical measurements, wood density and saturated water content determination.
- Several field campaigns to collect twig and leaf material from the upper canopy for determination of hydraulic conductivity, pressure-volume curves, wood anatomical traits, leaf morphology and leaf nutrient content using the tree climbing equipment and branch cutters.

### 2.3.3 Sap flow measurements

Stem xylem sap flux ( $J_s$ ,  $\text{g cm}^{-2} \text{d}^{-1}$ ) sensors were installed in the beginning of 2007 in 95 trees of eight of the most common species (Tab. 2.4) using the constant-heating (thermal dissipation) method after Granier (1985, 1987). Pairs of 25 mm long and 2 mm wide heating probes were inserted into the stem sapwood facing north and south. These probes were



manufactured according to the original design given by Granier (1985). Due to a thicker insulation of the heating wire, 73 windings resulted in a probe length of up to 25 mm instead of the original design of 20 mm, but this specification did not alter the resistance of the heating coil.



**Fig. 2.4:** Investigation of radial sap flow profiles with sap flux sensors inserted in five different xylem depths at breast height in a *Platea excelsa* tree individual.

The heating element of the upper probe used a constant current of 0.12 A with a heating power of 0.2 W. Sap flux velocity was calculated according to the empirical calibration equation given by Granier (1985, 1987):

$$J_s = 119 \cdot K^{1.231} \quad (1)$$

where  $K = (\Delta T_M - \Delta T) / \Delta T$ .  $\Delta T_M$  is the maximum temperature difference when sap flow is assumed to be zero.



**Tab. 2.4:** Biometric characteristics of the 8 common tree species investigated for sap flux in Pono Valley, Central Sulawesi on the control and roof plots. The number of investigated tree individuals (n), stem diameter at breast height (DBH) and total tree height (H) are given as well.

Family	Species	Control			Roof		
		n	DBH (cm)	H (m)	n	DBH (cm)	H (m)
Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	5	14.6 - 58.2	18.4 - 27.6	5	15.9 - 31.3	16.9 - 24.0
Compositae	<i>Vernonia arborea</i> Buch.-Ham.	3	20.1 - 43.0	21.6 - 28.7	4	13.0 - 20.5	20.1 - 25.1
Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	8	11.8 - 71.4	17.6 - 43.9	6	13.9 - 81.0	17.3 - 43.9
Lauraceae	<i>Cryptocarya laevigata</i> Blume	6	11.2 - 27.9	12.3 - 24.7	5	10.3 - 26.6	12.4 - 18.9
Icacinaceae	<i>Platea excelsa</i> Bl. var. <i>borneensis</i> (Heine) Sleum.	6	11.7 - 45.7	15.4 - 33.2	6	10.0 - 49.6	12.6 - 35.8
Myrtaceae	<i>Myrtaceae spec.</i>	7	11.0 - 33.6	13.1 - 27.9	6	10.2 - 34.7	8.8 - 33.1
Sapotaceae	<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	6	10.4 - 95.0	14.7 - 44.3	5	10.0 - 25.6	15.7 - 33.8
Sapotaceae	<i>Pouteria firma</i> (Miq.) Baehni	7	14.7 - 62.5	17.6 - 44.7	6	10.0 - 37.0	12.8 - 34.1

### 2.3.4 Derivation of the empirical sap flux velocity calibration equation

To assure that the modified sensor design did not alter the calculated sap flux densities, the empirical calibration equation given by Granier (1985, 1987) was derived in collaboration with Heinz Coners. Under conditions of thermal equilibrium of the system established between the sensor probe and its surroundings (wood and sap) and under a constant sap flux density, it can be assumed that the input of heat by the Joule effect is equal to the quantity of heat dissipated by convection and conduction at the wall of the probe (Granier 1985, Cabibel and Do 1991):

*Energy balance* (after Lu *et al.* 2004):

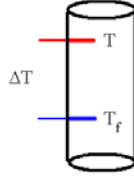
$$h \cdot S (T - T_f) = R \cdot I^2 \quad (2)$$

$h$	Coefficient of heat exchange	(W m <sup>-1</sup> °C <sup>-1</sup> )
$S$	Exchange surface area	(m <sup>2</sup> )
$T$	Temperature of the probe	(°C)
$T_f$	Temperature of the wood in absence of heating	(°C)
$R$	Electrical resistance of the heating element	(Ω)
$I$	Intensity of the electrical current	(A)

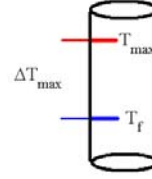
$$h = h_0 \left( 1 + \alpha F_d^\beta \right) \quad (3)$$

$h_0$	Thermal exchange coefficient at zero flux, i.e. $F_d = 0$
$\alpha, \beta$	Coefficients, depending on the quantity of heat applied
$F_d$	Sap flux density (m <sup>3</sup> m <sup>-2</sup> s <sup>-1</sup> )

$F_d \neq 0$  (sap flow is present)



$F_d = 0$  (no sap flow present)



Insert (3) in (2):

$$h_0 \left(1 + \alpha F_d^\beta\right) S (T - T_f) = R I^2 \quad (4)$$

Assume  $F_d = 0$ :

$$R I^2 = h_0 (1) S (T - T_f) \quad (5)$$

$$h_0 = \frac{R I^2}{S(T_{\max} - T_f)} \quad (6)$$

Resolve (3) for  $F_d$ :

$$h = h_0 \cdot \left(1 + \alpha F_d^\beta\right) \quad (7)$$

$$\left[ \frac{h - h_0}{h_0} \cdot \frac{1}{\alpha} \right]^{\frac{1}{\beta}} = F_d \quad (8)$$

Insert (2) and (6) in (8):

$$F_d = \left[ \frac{1}{\alpha} \cdot \frac{\left( \frac{R I^2}{S(T - T_f)} \right) - \left( \frac{R I^2}{S(T_{\max} - T_f)} \right)}{\left( \frac{R I^2}{S(T_{\max} - T_f)} \right)} \right]^{\frac{1}{\beta}} \quad (9)$$

$$F_d = \left[ \frac{1}{\alpha} \cdot \left( \frac{T_{\max} - T_f}{T - T_f} - 1 \right) \right]^{\frac{1}{\beta}} \quad (10)$$

*Original equation after Granier (1985) and in Lu et al. (2004)*

$$F_d = \left[ \frac{1}{\alpha} \cdot \left( \frac{\Delta T_{\max}}{\Delta T} - 1 \right) \right]^{\frac{1}{\beta}} \quad (11)$$

where  $K$  (sap flow index) is:

$$K = \frac{\Delta T_{\max}}{\Delta T} - 1 \quad (12)$$

According to the derivation of the original calibration equation, ‘exchange surface area’ and ‘electrical resistance of the heating element’ are crossed out. Our modified sensor design had the same number of windings (73) given by the original design and the resistance of the heating coil was unaltered. Accordingly, we could confirm that the modified sensor design did not alter the calculated sap flux density, even though the sensor was elongated.

### 2.3.5 Litter traps

In total, 72 litter traps ( $0.75 \times 0.75$  m aperture), 12 per plot, were installed in March 2007. The litter was collected every two weeks and sorted into leaves and other fine litter components (in particular flowers, fruits and small twigs). At every second sampling date, all leaves were scanned with a flat bed scanner to determine the leaf area using the software WinFolia 2005 (Régent Instruments, Quebec, Canada). Specific leaf area (SLA,  $\text{cm}^2 \text{g}^{-1}$ ) was calculated by relating measured leaf area to the corresponding dry weight (48 h,  $70^\circ \text{C}$ ).

### 2.3.6 Selected tree physiological and morphological parameters measured in 50 trees from the control plots

To analyse the influence of tree height or wood density on several tree physiological and morphological attributes, 50 trees from the control plots (Tab. 2.5), most of them equipped with sap flux sensors (Tab. 2.4), were chosen for the investigation of several parameters.

**Tab. 2.5:** Biometric characteristics of the 50 investigated tree individuals from the control plots. Number of tree individuals (n), range of tree height (H) and DBH, and total above ground biomass (AGB) per species for this forest stand for all trees DBH > 2 cm, for further information see Culmsee *et al.* (2010).

Species	Family	(n)	H (m)	DBH (cm)	AGB (MG ha <sup>-1</sup> )
<i>Santiria apiculata</i> A.W. Benn.	Burseraceae	8	17.4 - 29.4	14.6 - 58.2	7.3
<i>Vernonia arborea</i> Buch.-Ham.	Compositae	5	19.5 - 28.7	20.1 - 43.0	4.3
<i>Castanopsis acuminatissima</i> (Blume) Rheder	Fagaceae	12	17.6 - 50.6	11.8 - 66.0	52.4
<i>Platea excelsa</i> Bl. var. <i>borneensis</i> (Heine) Sleum.	Icacinaeae	5	15.4 - 33.2	11.7 - 45.7	5.6
<i>Cryptocarya laevigata</i> Blume	Lauraceae	8	12.3 - 24.7	11.2 - 27.9	2.0
<i>Myrtaceae spec.</i>	Myrtaceae	2	13.1 - 17.4	11.0 - 14.0	1.3
<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	Sapotaceae	3	31.8 - 44.3	53.7 - 95.0	30.9
<i>Pouteria firma</i> (Miq.) Baehni	Sapotaceae	7	12.8 - 36.1	14.7 - 66.5	19.7

The following parameters were measured:

- Diameter at breast height (DBH, cm).
- Tree height (*H*, m). See chapter 3.2.5.
- Stem wood density ( $\rho$ , g cm<sup>-3</sup>) determined with wood cores extracted at breast height. See chapter 4.2.2.
- Twig hydraulic properties. These were leaf-specific conductivity (LSC, kg m<sup>-1</sup> MPa<sup>-1</sup> s<sup>-1</sup>) and specific conductivity (ks, kg m<sup>-1</sup> MPa<sup>-1</sup> s<sup>-1</sup>). See chapter 3.2.3.
- Mean leaf size ( $A_L$ , cm<sup>2</sup>), specific leaf area (SLA, cm<sup>2</sup> g<sup>-1</sup>) and Huber value (HV, 10<sup>-4</sup>). See chapter 6.2.10.
- Leaf nutrient contents and isotope ratios of carbon, nitrogen and oxygen ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{18}\text{O}$ ). See chapter 6.2.10.
- Xylem sap flux density (XFD, g cm<sup>-2</sup> d<sup>-1</sup>). See chapter 2.3.3.

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### **3 THIRD CHAPTER**

#### **VESSEL DIAMETER AND XYLEM HYDRAULIC CONDUCTIVITY INCREASE WITH TREE HEIGHT IN TROPICAL RAINFOREST TREES IN SULAWESI, INDONESIA**

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## Vessel diameter and xylem hydraulic conductivity increase with tree height in tropical rainforest trees in Sulawesi, Indonesia

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### Abstract

In humid environments, where trees rarely experience severe soil water limitations, the hydraulic system of trees requires a functional architecture for an effective transport of water to the crown despite of a comparably low atmospheric evaporative demand for most of the year. Strategies in adapting hydraulic properties of tropical trees to an aseasonally wet climate are less studied, as is the impact of tree height growth on the hydraulic conductivity and vessel anatomy of tropical canopy trees. We analyzed the dependence of hydraulic architecture on tree height in several phylogenetically different canopy tree species growing under the aseasonally humid climate of a lower montane rainforest in Sulawesi, Indonesia. We determined leaf-specific conductivity (LSC), sapwood-area specific hydraulic conductivity ( $k_s$ ), and wood anatomy (vessel diameter and density) of exposed twigs and the trunk of 51 trees of eight abundant species ranging in tree height between 6.5 and 44 m. Rates of LSC as well as  $k_s$  significantly increased with tree height ( $r^2_{\text{adj}} = 0.50$  and  $0.46$ , respectively) and this increase with tree height was closely coupled with an increase in mean vessel diameters along the height gradient. We found this trend consistent for both the trunk ( $r^2_{\text{adj}} = 0.61$ ) and the twig ( $r^2_{\text{adj}} = 0.47$ ) xylem vessel diameters. In contrast, the negative relationship between vessel density and height was significant for twigs, but not for the trunks. We assume that under conditions of prevailing high atmospheric humidity, it seems more advantageous for tall trees to focus on a high plant hydraulic conductance in the trunk- as well as the upper crown conducting-tissue, rather than to minimize the drought-induced risk of xylem embolism. However, the tree size-effect in our study has to be validated at a broader species-level before universal rules could be deduced.

**Key words:** *adaptation, hydraulic architecture, leaf specific conductivity, tree size, vessel density, vessel size.*



### 3.1 INTRODUCTION

The principal path of mass water flow in trees is through vessels that form a continuous network from roots to shoots. The hydraulic conductivity of these elements is determined by their anatomical characteristics and strongly depends on the number, radius and length of the vessels. The size of the hydroactive xylem area depends on how long the xylem elements remain active.

When trees grow taller, it is essential that their vessels remain fully functional to secure sufficient water supply to the top of the canopy. Adaptations in the hydraulic architecture that contribute to maintain the water balance with height growth include the production of xylem vessels with higher conductivity (i.e., more and larger vessels) (Pothier *et al.* 1989) and a decrease in the transpiring leaf area in relation to the conductive xylem area (Vanninen *et al.* 1996, McDowell *et al.* 2002). A highly functional vessel system in tall trees is even more important since the total hydraulic resistance within the soil-plant-atmosphere continuum tends to increase with tree height (Martínez-Vilalta *et al.* 2007). A higher hydraulic resistance can cause leaf water deficits resulting in a declining leaf water potential and turgor and subsequent consequences for leaf growth and leaf metabolism. The resulting restrictions for photosynthetic carbon gain can ultimately constrain trees to grow taller (Ryan and Yoder 1997, Koch *et al.* 2004). Consequently, a high plant hydraulic efficiency (i.e., higher rates of leaf-specific and sapwood-area specific conductivity) supposed to be an important prerequisite for maintaining high levels of productivity in tall-growing forest trees (Tyree 2003). However, increasing conductivity in tall trees may conflict with the necessity to minimize the risk of embolism (i.e., the cavitation-induced breakdown of the hydraulic water flow in tree vessels, which can cause branch dieback and plant death).

The plasticity of plant hydraulic functioning with increasing size has stimulated numerous research efforts mostly in temperate ecosystems (Mencuccini *et al.* 1997, Williams *et al.* 2001, Oren and Pataki 2001, McDowell *et al.* 2002, Delzon *et al.* 2004, Aspelmeier and Leuschner 2004, Woodruff *et al.* 2007), but also in the seasonally dry tropics (Oberbauer *et al.* 1987, Borchert 1994, Phillips *et al.* 2001, Choat *et al.* 2005, Kume *et al.* 2007). Where seasonal drought stress occurs, trees can either drop their leaves (temperate broad-leaved or tropical deciduous trees) or can adapt their hydraulic architecture to withstand the greater xylem pressure gradient under dry season conditions. Adaptations include lower rates of leaf-specific hydraulic conductivity in drought-tolerant evergreen tropical species (Choat *et al.* 2005) as well as in conifers (Williams *et al.* 2001, Delzon *et al.* 2004, Koch *et al.* 2004,

Woodruff *et al.* 2007). Reducing stomatal conductance ( $g_s$ ) in response to elevated vapor pressure deficit (VPD) is another strategy to avoid reductions in leaf turgor and to decrease the risk of xylem embolism. These strategies are increasingly advantageous with growing tree height, when hydraulic resistance and water flow path way increase (Williams *et al.* 2001).

The situation may be different in humid environments, where trees rarely, if ever, experience severe soil water limitations. In a Panamanian humid forest, xylem sapwood characteristics and sap flow density were closely related to tree diameter at breast height (DBH) across several co-occurring canopy species (Meinzer *et al.* 2001). In contrast, Phillips *et al.* (1999) found no consistent relationship between sap flux density and DBH for the same region. In moist climates, the hydraulic system of trees requires a functional architecture for an effective transport of water to the crown despite of a comparably low atmospheric evaporative demand, which would help to force water through the plant. Growth and physiological functioning of tree species living in humid areas was closely related to the wood-hydraulic and -anatomical characteristics as well as to leaf-morphologic traits and chemical composition (Ryan and Yoder 1997, Reich *et al.* 1999). In a comparison of different forest biomes, specific leaf area, mass-based photo-synthesis and stomatal conductance were greatest in moist compared to drier sites, while leaf nitrogen content was negatively related to water availability and positively to leaf life span (Reich *et al.* 1999). However, strategies in the hydraulic properties and vessel anatomy of trees growing under aseasonally wet conditions have not been studied yet and if these strategies universally scale with tree size still has to be solved.

In this study, we aimed to analyze the dependence of hydraulic architecture on tree height across several phylogenetically different canopy species growing under an aseasonally wet tropical climate. The study covered 51 trees in a lower montane rainforest in Sulawesi, Indonesia, where we determined leaf-specific conductivity (LSC), sapwood-area specific hydraulic conductivity ( $k_s$ ), and wood anatomy (vessel size and density) of exposed twigs and the trunk of eight abundant species and their relationship to tree height. We hypothesized that the hydraulic architecture differs between small- and tall-growing canopy trees. In order to guarantee sufficient water transport to the top of the crown, tall canopy trees growing under prevailing high atmospheric humidity should show adaptive differences in their hydraulic system compared to smaller growing canopy trees.

## 3.2 MATERIALS AND METHODS

### 3.2.1 Study area and macroclimatic conditions

The study was carried out in a tropical rainforest at lower montane elevation (1050 m a.s.l.) in the Pono Valley located on the western boundary of the Lore Lindu National Park of Central Sulawesi, Indonesia (UTM 51M, 0172451, 9834650). The soils of this old-growth forest developed on metamorphic rocks, classified as Acrisols (FAO-classification). In the study area, mean annual precipitation is c. 3000 mm. At the most, two months per year receive < 100 mm rainfall, which classified this climate as perhumid (Holdridge *et al.* 1971). During the measurement year 2008 about 240 (66%) days received > 1.0 mm of rainfall. In 2008, mean annual atmospheric vapor pressure deficit (VPD) was 0.33 kPa and mean annual temperature was 20.6 °C (own unpublished data).

**Tab. 3.1:** Observed ranges of tree height (m), diameter at breast height (DBH; cm), Huber value ( $HV \times 10^{-4}$ , mean in parentheses) of the sampled trees of 8 species. Mean (SD in parentheses) empirical leaf-area specific hydraulic conductivity ( $LSC \times 10^{-4}$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) and branch-sapwood-area specific hydraulic conductivity ( $k_s$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) of exposed, upper-crown twigs of the measured tree species.

Species	<i>n</i>	Height	DBH	$HV \times 10^{-4}$	$LSC \times 10^{-4}$	$k_s$
<i>S. apiculata</i>	11	6.5 - 29.4	11.7 - 41.1	1.69 - 7.72 (2.80)	6.09 (3.35)	2.43 (1.38)
<i>V. arborea</i>	8	19.5 - 26.9	14.3 - 30.5	1.16 - 4.34 (2.06)	3.96 (2.54)	2.11 (1.42)
<i>C. acuminatissima</i>	10	27.5 - 44.2	22.2 - 131.8	0.71 - 2.44 (1.57)	15.90 (7.70)	10.49 (3.47)
<i>P. excelsa</i>	6	12.8 - 27.2	10.1 - 25.4	1.34 - 2.57 (1.99)	3.26 (2.63)	1.63 (0.89)
<i>C. laevigata</i>	4	12.7 - 22.8	17.5 - 22.7	1.29 - 2.19 (1.75)	3.95 (2.68)	2.14 (0.87)
<i>Myrtaceae sp. 8</i>	2	11.3 - 11.7	15.6 - 16.7	1.08 - 1.89 (1.48)	5.15 (9.43)	3.88 (1.51)
<i>Myrtaceae sp. 10</i>	3	11.0 - 29.0	11.7 - 18.0	1.35 - 2.00 (1.63)	8.79 (2.44)	5.34 (0.31)
<i>P. firma</i>	7	12.8 - 36.1	10.0 - 66.5	1.29 - 4.84 (2.50)	4.09 (2.57)	1.68 (0.80)

### 3.2.2 Tree selection

The hydraulic measurements were conducted at six plots of 40 x 40 m in nearly level terrain. We chose 51 tree individuals of eight common tree species with a DBH > 10 cm (Tab. 3.1) for xylem hydraulic conductivity measurements and xylem anatomical studies. Each species was represented by two to eleven tree individuals differing in canopy height. We focused on mature trees only and included species differing in their growth strategies in order to represent the variability of tree functional types and tree families in this species-rich tropical rainforest. Our species selection included slow-growing mid-story species (e.g., *Cryptocarya laevigata*, *Pouteria firma*, *Myrtaceae spec.*) as well as fast-growing canopy species (e.g., *Platea excelsa*, *Vernonia arborea*, *Castanopsis acuminatissima*). The broad selection of species implied that a given species could not be represented by individuals from all height classes (i.e., 10-20, 20-

30 and 30-50 m in our study). While most of the sampled trees ranged between 10 to 30 m in height, trees > 40 m were represented by *C. acuminatissima* only. In total we measured 51 trees ranging in height from 6.5 - 44.2 m (Tab. 3.1) which is representative for the average forest height structure in this forest.

### 3.2.3 Hydraulic conductivity ( $k_h$ )

We used branches from the upper crown of each tree individual for measuring the empirical axial hydraulic conductivity. Branches from trees < 12m were sampled with a pruner, while branches from taller trees were collected by climbing the trees. Per tree, 3-6 branches with a mean diameter of 7.7 mm ( $\pm 1.4$  SD) and a mean length of 85 mm ( $\pm 33.3$ ) together with the supported leaf material were collected. The branch segments were immediately stored in polyethylene tubes filled with water containing a sodium-silver-chloride complex (Micropur, Katadyn, Wallisellen, Switzerland) to prevent microbial growth. Samples were immediately taken to the laboratory and stored at 4 °C. Prior to hydraulic measurement, each segment was recut under water with a razor blade and measurements of  $k_h$  were conducted at least three times for each branch following Sperry *et al.* (1988). For the measurement, we used distilled water containing the same sodium-silver-chloride complex as described above. Before entering the branch segment, the solution was forced through a 0.20  $\mu$ m membrane filter (Maxi Capsule, Pall, U.S.A.). Water extruding from the distal end of the segment was collected and weighted at an accuracy of 0.1 mg.

Hydraulic conductivity ( $k_h$ ) can be expressed as:

$$(1) \quad k_h = F \cdot \frac{l}{\Delta P} = \frac{\Delta V}{\Delta t} \cdot \frac{l}{\Delta P} \left( \frac{\text{kg m}}{\text{MPa s}} \right)$$

where  $F$  is the water flux ( $\text{kg s}^{-1}$ ),  $l$  is the length of the branch segment (m),  $\Delta P$  is the pressure difference applied to the branch segment (MPa),  $\Delta V$  is the amount of water flowing out of the branch segment (kg) and  $\Delta t$  is the time interval (s). After measuring actual conductivity ( $k_h^{\text{act}}$ ), the segments were flushed at a pressure of 0.12 MPa to achieve maximum axial conductivity ( $k_h^{\text{max}}$ ).

For each species we established a cross-sectional factor (i.e., total cross-sectional area divided by xylem cross-sectional area without pith and bark), which was used to calculate the total branch cross-sectional area excluding pith and bark using the branch diameter. The branch cross-sectional area ( $\text{m}^2$ ) not including pith and bark and the supported leaf area ( $\text{m}^2$ ) were used to calculate sapwood-area specific ( $k_s$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) and leaf-specific conductivity

(LSC,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), respectively. We determined the Huber value (HV) as the ratio of the sapwood cross-sectional area to the supported leaf area distal to the measured branch segment. Length and mean diameter of the segments were determined and the samples stored in 70% ethanol for further anatomic analyses.

#### 3.2.4 Vascular anatomy

For the analysis of xylem anatomy of twigs, small cuts were taken from the transverse section of the branch segments used to measure kh. The cuts were immersed in Polyethylenglycol, (Type 2000, Merck Schuchardt, Hohenbrunn, Germany). After hardening, 10–20  $\mu\text{m}$  thick discs were cut with a sliding microtome (Hn 40, Reichert-Jung, Germany), mounted in microscope plates and submersed in Euparal (Chroma, Münster, Germany). Finally, the discs were oven dried for a week at 50 °C.

In the case of the stems, we took samples with an increment corer (5 mm diameter, Haglöf, Långsele, Sweden). With the sliding microtome, we obtained 10–20  $\mu\text{m}$  thick cuts from the radial side of the cores. Samples for microscope analysis were taken from the outer 1–2 cm. The same xylem analytical procedure as for twig samples was applied thereafter.

We photographed the cross-sections using a digital camera (PowerShot A620, Canon, Japan) connected with a light microscope (Photomikroskop III, Zeiss, Jena, Germany). As scale reference an object micrometer (resolution: 10  $\mu\text{m}$ ) was used. Images were analyzed with ImageJ (v1.36b, <http://rsb.info.nih.gov/ij>) via particle analysis-function to estimate the idealized radius ( $r$ ) of the vessels by means of lumen area ( $A = \pi r^2$ ), vessel density ( $n \text{ mm}^{-2}$ ) and total cross-sectional area of all vessels ( $\text{m}^2$ ). Several twig discs were too large to obtain a complete image within the smallest resolution of our micro-scope. To obtain the total cross-sectional area of these twig samples, four separate sections were compiled using Adobe Illustrator CS2 (Version 12.0.1, Adobe Systems Incorporated, U.S.) prior to the digital analyses of the disc area. Since xylem vessel studies are very labour intensive, we used fewer repetitions for the xylem anatomy analyses than for kh measurements (Tab. 3.1 and 3.2).

#### 3.2.5 Tree height

Tree height was measured using a laser tree height meter (Vertex III Forester, Haglöf, Långsele, Sweden). The slopes of the sites were taken into account by determining the angle of the stems for calculating total stem length.

### 3.2.6 Microclimate measurements

For determining differences in vertical microclimate with tree canopy heights, we installed microclimate sensors for air temperature and relative humidity (HOBO® H8 Pro Series, Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532) at four different height positions along stem and canopy of one single emergent tree (*Ficus spec.*) in June 2009 (days of year 159 - 170). The tree was selected by random and where the upper canopy could be accessed by climbing. Sensors were installed at 5, 10, 20 and 30 m representing lower canopy strata and upper canopy conditions. At each height, microclimate parameters were separately logged every 30 minutes for 12 days. This period resembled a low-rainfall period in the study area. A total of 15.52 mm precipitation fell during the measurement campaign, distributed among five nights (data not shown). For characterizing the vertical microclimate, we restricted analyses to the sun-light hours between 6 am and 6 pm relevant for plant hydraulic activity. We calculated the atmospheric vapor pressure deficit (VPD, kPa) from air temperature and relative air humidity following Allen *et al.* (1998).

### 3.2.7 Statistical analysis

We determined the relation of the hydraulic architecture with tree size by plotting hydraulic parameters (LSC,  $k_s$ , vessel diameter and vessel density) against tree height as the independent variable. Regression analyses were conducted across all eight measured species for analyzing data representative for tree height distribution in the stand and to reach at stand-level patterns in hydraulic efficiency.

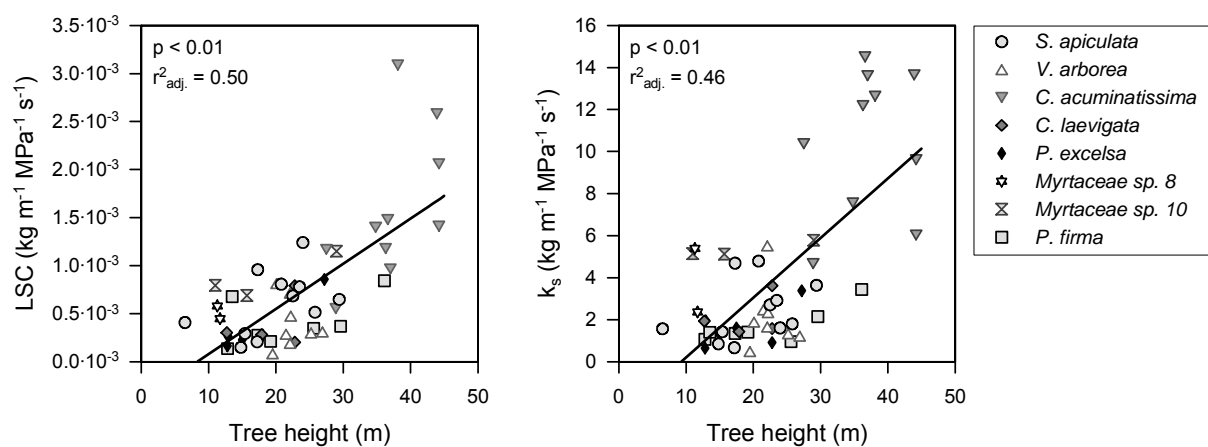
Significant differences in microclimate (VPD) along the vertical tree height gradient from 5 m and 30 m were determined by repeated measure ANOVA and Tukey's HSD as post hoc test. We tested for significant differences in the variance of VPD within two single days representing cloudy and cloudless conditions and within the entire 12-day campaign. Because values of VPD were highly skewed we log-transformed data prior to analyses.

## 3.3 RESULTS

### 3.3.1 Leaf- and sapwood-specific hydraulic conductivity and tree height

We found a significant positive correlation of LSC as well as  $k_s$  with increasing tree height across species (Fig. 3.1). Highest values of LSC and  $k_s$  were measured in twigs of the tall-growing *C. acuminatissima* (Fig. 3.1). Lowest values of LSC and  $k_s$  were not found in the

smallest measured tree; rather, low specific conductivities were found in twigs of various tree species ranging in height between 10 and 20 m. Hydraulic conductivities differed greatly between and within species. *V. arborea* showed consistently low values of LSC and  $k_s$  across a comparatively narrow range in tree height (19.5 - 26.9 m). Rates of LSC and  $k_s$  varied greatly among individuals of different height (6.5 - 29.4 m) in *S. apiculata* (Fig. 3.1). The steepest increase in LSC and  $k_s$  with increasing tree heights (27.5 - 44.2 m) was found in *C. acuminatissima*. Due to the absence of other tree species > 30 m in our sample, *C. acuminatissima* had a large influence on the height-related increase in LSC and  $k_s$  found in our study.

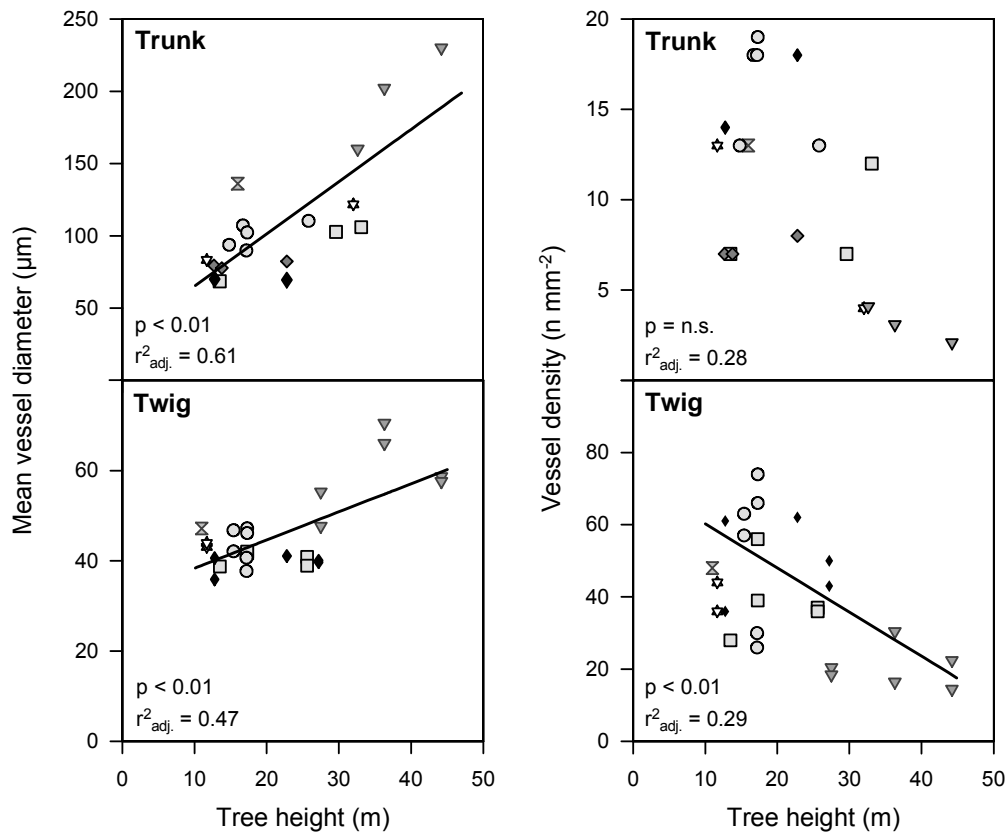


**Fig. 3.1:** Empirical leaf-specific (LSC) and sapwood-specific hydraulic conductivity ( $k_s$ ) of exposed upper-canopy twigs of 8 tree species as related to tree height. Regressions are based on each 2 to 11 tree individuals of the 8 species (see Tab. 3.1).

### 3.3.2 Vessel anatomy and tree height

Across species, we found a significant, positive correlation between tree height and the xylem vessel diameter of stems. Mean trunk vessel density was negatively related to tree height, though not significantly (Fig. 3.2). Plotting mean twig vessel diameter and mean twig vessel density against tree height was significant in both cases. The positive correlation between twig vessel diameter and height was less steep than for the trunk vessel sizes. Nevertheless, the negative relationship between twig vessel density and height was much more pronounced than found for the trunks (Fig. 3.2).

Within species, mean trunk vessel diameter showed an increasing and vessel density a declining trend with increasing tree height (Fig. 3.2). However, these correlations could not be verified statistically which is partly a consequence of low numbers of replicates per species (Tab. 3.2). Nevertheless, a general trend of increasing vessel diameter and decreasing vessel



**Fig. 3.2:** Mean vessel diameter and vessel density of trunks and twigs as related to tree height. Regressions are based on two to 11 tree individuals per species measured (see Tab. 3.1). For symbol explanation see Fig. 3.1.

density with tree height was observed across and within species and this trend could be found for the trunk as well as for the twig xylem tissues.

The correlation between vessel diameter and height was less rigid for upper canopy twigs than for the trunk xylem. Twigs from the upper crown varied less in diameter (values not shown) than the DBH across species (Tab. 3.1). The narrow range in twig diameter across trees most likely resulted in a more equalized xylem anatomy across species and hence showed a less pronounced increase in vessel size with tree height. However, species with a large (small) mean trunk vessel diameter also showed a large (small) mean twig vessel diameter (Tab. 3.2). Maximum vessel diameters were observed in *C. acuminatissima* for twig- and trunk-xylem. The largest conducting vessels of trunks and twigs in *C. acuminatissima* were accompanied by the lowest vessel densities. The smallest trunk and twig xylem vessel diameters accompanied by high vessel densities were found in *P. excelsa* (Tab. 3.2).

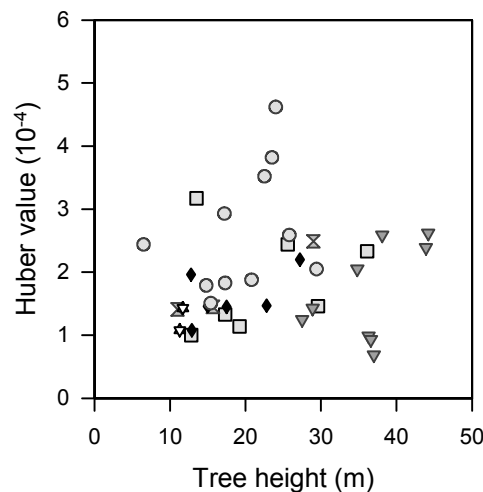


**Tab. 3.2:** Mean (SD in parentheses) xylem vessel diameter ( $\mu\text{m}$ ) and vessel density ( $\text{n mm}^{-2}$ ) of the trunks (at breast height) and of the exposed, upper-crown twigs of 7 species used for the hydraulic measurements.

Species	<i>n</i>	Trunk vessel diameter	Trunk vessel density	Twig vessel diameter	Twig vessel density
<i>S. apiculata</i>	5	100.3 (32.9)	16.3 (3.2)	44.1 (10.1)	52.7 (19.9)
<i>V. arborea</i>	-				
<i>C. acuminatissima</i>	3	199.2 (91.9)	2.9 (0.7)	60.3 (21.6)	20.1 (5.6)
<i>P. excelsa</i>	2	69.4 (26.1)	15.9 (2.7)	39.8 (7.9)	50.4 (11.2)
<i>C. laevigata</i>	3	80.3 (30.9)	12.6 (0.8)		
Myrtaceae sp. 8	2	103.8 (49.8)	7.4 (0.1)	43.5 (10.6)	40.0 (6.2)
Myrtaceae sp. 10	1	136.1 (40.0)	9.2 (0.1)	47.1 (12.1)	48.1 (8.0)
<i>P. firma</i>	3	105.4 (57.1)	6.4 (1.6)	40.7 (8.6)	39.1 (10.2)

### 3.3.3 Huber value and tree height

The calculated Huber value (HV) varied greatly across and within species. We found no clear trend of HV with increasing tree height across or within species (Fig. 3.3). Independent of tree height, HV averaged between 1.57 and 2.80 across species (Tab. 3.1).



**Fig. 3.3:** Huber value (HV; i.e., ratio of the cross-sectional area of sapwood to the distal leaf area) as related to tree height. For symbol explanation see Fig. 3.1.

### 3.3.4 Vertical microclimate

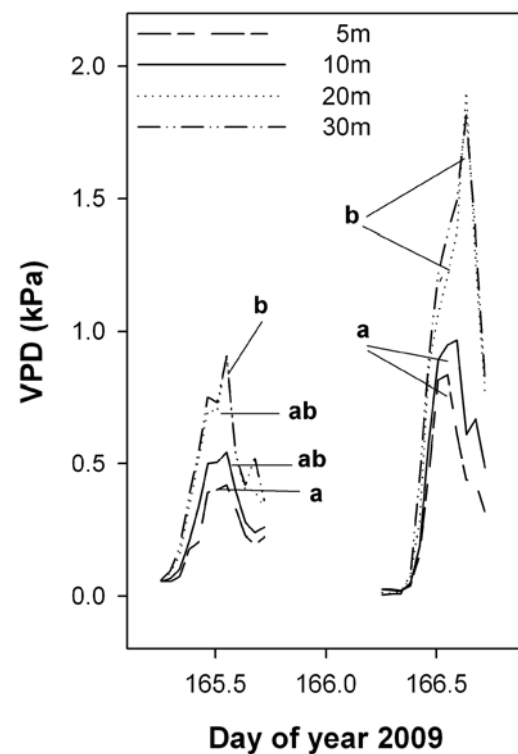
Vertical VPD significantly increased from 5 to 30 m, when analyzed for the 12-days-period (Tab. 3.3) and when analyzed for two single days differing in cloud cover (Fig. 3.4). However, differences in the diurnal course of VPD were not significant between 5 and 10 m and between 20 and 30 m at either of the analyzed time periods (Tab. 3.3, Fig. 3.4). Saturation deficits at 5 m reached daytime maxima of 0.4 and 0.9 kPa around noon at a cloudy and a

cloudless day, respectively. Maximum daytime values of VPD at 30 m were 0.9 around noon at a cloudy and 1.8 kPa in the early afternoon at a cloudless day.

**Tab. 3.3:** Vertical microclimate as measured between 5 and 30m height (h) along the stem and within the canopy of one single tree for 12 days in June 2009. Given are mean values of atmospheric vapor pressure deficit ( $VPD_{mean}$ , kPa; SD in parentheses) and maximum values ( $VPD_{max}$ ) for the 12-days-measurement campaign. Analyses are restricted to daytime hours (6 am to 6 pm). Different letters indicate significant differences between height positions ( $p < 0.001$ , Tukey's HSD).

h	$VPD_{mean}$	$VPD_{max}$
5m	0.28 (0.24) a	0.88
10m	0.36 (0.30) a	1.12
20m	0.58 (0.46) b	1.9
30m	0.63 (0.50) b	1.81

Differences in the daytime course of VPD between height positions were less pronounced on cloudy than on cloudless days (Fig. 3.4). As a consequence, differences in VPD between 10 and 30 m were significant at cloudless, but not at cloudy days (Fig. 3.4). Highest daytime maxima were measured at 20m height position during both a cloudy (0.91 kPa) and a cloudless (1.9 kPa) day, probably because the lower canopy maintained a higher over-temperature during sun-light hours than the exposed upper canopy.



**Fig. 3.4:** Diurnal courses of atmospheric vapor pressure deficit (VPD) at four different height positions along a vertical gradient in one single tree as measured on a cloudy (left) and a cloudless (right) day. Different letters indicate significant differences in VPD among height positions within one day ( $p < 0.05$ ).

### 3.4 DISCUSSION

We found a significant increase in LSC as well as in  $k_s$  with tree height across eight common tropical rainforest tree species growing under aseasonally wet conditions (Fig. 3.1). Rates of water supply with increasing size depend on the steepness of the water potential gradient between soil and leaf and the hydraulic resistance of the water flow pathway. To increase the hydraulic efficiency (i.e., high rates of leaf- and sapwood-specific conductivity) despite longer water pathways, increasing gravitational forces and increasing resistances with tree

height, large trees tend to widen their vessels (Pothier *et al.* 1989, West *et al.* 1999). Greater vessel diameters accompanied by high conductivities for rapid water transport usually lead to an elevated risk of xylem embolism and hence xylem dysfunction (Williams *et al.* 2001). Therefore, hydraulic conductivities were often found to decline with increasing tree height, in particular in partially dry environments (Williams *et al.* 2001, Delzon *et al.* 2004, Koch *et al.* 2004, Choat *et al.* 2005, Woodruff *et al.* 2007). In contrast to these observations, in our study, the hydraulic conductance increased with height and was accompanied by a strong height-related increase in mean vessel diameter in trunks and twigs across species (Fig. 3.2 and Fig. 3.3). In addition, the tallest species (*C. acuminatissima*) exhibited the largest mean vessel diameter and the highest empirically determined hydraulic conductivities. Despite large vessel diameters, the xylem of *C. acuminatissima* was not found to be more sensitive to embolism than in trees with smaller vessels (data not shown). In two neotropical *Piper* congeners, Engelbrecht *et al.* (2000) found greater vessel sizes and lengths in the *Piper* species from the wetter region compared to the species from drier environments. The drought-adapted *Piper* showed considerably lower hydraulic conductance and LSC values than its relative from the moist habitats. Higher hydraulic conductance and greater vessel sizes with increasing height as found in our sample may be interpreted as adaptive response with respect to water transport efficiency under relatively low soil-to-leaf water potential gradients for most of the year. The trees in our study developed under aseasonally wet conditions with a precipitation during the measurement year 2007 of c. 3000 mm. At least 66 % of the days in 2008 received more than 1.0 mm of rainfall (unpublished data). Although vertical daytime courses of VPD can differ considerably between lower and upper canopy strata on cloudless days, these differences were less pronounced under cloud cover (Fig. 3.4). Our measurements of vertical microclimate did not include typical rainy days. However, in the study area, foliage surfaces remained wet for about 50 % of the time with no differences in patterns of leaf surface wetness along a vertical gradient from 1.5 to 33 m during rainy periods (Dietz *et al.* 2007). Leaf wetness must coincide with very low VPD at the leaf surface and must hence limit plant transpiration. We assume that the diurnal courses of VPD tend to approximate along the vertical gradient from lower strata to the top of the canopy during rainy days, which account for most of the days per year. As a consequence, for our tree species studied, it might have been more advantageous to optimize for high hydraulic conductance rather than for the avoidance of embolism.

It has been recognized that forests with greater precipitation or high soil moisture availability tend to hold more leaf area per sapwood area (Waring *et al.* 1982, White *et al.* 1998). Under conditions of high air humidity and hence low evaporative demand, the stem requires a higher

leaf area per conducting sapwood area to maintain sufficient water flow despite the comparatively low soil-to-leaf water potential (Tyree and Ewers 1991). Hence, the hydraulic system of trees growing in humid environments should be characterized by high rates of LSC and  $k_s$ , but low HV, i.e., a high leaf area per conducting xylem cross-sectional area. Under the perhumid climate of Central Sulawesi, we could not find any clear trend in HV and hence in sapwood-to-leaf area ratios with tree height in the 51 measured trees. Instead, plotting HV against tree height revealed a highly scattered data set (Fig. 3.3). A possible explanation for the absence of a height dependence of HV was that the species selected for our study differed greatly in morphology and phylogenetic relatedness. Combining inherently slow- and fast-growing tree species with small and large mean leaf areas (data not shown) might indeed have masked an assumed HV-dependence on tree height. Nevertheless, hydraulic conductivity and HV behaved clearly different because LSC and  $k_s$  showed a clear increase with tree height.

The increasing LSC and  $k_s$  with tree height were closely coupled with an increase in mean vessel diameters along the height gradient and this trend was consistent for both, the trunk and the twig xylem. These results suggest that under the perhumid conditions of our study region, the adjustment of xylem vessel anatomy with tree height might be crucial for enhancing hydraulic efficiency and hence to allow for sufficient water supply to the canopy. It should be mentioned that LSC and  $k_s$  significantly increased with tree height across species at the stand-level, but this trend could not be generalized for the species-level in our sample (Fig. 3.1, statistics not shown). Due to the lack of other tall-growing species across our height gradient, trees > 30 m were mainly represented by *C. acuminatissima*. Information on LSC and  $k_s$  for small individuals of *C. acuminatissima* does not exist in our plots. Data was also missing on the hydraulic properties of other tall growing tropical species. Consequently, it cannot be entirely excluded that the observed height-related increase in LSC and  $k_s$  was due to a species-specific higher hydraulic efficiency being a characteristic of *C. acuminatissima*, but is missing in other species. Moreover, it remains to be shown as to whether hydraulic conductivity increases with tree height in tropical lowland forests with lower atmospheric humidity as well.

### 3.5 CONCLUSIONS

Across several co-occurring canopy tree species, the leaf-specific and sapwood-area specific hydraulic conductivity of twigs significantly increased with tree height in aseasonally wet tropical forest of Central Sulawesi. Our results suggest that the long distance water transport in large trees developing under perhumid conditions may depend on intrinsic adjustments of the plant hydraulic system, not only to compensate for the longer water flow path with tree

height, but also to compensate for a comparatively low leaf-to-soil water potential gradient for most of the year. Where soil water is sufficient and often atmospheric humidity close to saturation, the potential gradient between soil and canopy leaves is small. Under such conditions, it seems to increase the fitness of the tree to focus on a high plant hydraulic conductance in the trunk- as well as the upper crown conducting-tissue, rather than to minimize the drought-induced risk of xylem embolism. However, if the observed pattern is indeed universal or the result of a species-specific high efficiency of the hydraulic system of the tall-growing canopy species *C. acuminatissima* remained unsolved. In the light of the ongoing debate about the factors controlling the hydraulic architecture of trees differing in height (McDowell *et al.* 2002, Koch *et al.* 2004, Meinzer *et al.* 2005), it is therefore essential to verify the generality of evidence found in this study. In this context, changes in the hydraulic architecture with height in tropical trees still have to be validated at the species-level to gain deeper insight in the driving forces of plant water transport with increasing tree height under conditions of prevailing low evaporative atmospheric demands.

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## **4 FOURTH CHAPTER**

### **CHANGES IN VESSEL DIMENSIONS AND HYDRAULIC PROPERTIES OF THE XYLEM ALONG THE ROOT-TO-SHOOT FLOW PATH IN TROPICAL RAINFOREST TREES**

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## Changes in vessel dimensions and hydraulic properties of the xylem along the root-to-shoot flow path in tropical rainforest trees

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### Abstract

It has been hypothesized that conduits in the root xylem tend to be wider than in the stem and branches of a plant and that small-diameter roots may be particularly vulnerable to cavitations, thus acting as sort of ‘hydraulic fuse’ in the conducting system upon soil drying. Such a mechanism would restrict hydraulic failure to ‘expandable’ organs that are subsequently replaced. With this study in five tree species of a perhumid tropical rainforest in Sulawesi (Indonesia), we searched for patterns in hydraulic architecture and axial conductivity along the flow path from small-diameter roots (mean diameter 4.3 mm) through strong roots (mean diameter 130 mm) and the trunk to the terminal sun-canopy twigs (mean diameter 7.8 mm) and assessed the putative evidence in support of the ‘hydraulic fuse’ theory. Wood density differed by not more than 10 % among the organs of a species. In contrast to findings from conifers and certain dicotyledonous species, trunks and strong roots always had the largest vessels along the flow path while twig and small-root xylem had significantly smaller vessel diameters. Relative vessel lumen area as percentage of sapwood area linearly decreased from the small roots to the twigs reflecting the increase in sclerenchymatic tissue and tracheids in the xylem toward the canopy. Theoretical hydraulic conductivity was largest in strong roots and in the trunk and smallest in the sun-canopy twigs with a considerable variation among the five co-occurring species. We conclude that, at least in tropical trees from a perhumid climate, the xylem anatomy and hydraulic properties of small-diameter roots do not fit into the patterns predicted by the ‘hydraulic fuse’ theory. If xylem embolism occurs in small-diameter roots despite their relatively small conduits, rapid embolism reversal is more likely than permanent dysfunction with the need to replace the roots.

**Key words:** *Conduit tapering, hydraulic architecture, hydraulic conductivity, hydraulic fuse theory, vessel anatomy, vessel diameter, wood density.*

## 4.1 INTRODUCTION

A characteristic feature of tropical forests is their high tree species diversity which is linked to a considerable number of coexisting tree functional types (Meinzer *et al.* 2001, Culmsee *et al.* 2010, Poorter *et al.* 2010). Functional diversity is further enhanced by the fact that tree species with contrasting tree heights at maturity are often growing in the same stand (Turner 2001). So far, not much is known about the morphology and functionality of the hydraulic system of co-occurring tropical trees with contrasting phylogeny or size, and if convergent patterns in their hydraulic architecture exist.

Continuous supply of water is a prerequisite for the existence of evergreen humid and perhumid tropical rainforests (Whitmore 1993). These aseasonal forests generally possess more shallow and horizontally spreading root systems with most of the fine root mass concentrated within the top 20 cm of the soil profile (Schenk and Jackson 2002, Machado *et al.* 2007, Hertel *et al.* 2009, Jimenez *et al.* 2009). It may well be that deep-rooting as reported from certain Amazonian rainforests (e.g. Markewitz *et al.* 2010 and references therein) is a characteristic only of forests growing in a tropical humid climate with a distinct dry season, while true perhumid forests may lack this adaptation.

Roots lower their water potential in response to drying soil in order to guarantee continuous root water absorption. Beyond a certain threshold, that may depend on species and root diameter, roots may get embolized. According to his ‘segmentation hypothesis’ Zimmermann (1983) assumed that woody plants might restrict hydraulic failure to redundant organs that are readily replaced, in analogy with an electric circuit. Small-diameter roots with higher vulnerability to cavitation might act as ‘hydraulic fuses’ during soil drying, localizing failure to relatively ‘expendable’ units compared to tap roots, stems and branches (Jackson *et al.* 2000, Sperry *et al.* 2002). Additionally, embolized surface roots in dry soil layers might allow roots in wetter soil layers to continue transporting water due to translocation of negative root water potentials. These assumptions are mainly based on three findings: (a) Conduits tend to be wider in roots than in stems in the case of conifers and dicotyledons (Aloni 1987, Ewers *et al.* 1997, Gartner 1995, Psaras and Sofroniou 1999, Carlquist 2001, Martinez-Vilalta *et al.* 2002, Tyree and Zimmermann 2003, McElrone *et al.* 2004, Psaras and Sofroniou 2004, Goncalves *et al.* 2007, Petit *et al.* 2009, and references therein). (b) Increasing conduit size is related to higher conductivity according to the Hagen-Poiseuille equation, but simultaneously vulnerability to cavitation increases markedly (e.g. Tyree and Zimmermann 2003, Wheeler *et al.* 2005, Willson and Jackson 2006, Zhu and Cao 2009, Awad *et al.* 2010, Cai and Tyree

2010, Hacke *et al.* 2010). (c) Consistently, the root system of conifers, temperate or Mediterranean, Californian chaparral shrub and desert dicotyledons was found to be much more vulnerable to cavitation than the stems or branches of these species (Sperry and Saliendra 1994, Alder *et al.* 1996, Hacke and Sauter 1996, Mencuccini and Comstock 1997, Sperry and Ikeda 1997, Martinez-Vilalta *et al.* 2002, Maherali *et al.* 2006, Pratt *et al.* 2007, Domec *et al.* 2009, Gonzales-Benecke *et al.* 2010).

However, the ‘hydraulic fuse’ theory might only hold true for species adapted to the more or less frequent occurrence of drought- or frost-induced embolism, since in more humid regions the stem wood is known to produce larger vessels than the main root (Machado *et al.* 2007). We therefore postulate that in the perhumid rainforest of Central Sulawesi with annual precipitation rates > 2500 mm and a constantly high relative air humidity > 80 %, the stem wood should contain the largest vessels along the flow path in order to guarantee sufficient water flow to the canopy despite low evaporative demand. According to the model proposed by West *et al.* (1999), and the findings of the studies by Anfodillo *et al.* (2006), Petit *et al.* (2008, 2009) and others, we further assume conduits to taper acropetally from the trunk base towards the upper canopy, with the smallest vessels occurring in the terminal branches and twigs.

Vessel anatomy can provide important information needed to assess the risk of cavitation in a plant’s conducting system. Despite some controversy about the role of vessel diameter for cavitation vulnerability (e.g. Tyree and Sperry 1989, Tyree and Zimmermann 2003), it is now widely accepted that the cavitation risk increases with conduit diameter (e.g. Awad *et al.* 2010, Cai and Tyree 2010), be it due to an increasing pit pore area with increasing vessel size (Martinez-Vilalta *et al.* 2002), or another attribute linked to vessel diameters like increasing vessel length (Ewers *et al.* 1990, Cai *et al.* 2010). The link between anatomy (vessel diameters and vessel density per sapwood area) and cavitation vulnerability is also supported by indirect evidence obtained along rainfall gradients: while several studies reported a decrease in mean vessel diameters with decreasing precipitation (Carlquist 1975, 1977, Carlquist and DeBuhr 1977, Lens *et al.* 2004, Machado *et al.* 2007, DeMicco *et al.* 2008, Sterck *et al.* 2008), Maherali *et al.* (2004) could prove a decrease in cavitation vulnerability across species with decreasing rainfall. Thus, comparative xylem anatomical investigations among different organs of a tree (root – trunk – twigs) and among different species may give hints on the structure of the hydraulic system of trees, its capacity for rapid water transport under high evaporative demand and its vulnerability to dysfunction and where it can be expected to occur. Clearly, anatomical studies and models of hydraulic conductivity cannot

replace empirical studies on cavitation vulnerability and maximal conductivity in tree organs under realistic environmental conditions.

With this study in five tree species of a perhumid paleotropical rainforest, we searched for patterns in hydraulic architecture and axial conductivity along the flow path from small-diameter roots through the trunk to the distal sun-canopy twigs. In particular, we investigated putative evidence from xylem anatomy and flow path hydraulics in support of the ‘hydraulic fuse’ theory and its applicability to small-diameter tree roots in a perhumid climate. We tested the following hypotheses:

- (i) In trees growing in a perhumid climate, the vessels with the largest diameter are occurring at the trunk base, where thus the specific conductivity is highest along the root-to-twig flow path.
- (ii) The average xylem vessel diameter tapers acropetally from the trunk base towards the upper canopy, and basipetally from the trunk base to the terminal fine roots.
- (iii) Despite smaller vessels in small-diameter roots compared to the trunk, specific conductivity exceeds that in twigs manifold due to a higher vessel density in the roots.

## 4.2 MATERIAL AND METHODS

### 4.2.1 Study site and plant material

The study was carried out in a pre-montane rainforest in Pono Valley on the western boundary of Lore Lindu National Park in Central Sulawesi, Indonesia (S 01°29.6' E 120°03.4', elevation 1050 m). The climate of the study area is perhumid with a mean annual precipitation of 2901 mm, a mean annual temperature of 20.6 °C and a mean relative air humidity of 88.7 % (data derived from measurements in 2008). The forest has a canopy height of about 45 m with a few trees reaching a tree height ( $H$ ) of 55 m. Tree species diversity is high with about 130 species ha<sup>-1</sup> (Culmsee and Pitopang 2009, Culmsee *et al.* 2010). Trees with a DBH > 10 cm of five of the most common species were investigated for xylem anatomy and xylem hydraulic conductivity (Tab 4.1).

We collected wood samples of small and strong roots (according to the classification of Sutton and Tinus 1983, Tab. A4.1), trunks, and twigs. Small roots (mean diameter 4.3 mm)

and all appending fine roots were excavated with shovels by tracking a root from the trunk toward the fine branch roots.

**Tab. 4.1:** Stand characteristics of the five investigated species for trees with a DBH > 10 cm. Diameter at breast height (DBH, mean  $\pm$  1 SE), tree height (H, mean  $\pm$  1 SE), maximum tree height ( $H_{\max}$ ), above ground biomass (AGB) and stem density (SD). For further explanation see Cushman et al. (2010). The number (n) of sampled tree individuals varied per investigated organ (see Tab. 3).

Family	Species	n	DBH (cm)	H (m)	$H_{\max}$ (m)	AGB (MG ha <sup>-1</sup> )	SD (n ha <sup>-1</sup> )
Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	2 - 7	27.5 $\pm$ 2.4	21.1 $\pm$ 3.4	29.4	7.3	14.6
Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	2 - 5	33.1 $\pm$ 2.0	25.2 $\pm$ 7.8	50.6	51.1	98.6
Icacinaeae	<i>Platea excelsa</i> Bl. var. <i>borneensis</i> (Heine) Sleum.	3 - 4	17.9 $\pm$ 1.9	18.5 $\pm$ 5.1	35.7	4.3	23.6
Lauraceae	<i>Cryptocarya laevigata</i> Blume	2 - 3	17.1 $\pm$ 1.2	16.8 $\pm$ 4.8	24.7	1.9	13.9
Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	2 - 4	28.7 $\pm$ 4.3	24.4 $\pm$ 4.9	45.0	19.7	19.4

Strong root (mean diameter 130 mm) and trunk wood samples were collected with an increment corer (5 mm diameter, Haglöf, Långsele, Sweden). The twig samples were collected either with a long-reach branch cutter at 12 m height in trees of lower strata or with tree climbing equipment from the upper crown. All twigs were located either in canopy gaps or in the upper crown, where they were exposed to the full sun at least part of the day.

Since most of our results are concerned with species-specific properties, we aimed at calculating species averages of the variables investigated. We took care to select individuals of similar size and vertical position in the stand.

#### 4.2.2 *Measurement of wood density*

The wood density ( $\rho$ ) of strong roots (mean diameter  $\pm 1$  SE of the investigated root sections  $13.0 \pm 1.3$  cm,  $n = 3$  per species) and trunks (diameter at breast height  $34.5 \pm 1.5$  cm,  $n = 15-52$ ) was determined in cores taken close to the stem base. Stem cores were extracted at 1.5 m height above ground or immediately above the height where the main trunk inserts due to buttress roots. The volume of the fresh wood cores was calculated from the diameter of the increment corer and the length of the sample after removing bark and phloem. From the upper canopy, twig segments ( $7.0 \pm 0.2$  mm,  $n = 15$ ) were completely harvested. In addition, branches of  $29.0 \pm 0.3$  mm diameter ( $n = 40-103$ ) were also analyzed for wood density for comparison. The volume of these woody organs was gravimetrically determined immediately after harvest through the replacement of water after removing bark and phloem. After volume measurement, all samples were oven-dried at  $105^\circ\text{C}$  for at least four days. The dry wood cores were weighed at a precision of 0.1 mg due to their small weight and volume, the branch and twig segments at a precision of 10 mg. The dry mass of the sample was then related to the volume of the wood segment to obtain  $\rho$ .

#### 4.2.3 *Xylem anatomy, vessel size distribution and theoretical hydraulic conductivity*

Anatomical measurements (vessel lumen area, vessel diameters and densities) were conducted on cross-sections of small and strong roots, trunk wood and sun-canopy twig segments. Per species and organ, 55 to 16,700 vessels were analyzed (Tab. A2). The number of replicate organ samples varied between 3 and 16, and the number of tree individuals from 2 to 7 (see Tab. 4.3).

In addition to trunk samples extracted at breast height, three individuals of *Castanopsis acuminatissima* (Blume) Rheder (A: DBH 56.2 cm,  $H$  35.6 m; B: DBH 66.7 cm,  $H$  50.6 m; C: DBH 41.1 cm,  $H$  35.7 m) were climbed to obtain trunk cores from different stem heights (7.5, 15.0, 22.5 and 30.0 m) for analysing changes in xylem anatomy with stem height.

A sliding microtome (Hn 40, Reichert-Jung, Nußloch, Germany) was used to obtain thin transverse sections (10-20  $\mu\text{m}$ ) of root, trunk and twig wood for analyzing xylem anatomy and to calculate the theoretical hydraulic conductivity from vessel diameters according to the Hagen-Poiseuille equation (Tyree and Zimmermann 2003). Prior to microtome cutting, root and trunk cores and small twig segments were embedded in polyethylenglycol (PEG 2000, Merck Schuchardt, Hohenbrunn, Germany). The cross-sections were mounted on slides, submersed in Euparal (Chroma, Münster, Germany) and oven-dried for a week at 50 °C. Subsequently, the transverse sections were photographed at 25x or 100x magnification using a light microscope (DM5000B, Leica Microsystems, Wetzlar, Germany) equipped with a digital camera (DFC 300FX, Leica Microsystems, Wetzlar, Germany). The images were analyzed with the software ImageJ (v1.42q, <http://rsb.info.nih.gov/ij>) using the particle analysis-function to estimate single and cumulative vessel lumen area ( $\text{m}^2$ ), vessel density ( $VD$ ,  $\text{n mm}^{-2}$ ) and idealized vessel diameters ( $d$ ) from major (a) and minor (b) vessel radii using the equation given by White (1991):

$$d = \left( \frac{32 \cdot (a \cdot b)^3}{a^2 \cdot b^2} \right)^{1/4} \quad (1)$$

Single vessel diameters ( $d$ ) were used to calculate the hydraulic mean diameter ( $d_h$ ) according to Sperry *et al.* (1994):

$$d_h = \frac{\sum d_i^5}{\sum d_i^4} \quad (2)$$

By this transformation, every vessel is weighted according to its contribution to total hydraulic conductivity. According to the Hagen-Poiseuille equation, the theoretical hydraulic conductivity ( $k_h^{\text{theo}}$ ,  $\text{m}^4 \text{MPa}^{-1} \text{s}^{-1}$ ) was calculated as (Löscher 2001):

$$k_h^{\text{theo}} = \frac{\pi \sum r^4}{8\eta} \quad (3)$$

In these calculations, we used the viscosity of water ( $\eta$ ) at 20 °C ( $1.002 \cdot 10^{-3} \text{ Pa s}$ , Zwieniecki *et al.* 2001).  $k_h^{\text{theo}}$  was used to calculate the theoretical vessel lumen area-specific conductivity



( $k_s^{\text{theo}}$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) by dividing by cumulative vessel lumen area ( $A_{\text{Xylem}}$ ) and multiplying  $k_s^{\text{theo}}$  with the density of water ( $\rho$ ) at 20 °C ( $998.20 \text{ kg m}^{-3}$ , James *et al.* 2003):

$$k_s^{\text{theo}} = \frac{k_h^{\text{theo}} \cdot \rho}{A_{\text{Xylem}}} \quad (4)$$

#### 4.2.4 Root- and leaf-specific conductivity

The total fine root and leaf area distal to the analyzed xylem sections used for anatomical investigation (small roots and twigs) were calculated with the programs WinFOLIA and WinRHIZOR (Regent Instruments Inc.). The total surface area of all appending fine roots was used to obtain theoretical root-specific conductivity ( $\text{RSC}^{\text{theo}}$ ), total leaf area for calculating  $\text{LSC}^{\text{theo}}$  by dividing  $k_h^{\text{theo}}$  by the respective leaf or root areas.

#### 4.2.5 Statistical analyses

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. Comparisons of normally-distributed parameters were made with three-way general linear models (GLM). In cases of non-Gaussian distribution, the datasets were tested for significant differences between means with a non-parametric Mann-Whitney U test for pair-wise comparison. Significance was assumed at  $p \leq 0.05$  in all cases. These calculations were conducted with the SAS System for Windows 9.1 (SAS Institute, Cary, NC, USA). Linear and non-linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany).

### 4.3 RESULTS

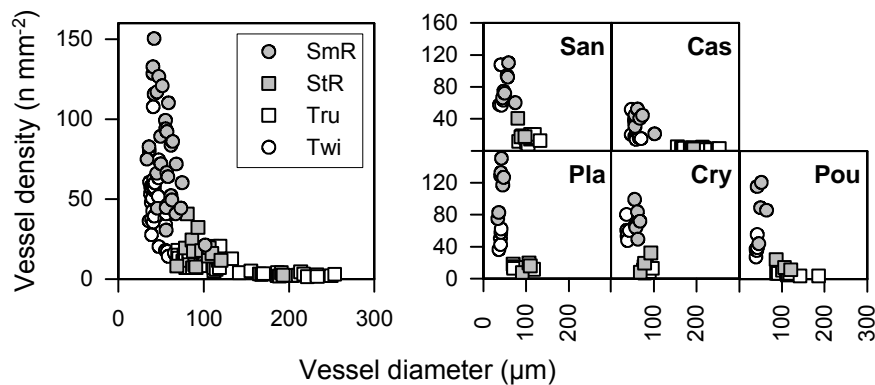
#### 4.3.1 Variation in wood density and xylem anatomy from root to twig and between species

The variability in wood density ( $\rho$ ) among the four investigated organs of a species (strong roots, trunks, branches and twigs) was low, differing by no more than 10 percent (Tab. 4.2). When averaged over the four organs,  $\rho$  varied between 0.44 and 0.48  $\text{g cm}^{-3}$  in four of the five species but was significantly smaller in *P. excelsa* (0.31  $\text{g cm}^{-3}$ ).  $\rho$  could not be related to other hydraulic or wood anatomical parameters, neither among the organs along the flow path nor across species.

**Tab. 4.2:** Wood density (WD, kg m<sup>-3</sup>) of strong roots, trunks, branches and twigs of five tree species in the Pono forest (means  $\pm$  1 SE, the number of replicates is indicated right to the organ). For the diameter of investigated samples see Methods section. Different small letters just right to the SE indicate significant differences between the organs of a species, different capital letters significant differences between the species for a given organ.

	Strong roots	n	Trunks	n	Branches	n	Twigs	n
<i>S. apiculata</i>	503.4 $\pm$ 3.2 a (a)	3	476.7 $\pm$ 10.4 a (ac)	25	467.9 $\pm$ 10.1 a (a)	56	481.6 $\pm$ 22.1 a (a)	15
<i>C. acuminatissima</i>	425.9 $\pm$ 7.6 ac (b)	3	493.3 $\pm$ 10.6 a (a)	52	539.4 $\pm$ 8.6 b (b)	103	431.8 $\pm$ 10.2 c (b)	15
<i>P. excelsa</i>	293.9 $\pm$ 11.4 acd (c)	3	330.9 $\pm$ 7.0 bc (b)	36	326.7 $\pm$ 8.6 c (c)	52	290.5 $\pm$ 13.1 d (c)	15
<i>C. laevigata</i>	528.4 $\pm$ 32.3 a (a)	3	430.8 $\pm$ 14.6 b (c)	15	426.6 $\pm$ 16.2 bc (d)	40	383.6 $\pm$ 18.3 c (d)	10
<i>P. firma</i>	455.2 $\pm$ 20.1 ab (ab)	3	476.3 $\pm$ 13.6 a (ac)	23	446.8 $\pm$ 7.3 b (e)	67	457.3 $\pm$ 18.2 ab (ab)	15

The comparison of wood anatomical properties across the four organs in a given species revealed a striking similarity between the terminal organs of the flow path, i.e. small roots and twigs that differed significantly from strong roots and the trunk in their vessel traits (Fig. 4.1, Tab. 4.3).



**Fig. 4.1:** Mean vessel diameter ( $d$ ) in relation to vessel density (VD) in four organs (small roots, strong roots, trunks and twigs) along the flow path for the five tree species (San = *S. apiculata*, Cas = *C. acuminatissima*, Pla = *P. excelsa* and Pou = *P. firma*, Cry = *C. laevigata*). Left: all five species pooled, right: species-specific plots. A decay function of the form  $y = 99377x^{-1.9529}$  was fitted to the pooled data ( $r^2 = 0.79$ ,  $p < 0.01$ ).

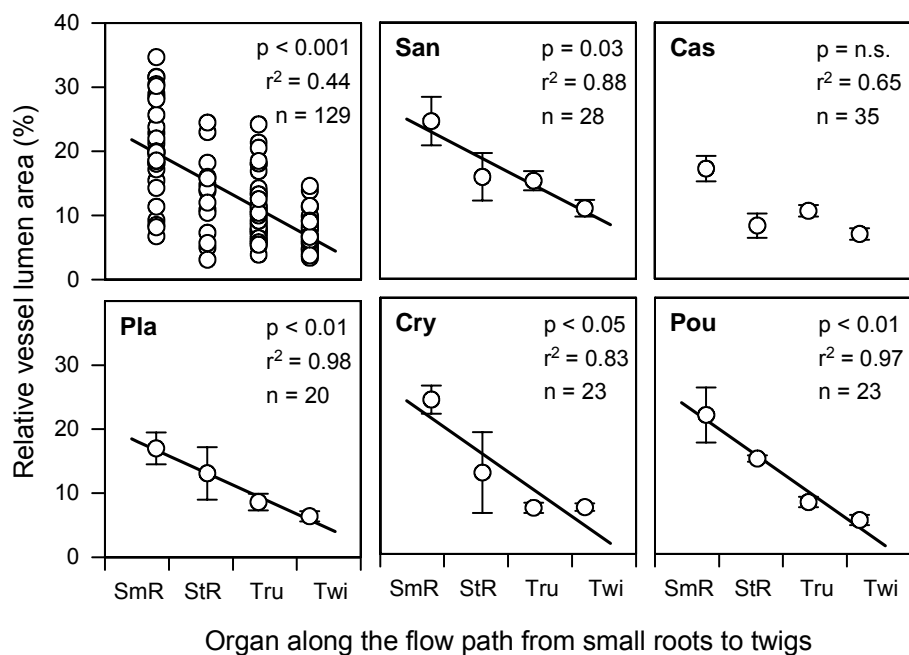
*P. excelsa* and *P. firma* deviated somewhat from this pattern by having two times higher vessel densities in their small roots than in their twigs (Tab. A4.2). Along the flow path, strong roots and trunks always had significantly larger vessels and lower vessel densities than in the more distal organs (Fig. 4.1, Tab. A4.2, Tab. A4.3).

**Tab. 4.3:** Hydraulic mean vessel diameter ( $d_h$ ,  $\mu$ m) of small and strong roots, trunks and twigs of the five species based on the microscopic analysis of vessel anatomy (means  $\pm$  1 SE, the number of tree individuals investigated is indicated right to the organ, the number of samples in parentheses). For further explanations see Tab. 4.2.

	Small roots	n	Strong roots	n	Trunks	n	Twigs	n
<i>S. apiculata</i>	87.2 $\pm$ 7.5 a AC	2 (6)	107.4 $\pm$ 2.4 a A	3 (3)	133.5 $\pm$ 3.3 b AC	7 (13)	52.0 $\pm$ 2.4 c A	3 (6)
<i>C. acuminatissima</i>	112.5 $\pm$ 9.5 ac A	2 (6)	219.6 $\pm$ 1.9 b B	3 (3)	269.5 $\pm$ 9.5 b B	5 (16)	78.0 $\pm$ 3.6 c B	5 (10)
<i>P. excelsa</i>	51.9 $\pm$ 3.6 a BC	4 (7)	117.4 $\pm$ 10.0 b A	3 (3)	106.8 $\pm$ 9.0 b A	3 (5)	46.5 $\pm$ 2.0 a A	3 (5)
<i>C. laevigata</i>	92.8 $\pm$ 2.6 a AC	2 (6)	103.6 $\pm$ 13.5 b A	3 (3)	108.0 $\pm$ 5.5 b A	3 (8)	52.1 $\pm$ 2.2 a A	3 (6)
<i>P. firma</i>	80.1 $\pm$ 6.6 ac C	2 (5)	139.2 $\pm$ 11.0 a A	3 (3)	168.8 $\pm$ 12.2 b C	4 (10)	48.7 $\pm$ 1.8 c A	3 (5)

Within a species, no significant differences between strong roots and trunks or between small roots and twigs were observed (except in *C. laevigata*). In general, larger vessels were associated with lower vessel densities in the five species. Despite distant phylogenies, the vessel diameters of a given organ tended to be rather similar among the species with mean diameters ranging between 40 and 60  $\mu\text{m}$  in small roots and twigs, and between 80 and 105  $\mu\text{m}$  in strong roots and the trunk. An exception was *C. acuminatissima*, which possessed significantly larger vessel diameters in all organs than the other four species (Fig. 4.1, Tab. A4.2).

Even though small roots and twigs at the two ends of the flow path were similar with respect to vessel diameter, a linear decrease in relative vessel lumen area (percentage of sapwood area) was detected along the flow path in all species reflecting the generally higher vessel density in the small roots (Fig. 4.2). As an average of the five species, vessels occupied 20.9 % of the sapwood area in small roots, but only 7.4 % in sun-canopy twigs, revealing a similar trend in all species.



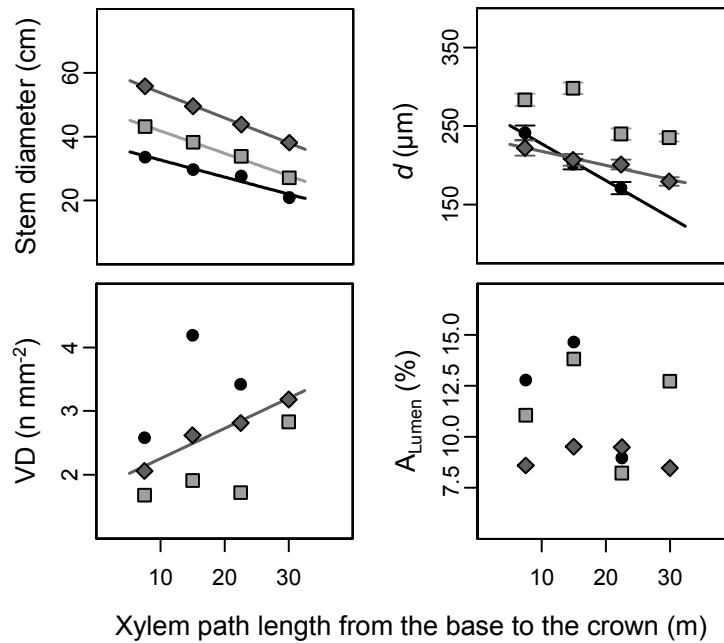
**Fig. 4.2:** Cumulative vessel lumen area as a percentage of sapwood area in the four organs (SmR = small roots, StR = strong roots, Tru = Trunks, Twi = Twigs) for the five tree species (San = *S. apiculata*, Cas = *C. acuminatissima*, Pla = *P. excelsa*, Cry = *C. laevigata*, Pou = *P. firma*). The pooled data set is also depicted (top left). Values are means  $\pm 1$  SE,  $n$  gives the number of replicate samples.

An investigation of changes in vessel anatomy with tree height in the trunk of three tall *C. acuminatissima* trees showed a significant decrease in mean vessel diameter and an increase in vessel density from 7.5 to 30 m stem height (trends significant in at least one tree). Relative

vessel lumen area remained invariant with height despite significant conduit tapering and associated increase in vessel density (Fig. 4.3).

#### 4.3.2 Specific hydraulic conductivity

The calculated theoretical axial conductivity, which bases on vessel diameter and Hagen-Poiseuille's law ( $k_s^{\text{theo}}$ ), varied considerably among the four organs along the flow path, when the species averages are considered (Tab. 4.4). Nevertheless, twigs as the most distal organ investigated along the flow path showed the smallest specific conductivities in all species, while strong roots and/or the trunk revealed the highest specific conductivities.



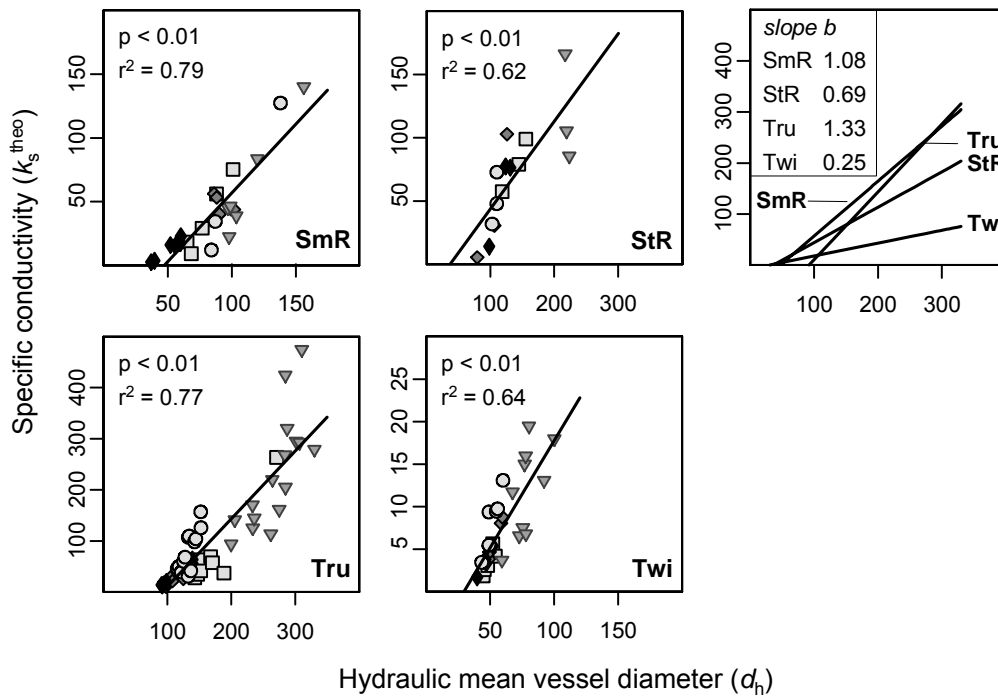
**Fig. 4.3:** Changes in stem diameter (cm), mean vessel diameter ( $d$ , means  $\pm$  SE), vessel density (VD) and percentage lumen area in the sapwood area of the trunk with stem height as a proxy for xylem path length from the base to the crown in three individuals of *C. acuminatissima* (□ = A; ♦ = B; ● = C). Coefficient of determination ( $r^2$ ) and levels of significance ( $p$ ) for the linear regressions were: Tree A: Stem diameter:  $p < 0.01$ ,  $r^2 = 0.99$ ,  $d$ :  $p = \text{n.s.}$ ,  $r^2 = 0.70$ , VD:  $p = \text{n.s.}$ ,  $r^2 = 0.61$ , Tree B: Stem diameter:  $p < 0.01$ ,  $r^2 = 1.00$ ,  $d$ :  $p = 0.01$ ,  $r^2 = 0.96$ , VD:  $p = 0.01$ ,  $r^2 = 0.96$ , Tree C: Stem diameter:  $p = 0.01$ ,  $r^2 = 0.95$ ,  $d$ :  $p = 0.02$ ,  $r^2 = 0.99$ , VD:  $p = \text{n.s.}$ ,  $r^2 = 0.27$ .

Again, *C. acuminatissima* differed from the other species by exceptionally high  $k_s^{\text{theo}}$  values; this species had particularly high  $k_s^{\text{theo}}$  values in the trunk. While vessel diameter reached a maximum and vessel density a minimum in the trunk and strong roots, the variation of axial conductivity along the flow path was characterized by four to twenty times smaller values in the twigs than in the other three organs.

**Tab. 4.4:** Theoretical axial hydraulic conductivity ( $k_s^{\text{theo}}$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) normalized to the cumulative vessel lumen area in the xylem of small and strong roots, trunks and twigs ( $k_s^{\text{theo}}$ ) of the five species based on the microscopic analysis of vessel diameter and Hagen-Poiseuille's law (means  $\pm$  1 SE). For number of replicate samples see Tab. 4.3. For further explanations see Tab. 4.2.

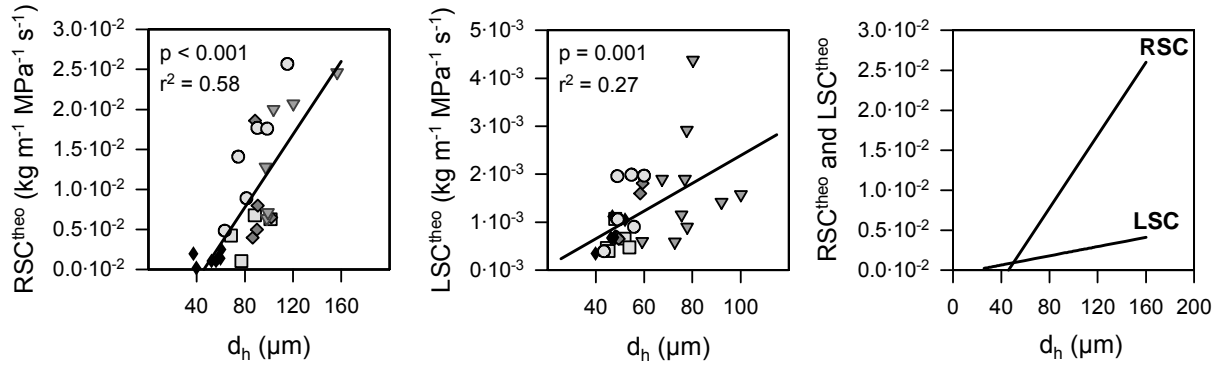
	Small roots	Strong roots	Trunks	Twigs
<i>S. apiculata</i>	51.9 $\pm$ 15.6 ab A	51.0 $\pm$ 11.9 ab A	79.6 $\pm$ 10.9 a A	8.4 $\pm$ 1.4 b AC
<i>C. acuminatissima</i>	61.4 $\pm$ 17.5 a A	117.7 $\pm$ 24.3 ab BC	229.6 $\pm$ 27.8 b B	11.6 $\pm$ 1.7 a A
<i>P. excelsa</i>	13.7 $\pm$ 2.9 a A	56.1 $\pm$ 20.9 a AC	30.2 $\pm$ 9.8 a A	3.9 $\pm$ 0.7 b BD
<i>C. laevigata</i>	46.4 $\pm$ 2.8 ab A	46.4 $\pm$ 29.2 bc ABC	24.0 $\pm$ 5.1 c A	5.6 $\pm$ 0.9 d CD
<i>P. firma</i>	37.7 $\pm$ 12.3 ac A	78.5 $\pm$ 12.0 b C	70.1 $\pm$ 21.9 ab A	3.5 $\pm$ 0.7 c D

As follows from the Hagen-Poiseuille equation,  $k_s^{\text{theo}}$  was positively correlated with hydraulic mean vessel diameter in all four organs, but the slope was largely different. Small roots and the trunk showed the steepest increase of  $k_s^{\text{theo}}$  with increasing  $d_h$ , followed by strong roots. The distal twigs had by far the smallest increase in  $k_s^{\text{theo}}$  with  $d_h$  (Fig. 4.4).



**Fig. 4.4:** Hydraulic mean vessel diameter ( $d_h$ ,  $\mu\text{m}$ ) in relation to theoretical specific conductivity ( $k_s^{\text{theo}}$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) in small (SmR, top left) and strong (StR, top middle) roots, the trunk (Tru, bottom middle) and twigs (Twi, bottom left) of five tree species ( $\circ$  = *S. apiculata*,  $\nabla$  = *C. acuminatissima*,  $\blacklozenge$  = *P. excelsa*,  $\square$  = *C. laevigata* and  $\blacklozenge$  = *P. firma*). Note different scale of the y-axes. The joint plot of all four organs (top right) gives also the slopes  $b$  of the regression lines. For further explanations see Tab. 4.3.

Theoretical root- and leaf-specific conductivity ( $\text{RSC}^{\text{theo}}$ ,  $\text{LSC}^{\text{theo}}$ ), i.e.  $k_h^{\text{theo}}$  normalized by fine root surface area or leaf area, were also positively correlated with  $d_h$ , and again the increase of area-specific conductivity with  $d_h$  in small roots exceeded the corresponding increase in twigs considerably (Fig. 4.5).



**Fig. 4.5:** Theoretical root-specific ( $RSC^{theo}$ , left) and leaf-specific conductivity ( $LSC^{theo}$ , middle) in relation to mean hydraulic vessel diameter ( $d_h$ ) for a pooled sample of the five species. Note different scales for  $RSC^{theo}$  and  $LSC^{theo}$ . The slopes of the regression lines in the joint plot (right) were 20.0 (RSC) and 2.89 (LSC)  $\times 10^{-5}$ . For symbol explanation see Fig. 4.4.

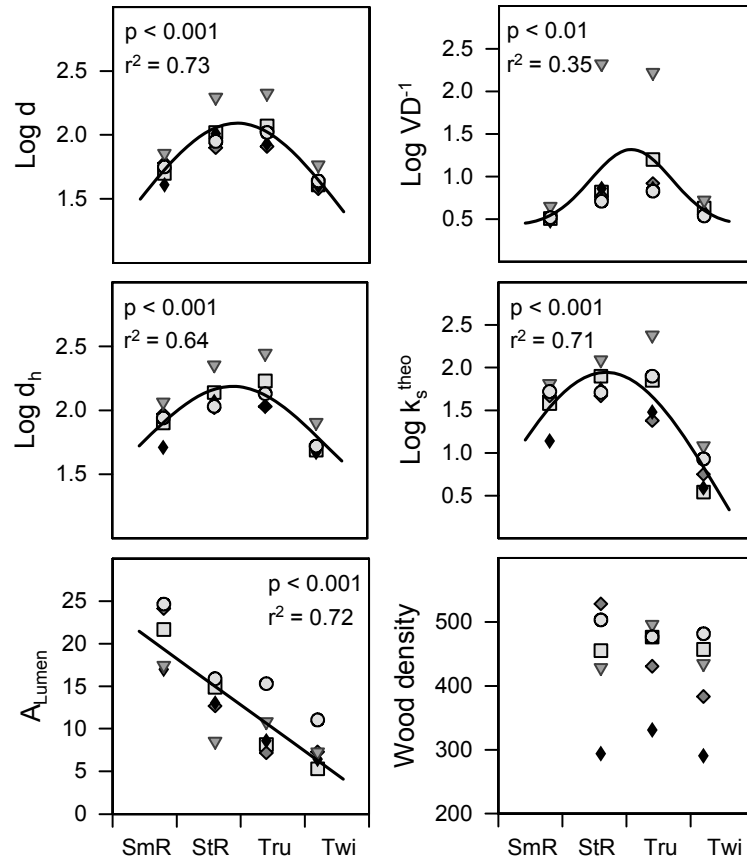
## 4.4 DISCUSSION

### 4.4.1 Variation in vessel dimensions along the flow path from small roots to distal twigs

As formulated in our first hypothesis, we found the largest vessels along the flow path in the trunk wood, but conduits of similar diameter occurred also in strong roots (mean diameter: 13 cm in our sample). According to the pipe model theory of Shinozaki *et al.* (1964a, b) and Murray's law (McCulloh *et al.* 2005), we assume that these woody organs fulfill similar functions, notably for the mass flow of water at high velocities, carbohydrate and nutrient storage, and for the structural support. A striking anatomical similarity also exists for the hydraulic architecture of the terminal organs of the flow path, i.e. small roots and twigs. These two fulfill highly different tasks within the flow path. Due to the high hydraulic resistance in the small terminal twigs of the upper sun-canopy, the trees can effectively control the distribution of water in the crown regardless of how far it must travel (Zimmermann 1978). In the terminal twigs and leaves, the most negative water potentials of the plant occurs, and these organs are also exposed to the highest mechanical stress during storm events. Not surprisingly, we found the smallest relative lumen area per cross-section and the smallest lumen area-specific conductivity in twigs, and the xylem of twigs contains only small vessels with more fibres and tracheids.

Among the five tree species investigated, *C. acuminatissima* showed the largest vessels and the smallest vessel densities in all four investigated organs. According to Tyree (2003), a high hydraulic conductance across the plant is an essential prerequisite for a high productivity in forest trees; consistently, this species is among the tallest in the forest and contributes the

highest aboveground biomass of all species in the forest (Culmsee *et al.* 2010). Despite the fact that *C. acuminatissima* had vessels with twice the diameter of the other four species, we found convergent patterns in the hydraulic architecture of these five co-occurring species (Fig. 4.6). In support of our second hypothesis, optimum curves described the change in vessel dimensions (and the reciprocal of vessel density) and also in specific conductivity along the flow path from small roots acropetally towards the terminal twigs.



**Fig. 4.6:** Changes in vessel traits along the flow path from small roots (SmR) over strong roots (StR), the trunk (Tru) to the terminal twigs (Twi) for the five species. Logarithmized mean vessel diameter ( $d$ ,  $\mu\text{m}$ ), reciprocal vessel density ( $VD$ ,  $\text{n mm}^{-2}$ ), hydraulic mean vessel diameter ( $d_h$ ,  $\mu\text{m}$ ), theoretical specific conductivity ( $k_s^{\text{theo}}$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), relative vessel lumen area ( $A_{\text{Lumen}}$ , %) and wood density ( $\rho$ ,  $\text{kg m}^{-3}$ ). The non-linear fits were done with equations of the form  $y = a + b \cdot \exp(-((x-c)/d)^2)$ . For  $VD$  the reciprocal was used. For symbol explanation see Fig. 4.4.

A contrasting pattern existed for relative vessel lumen area, that decreased linearly by 70 % along the flow path in all five species. One explanation for the reduction in relative lumen area may be that the mechanical stress is generally higher and the water potentials lower in the aboveground environment than belowground, which explains the need for more fibres and tracheids for structural support in the aboveground flow path. We were, however, surprised not to find significantly higher vessel densities in small roots compared to twigs in three of the five species. It is possible that these species achieve a sufficient root axial conductivity by a higher fine root biomass, i.e. more roots that operate in parallel. In any case, the hydraulic

mean vessel diameters were on average 30 % larger in the small roots, resulting in on average 85 % higher theoretic specific conductivities in roots compared to twigs in the five species, thereby supporting our third hypothesis.

To our knowledge, only one study showed so far that vessels of plants in humid environments tend to be largest in the trunk wood (Machado *et al.* 2007). In most relevant studies it is generally assumed that the largest vessels in woody plants occur in the root system, with conduits tapering continually along the flow path up to the distal twigs (e.g. Tyree and Zimmermann 2003). From our findings, it seems more likely that only woody plants frequently exposed to the occurrence of drought- or frost-induced embolism show this vessel diameter pattern. It appears that this paradigm needs to be reconsidered. First, results from conifers should be discussed separately from those of dicotyledons, and within the large group of dicotyledons a distinction between plants adapted to different environments is needed. Secondly, a clear terminology is required when talking of roots. Coarse roots, which show secondary growth, are mainly responsible for anchorage and water transport. Coarse roots will most likely possess larger conduit dimensions than fine or small roots. To illustrate the variety of root dimensions investigated, Ewers *et al.* (1997) took their samples close to the trunk base, which must be strong roots, while Martinez-Vilalta *et al.* (2002) studied small and medium-sized roots (3.0-11.8 mm, pers. communication). Even though both studies found the largest vessels in their root samples, the comparability of the data must be questioned.

More recent studies emphasize that root functions vary according to the position of the root segment on the branches of the entire root system. The term ‘root order’ was introduced to categorize this position (e.g. Rewald *et al.* 2010 and references therein) which also defines the age of the root. The terminal fine root represents the 1<sup>st</sup> order root, while every further branching increases the root order. Accordingly, the root function, such as water transport efficiency, should correspond to root age and related anatomy and not necessarily to root diameter. In support of this concept, Valenzuela-Estrada *et al.* (2008) found a linear increase in mean vessel diameters from 1<sup>st</sup> to 6<sup>th</sup>-order fine roots in *Vaccinium corymbosum*.

The assumed functional differentiation belowground according to root orders and age is not mirrored aboveground where wood samples of trunks differing in diameter show a more or less comparable hydraulic architecture. For example, Mencuccini *et al.* (1997) found no significant change in conduit diameter with tree age, but the hydraulic conductivity of the sapwood increased due to higher conduit densities. For several trees of our sample, we also found a linear decrease in  $k_s^{\text{theo}}$  from the cambium to the centre of the stem by up to 80 %, i.e.



from younger to older tissue, but mean vessel diameter stayed more or less constant while vessel density decreased (Schuldt, unpublished). In the aboveground part of the flow path, it appears that differences in tree height, and thus in gravity, determine the diameter of a conduit. In the trunk and canopy, conduits are tapering in parallel with a decrease in stem diameter with increasing height. If the tube diameter would remain constant, the hydraulic resistance of a capillary tube would increase linearly with transport distance (Becker *et al.* 2003).

#### 4.4.2 Evidence in support of the ‘hydraulic fuse’ theory in small-diameter roots

Large conduits possess higher conductivities but, in parallel, vulnerability to dysfunction due to drought-stress induced cavitation increases. The ‘hydraulic fuse’ theory bases on a number of empirical studies that found the largest vessel diameters in the root system. It was assumed that the large vessels were required to secure water uptake, while they would cause cavitation to occur first in roots. This was interpreted as an advantage in terms of carbon investment, because small-diameter roots can be replaced cost-efficiently, avoiding cavitations in trunk and branches. From the pattern of vessel diameters along the flow path, we obtained no evidence in support of the ‘hydraulic fuse’ theory for our sample of tropical tree species. Rather, the cavitation risk should be larger in the trunk and in strong roots than in small diameter roots, which can be replaced more easily.

However, other factors than vessel diameter may also be decisive for assessing the risk of cavitation. First, small-diameter roots with their high relative vessel lumen area and consequently a smaller amount of tracheids and sclerenchymatic tissue may be particularly sensitive to embolism because the physical strength of the tissue should be lower than in the trunk, twigs or strong roots. Second, damage to small-diameter roots caused by burying soil animals or rhizophagous organisms may occur quite frequently, which could promote the development of embolisms. Finally, roots may experience relatively low tissue water potentials when the soil dries out and a partial reversal of the root-to-shoot water potential gradient with reverse water flow may occur (Burgess *et al.* 1998, Olivera *et al.* 2005, Scott *et al.* 2008, Hao *et al.* 2010). A higher vulnerability to cavitation of small-diameter roots as compared to twigs of similar diameter was reported for temperate oak and beech trees by Rewald (2008) supporting the assumption that fine and other small-diameter roots may indeed be affected by cavitations despite rather small conduit diameters. However, these attributes may not be qualified to sustain the proposition that a “small-diameter” functions as a “hydraulic fuse” in trees.

Gonzales-Benecke *et al.* (2010) argued that the term ‘hydraulic fuse’ should be reconsidered, since roots are not necessarily an ‘expandable’ organ. The construction costs of 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. Thus, we can assume that the plant cannot afford to loose all embolized root segments after a severe drought event, especially if root embolism is perceived as a dynamic control mechanism of water flow in analogy with stomatal regulation (Salleo *et al.* 2000, Chaves *et al.* 2003). Further, the development of new roots will take at least weeks or month which may be too long to secure the supply of water and nutrients.

Recent studies showed that xylem embolism may be reversible within hours after additional water has reached the embolized cell (Zwieniecki and Holbrook 2009). Low-molecular weight sugars might be the principle osmoticum being active in refilling. If embolism reversal is a frequent process, it may be an advantage for the plant to confine it to somewhere close to the soil water source in the roots, where the flow path is much shorter than when it occurs in the crown. It may well be that small-diameter roots of trees are embolized despite relatively small vessel diameters with a subsequent blocking of the water flow in the direction of the trunk. However, we doubt that this will inevitably result in the necessity to replace these roots by growing new fine and small roots as was postulated by Zimmermann (1983) on his ‘segmentation hypothesis’. The inhibition of xylem water flow should rather be of limited duration because embolism may be reversed as long as sufficient mono- and disaccharides can be mobilized as osmoticum. Field studies with in-situ monitoring of sap flow in small-diameter roots (2-5 mm in diameter) in temperate oak and beech trees support this conclusion. The continuous measurement with miniature sap flow gauges showed that root water flow ceased during longer periods of soil drying, probably caused by root cavitation, but started again within 3-4 hours after soil rewetting (Coners and Leuschner, unpublished). In any case, more empirical data on the vulnerability of roots to cavitation – despite rather small vessels – and the process of vessel refilling are needed to fully reject or confirm the ‘hydraulic fuse’ hypothesis for small-diameter tree roots.

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## 4.5 APPENDIX

**Tab. A4.1:** Root classification using the diameter ranges after Sutton and Tinus (1983).

Root diameter	Classification
Ø >50 mm	strong roots
Ø 20-50 mm	very large roots
Ø 10-20 mm	large roots
Ø 5-10 mm	medium roots
Ø 2-5 mm	small roots
Ø 1-2 mm	fine roots
Ø ≤ 1 mm	very fine roots

Ø >2 mm (coarse roots)

Ø ≤ 2 mm (fine roots)

**Tab. A4.2:** Mean vessel diameter ( $d$ , µm) in the wood of small and strong roots, trunks and twigs of the five tree species (means ± 1 SD, the number of vessels measured are indicated right to the organ). For further explanations see Tab. 4.2.

	Small roots	n	Strong roots	n	Trunks	n	Twigs	n
<i>S. apiculata</i>	55.1 ± 24.8 a A	4696	89.3 ± 23.0 b A	146	104.8 ± 33.8 b A	2135	44.1 ± 10.1 a A	8598
<i>C. acuminatissima</i>	80.0 ± 43.5 a B	766	191.0 ± 48.9 b B	55	199.2 ± 91.9 b B	388	56.4 ± 21.2 a B	7386
<i>P. excelsa</i>	40.6 ± 12.3 a A	2338	104.3 ± 23.6 b A	146	88.9 ± 28.5 b A	1146	39.8 ± 7.9 a A	6218
<i>C. laevigata</i>	59.4 ± 25.0 a AB	2039	81.8 ± 27.9 b A	186	80.3 ± 30.9 b A	1026	37.6 ± 12.8 c A	16696
<i>P. firma</i>	50.2 ± 21.7 a AB	2288	104.0 ± 38.6 b A	181	105.4 ± 57.1 b A	743	40.7 ± 8.6 a A	3802

**Tab. A4.3:** Vessel density (VD, n mm<sup>-1</sup>) in the wood of small and strong roots, trunks and twigs of the five tree species (means ± 1 SD, the number of tree individuals investigated is indicated right to the organ, the number of samples in parentheses). For further explanations see Tab. 4.2.

	Small roots	n	Strong roots	n	Trunks	n	Twigs	n
<i>S. apiculata</i>	82.5 ± 19.3 a AB	2 (6)	25.3 ± 13.4 b A	3 (3)	16.0 ± 4.0 b A	7 (13)	71.0 ± 19.1 a A	3 (6)
<i>C. acuminatissima</i>	37.1 ± 13.8 a A	2 (4)	2.7 ± 1.1 b B	3 (3)	2.9 ± 1.0 b B	5 (16)	26.6 ± 13.4 a B	5 (10)
<i>P. excelsa</i>	116.2 ± 27.5 a B	4 (7)	14.4 ± 6.2 bc A	3 (3)	14.3 ± 2.3 b A	3 (5)	49.9 ± 10.6 c C	3 (5)
<i>C. laevigata</i>	66.0 ± 14.0 a AB	2 (4)	19.9 ± 12.1 b A	3 (3)	12.0 ± 3.3 b A	3 (7)	59.8 ± 11.2 a AC	3 (6)
<i>P. firma</i>	83.8 ± 29.5 a AB	2 (4)	16.8 ± 6.7 bc A	3 (3)	7.1 ± 2.1 b C	4 (9)	39.1 ± 10.2 c BC	3 (5)

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## **5 FIFTH CHAPTER**

### **ENVIRONMENT AND TREE SIZE CONTROLLING STEM SAP FLOW IN A PERHUMID TROPICAL FOREST OF CENTRAL SULAWESI, INDONESIA**

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## Environment and tree size controlling stem sap flow in a perhumid tropical forest of Central Sulawesi, Indonesia

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### Abstract

Among-species variation of sap flux density in the stems of seven common tree species was studied in a tropical pre-montane rainforest of Central Sulawesi, Indonesia and analyzed with regard to the effects of tree size and environmental controls. The study covered 39 individuals from 6 different families common in the area.

Sap flux density  $J$  in the outermost xylem varied considerably among the tree species and was highest in the Fagaceae *C. acuminatissima* which is characterized by a high stem hydraulic conductivity. Across all seven species a tight correlation was found between daily water use and tree size.

Over the study period, daily sap flux showed a better correlation to the atmospheric vapor pressure deficit ( $D$ ) than to shortwave radiation ( $R$ ) or to soil moisture (SWC), in spite of the permanently high atmospheric humidity. The soil moisture effect on sap flux was negligible in all species, with an  $r^2 > 0.03$ . The area of the diurnal hysteresis loop of a plot of  $J$  against radiation was for all species larger for  $R$  than for a plot against  $D$ , indicating a better coupling of the diel flux variation to  $D$ .

In conclusion, all seven species revealed convergent patterns in the regulation of sap flux by environmental factors, while species-specific differences in the hydraulic architecture and in the canopy position may lead to considerable differences observed in the water consumption of coexisting trees in this species rich tropical perhumid forest.

**Key words:** *Castanopsis acuminatissima*, Granier method, radiation, saturation deficit, soil moisture, stand transpiration, tree height, tropical families, water consumption.

## 5.1 INTRODUCTION

Tropical moist forests are known for their exuberant species richness. This species diversity may harbour a high number of tree functional types with contrasting sizes and ontogeny. Tyree and Ewers (1996) predicted a high variation in the diel patterns of stem water flux in tropical forest trees as a consequence of a high diversity in hydraulic structures. This prediction seems to contradict the conclusion of Meinzer (2003) that tree species from closed tropical rainforests tend to converge in their patterns of transpiration control and response to drought, emphasizing similarities among different tree species due to certain uniformity of environmental constraints.

Similar to other forest biomes, atmospheric water vapor saturation deficit ( $D$ ), solar radiation ( $R$ ) and soil water availability (SWC) are the main environmental factors controlling the transpiration of tropical forests (Meinzer 2003, O'Brien *et al.* 2004, Andrade *et al.* 2005). However, the influence of these three variables may differ among trees of different sizes and ontogenetic stages. A close correlation has been found between sap flow and tree diameter of tropical trees (Meinzer 2003), with tree diameter being a surrogate for tree size or age. Tree height has also been identified as another size parameter influencing water consumption (Andrade *et al.* 1998, Becker 1996, Goldstein *et al.* 1998, Meinzer *et al.* 2001). According to Phillips *et al.* (1999), tall trees growing on moist soils exhibit high water flow rates because their canopies are exposed to a higher evaporative demand and higher radiation fluxes than smaller trees. The exposure to a higher evaporative force results in larger water potential gradients, which under conditions of non-limiting water supply (e.g. in moist tropical forest) would lead to continuous high transpiration rates. Nevertheless, for a number of tropical tree species, a sensitive stomatal response to  $D$ , leading to partial stomatal closure at saturation deficits  $> 1$  kPa, has been reported (e.g. Fetcher *et al.* 1994). This may indicate a conservative use of water of certain trees in tropical forests which may be an adaptation to short regular, or irregular dry periods (Granier *et al.* 1992, O'Brien *et al.* 2004).

In the perhumid montane rainforests of Central Sulawesi (Indonesia) with about 3000 mm of annual precipitation, temperature, solar radiation, rainfall, and vapor pressure deficit vary only slightly throughout the year. A short and usually tenuous dry period lasts at the maximum one to two months, usually shorter, and the intensity and duration of these events are quite unpredictable (Withmore 1975). Thus, droughts occur only irregularly in this environment which makes permanent adaptive responses to water shortage less economic, but may favor an increased morphological and physiological plasticity with respect to water transport and

flow control. Moreover, Zach *et al.* (2010) found a good correlation between tree height and the diameter of the conducting vessels. This finding highlights the adaptation of the hydraulic architecture of tall trees to secure the transport of water to the top of their canopies under the low evaporative demand in the perhumid climate of this region.

In the present study, we examine the sap flux dynamics of seven common tree species in the tropical premontane rainforest of Central Sulawesi, Indonesia, during a typical humid year and relate them to stand structural properties and climatic variables. These species are members of six families with contrasting phylogenetic and biogeographic background. The following questions were addressed:

- (i) How do coexisting species differ in their diurnal and seasonal patterns of sap flow?
- (ii) Does the environmental control of tree sap flux density vary among tree species or is there convergence in the species response to environmental variation in this perhumid climate?
- (iii) What is the effect of tree size on sap flux among different species?

We compare individual trees and tree species because this provides insights into the relative contribution of physiological regulation and structural limitations of tree water use. These factors are often species-specific and relevant when upscaling from tree to stand water consumption in highly diverse tropical forests.

## 5.2 MATERIALS AND METHODS

### 5.2.1 Study sites

The study was carried out at pre-montane elevation (1050 m a.s.l.) in the tropical rainforest of Pono Valley located on the western boundary of Lore Lindu National Park in Central Sulawesi, Indonesia (UTM 51M, 0172451, 9834650). The soils of this old-growth forest developed as Acrisols (FAO- classification) over metamorphic rocks. The climate of the study area is wet all year long, with a mean annual precipitation of around 3500 mm. A short dry period with less than 100 mm rainfall per month usually occurs between July and August. According to the Holdridge classification, the study area falls into the perhumid category (Holdridge *et al.* 1971). Mean annual air temperature is 20.8 °C.

### 5.2.2 Tree selection

To study the floristic structure of the forest and the effect of experimental drought on tree vigor and forest dynamics, six permanent plots of 40 m by 40 m were established within the frame of the Sulawesi Throughfall Displacement Experiment (STDE) in Pono Valley. Half of the plots were covered by a sub-canopy roof to control the amount of precipitation reaching the ground, while the other three plots served as control. On the three control plots, we chose 39 tree individuals of seven common tree species with a diameter at breast height (DBH, measured at 1.3 m above the ground) of >10 cm (Tab. 5.1). Each species was represented by a minimum of three and a maximum of eight tree individuals differing in tree height ( $H$ ) and DBH. We focused on trees from different canopy layers and included species from different families with slow-growing mid-story species (e.g. *Cryptocarya laevigata*, *Pouteria firma*) as well as fast-growing canopy species (e.g. *Platea excelsa*, *Castanopsis acuminatissima*) being represented. Most of the sampled trees ranged between 10 and 30 m in height. Some *C. acuminatissima* and *Palaquium luzoniense* individuals exceeded 40 m. The vegetation composition of all six plots is described in detail in Culmsee *et al.* (2010).

Biometric parameters for structure analysis included basal area (BA) as calculated from stem diameter at breast height (DBH) measured at 1.30 m above the ground and assuming a circular stem cross area; tree height ( $H$ ) as the measured distance between the base of the trunk and the top of the crown using a laser meter sensor (Vertex III Forester, Haglöf, Långsele, Sweden). Sapwood area (SA) was estimated from an empirically developed relationship with DBH that was established in a sample of 57 trees of different species and sizes. Sapwood depth at breast height was estimated in these trees using a staining method (Goldstein *et al.* 1998, Meinzer *et al.* 2001). During the morning hours (from 8:00-11:00 a.m.), when transpiration rates start rising, a first core was taken at 1.3 m height with a 5 mm diameter increment borer (Suunto Oy, Vaanta, Finland) to the centre of the trunk. Immediately after coring, a 0.1 % indigo carmine-solution was injected into the hole and refilled if needed. After two to four hours, when the dye had been carried upwards with the xylem flux, a second core was taken 3-5 cm above of the injection point. The stained depth of the sapwood was determined visually and was taken as the sapwood depth. Sapwood area was then calculated as the area of the stem ring with a radius equal to the estimated sapwood depth.

### 5.2.3 Sap flux measurements

We measured xylem sap flux density ( $J$ ,  $\text{kg m}^{-2} \text{d}^{-1}$ ) in the stem xylem using heat dissipation sensors (Granier 1985, 1987). Pairs of 20 mm-long and 2 mm-wide heating probes were inserted in northern and southern trunk directions into the stem sapwood of each tree. The probes were manufactured according to the original design given by Granier (1996). The upper probe was heated with a constant power of 0.2 W. The temperature difference between the two sensors was recorded with copper-constantan (Cu-Ni) thermocouples placed at the centre of the heating coil. The lower probe was not heated and served as reference for the upper probe. The distance between the two sensor probes was kept at about 15 cm to avoid thermal interference. Sap flux velocity was calculated according to the empirical calibration equation given by Granier (1985, 1987, 1996):

$$J_s = 119 \times K^{1.231} \quad (1)$$

where  $K$  is a temperature constant determined as follows

$$K = \frac{(\Delta T_0 \times \Delta T)}{\Delta T} \quad (2)$$

$\Delta T_0$  is the maximum temperature difference when sap flow is assumed to be zero and  $\Delta T$  is the actual temperature difference between the two probes.

Mean daily water consumption per tree ( $\text{kg d}^{-1}$ ) was estimated using the mean daily xylem flux density in the outer xylem and the stem hydroactive sapwood area ( $\text{SA}$ ,  $\text{m}^2$ ). An exponential decrease in sap flux density from the outer to the inner xylem was assumed for up-scaling to daily water uptake (Becker 1996, Phillips *et al.* 1996, James *et al.* 2003, Delzon *et al.* 2004, Hölscher *et al.* 2005, Kubota *et al.* 2005, Motzer *et al.* 2005).

Stand daily transpiration rate  $E_c$  (in  $\text{mm d}^{-1}$ ) was calculated for  $n$  tree height classes as:

$$E_c = \frac{1}{n} \sum_{j=1}^n DWU_j \times SAI_j \quad (3)$$

where  $DWU_j$  is the mean daily tree water uptake (in  $\text{g H}_2\text{O m}^{-2} \text{sapwood d}^{-1}$ ) of the tree height class  $j$  and  $SAI_j$  is the sapwood area index for the tree height class  $j$ .  $SAI_j$  ( $\text{m}^2 \text{m}^{-2}$ ) is calculated as the sapwood to ground area ratio for each tree height class. We considered different tree height classes in the calculation of stand transpiration because of the significant relationship found by Zach *et al.* (2010) between tree height and hydraulic conductivity across different co-occurring tree species in the perhumid forest of Sulawesi.

#### 5.2.4 Microclimatic and hydrologic measurements

Above-canopy incoming shortwave radiation ( $R$ ) was measured with a pyranometer (CS 300, Campbell Scientific, UK). Air temperature and relative humidity were recorded with a combined temperature and humidity probe (CS 215, Campbell Scientific, U.K.). Rainfall was measured to the nearest 0.1 mm with a tipping bucket rain gauge (ARG100, Campbell Scientific, U.K.). All sensors were mounted on a 16 m tall tower located in a large natural forest gap several hundred meters away from the study plots. All values were registered at half-hour intervals by a Campbell CR1000 data logger (Campbell Scientific, U.K.). Atmospheric vapor pressure deficit ( $D$ ) was calculated from air temperature and relative humidity according to Goff and Gratch (1946).

Volumetric soil water content (SWC) was recorded half-hourly with time domain reflectometry probes (TDR, Campbell Scientific, U.K.) in the three stands. At each plot, three soil pits were dug for soil profile description and soil moisture measurements at different depths. TDR probes were inserted at depths of 10, 20, 40, 75, 150 and 250 cm (M. Köhler, unpubl. data). For our analysis, we used the volumetric soil moisture data from 10 cm depth where the highest fine root density was found. Deeper in the soil profile, fine root biomass was strongly reduced (Hertel *et al.* 2009). The sap flux data analyzed in this study correspond to the period from July 2007 to December 2008.

#### 5.2.5 Data analysis

Species differences in mean sap flux density were tested by means of ANOVA. To test for the effect of tree size as a covariate in the inter-species comparison of mean sap flux we ran an ANCOVA test using the biometric factor that showed the best correlation to sap flux density as a covariate.

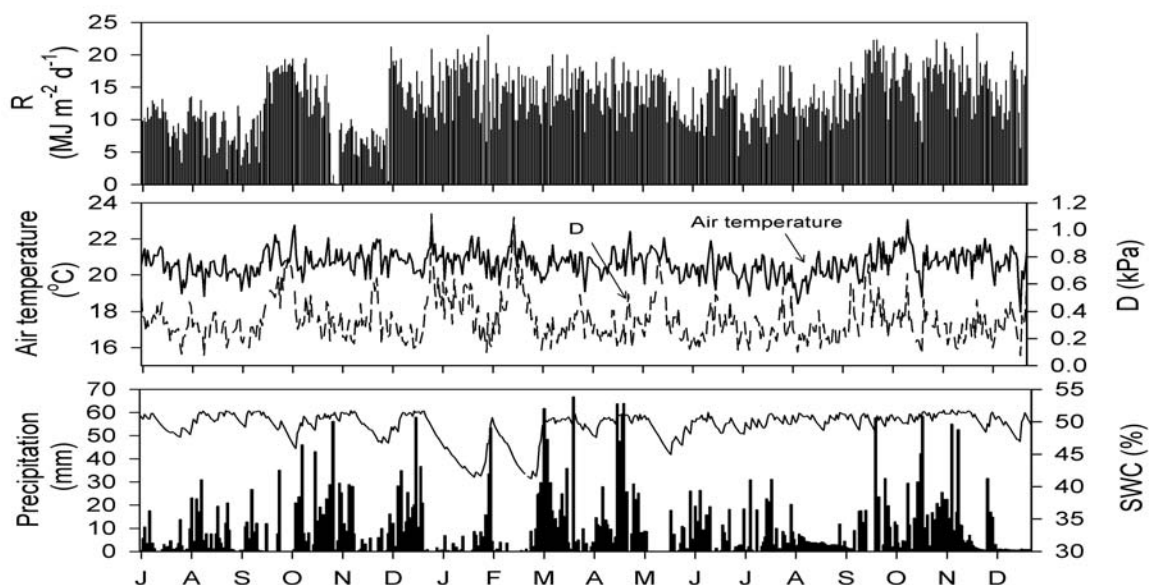
Daily hysteresis in xylem flux density with variation in  $D$  ( $H_D$ ) and  $R$  ( $H_R$ ) was estimated for every tree during 2007. Mostly sunny days with less than 2 mm rainfall were selected for this calculation ( $n = 123$  days). Here, hysteresis is defined as the difference in  $J$  at same  $D$  and  $R$  values registered either during morning or afternoon hours. We estimated the hysteresis area according to Zeppel *et al.* (2004) by fitting a polynomial regression to the upper part of the hysteresis loop and one to the lower part of the loop for the relationship between stem sap flux and  $D$  or  $R$ . The hysteresis area was then estimated by subtracting the area between the lower polynomial and the x-axis from the area of the upper polynomial and the x-axis.

Simple regressions were conducted to analyze the relationship between sap flux density and environmental parameters ( $D$ ,  $R$ , and SWC) for each species. Multiple regression analysis was used to compare the effect of  $D$  and  $R$  as controlling environmental factors and tree height and DBH as controlling biometric parameters of daily stem sap flux. These calculations were conducted with the SAS System for Windows 9.1 (SAS Institute, Cary, NC, USA) and Sigma Plot 10.0 (Systat software, Inc.).

## 5.3 RESULTS

### 5.3.1 Climate

During the study period between July 2007 and December 2008, volumetric soil moisture at 10 cm depth varied between 41.2 and 52.1 %. Mean atmospheric saturation deficit  $D$  during this period was 3.3 hPa with a maximum of 27.2 hPa at the end of September 2007. Total precipitation was 1375 mm between July and December 2007 and 2901 mm during 2008. In July 2007, and in January and December 2008, less than 100 mm of precipitation fell in each month. Highest monthly precipitation was registered in March 2008 (541 mm). Global radiation was highest at the end of January and at the end of December 2008 (23.05 and 23.36  $\text{MJ m}^{-2} \text{d}^{-1}$ , respectively). Soil water content decreased to a minimum of 41 vol. % at the end of February 2008 (Fig. 5.1).



**Fig. 5.1:** Daily totals of global radiation (top), daily mean air temperature and vapour pressure deficit (centre) and daily precipitation and mean volumetric soil water content (bottom) during the measurement interval from July 2007 to December 2008 in Pono Valley in Central Sulawesi, Indonesia. Air temperature, radiation and precipitation were measured on a 16 m tall tower located in a forest gap. Volumetric soil water content data are means of 3 plots with 3 measurement locations each (soil depth of 10 cm). Due to malfunction of the radiation sensor, data of  $R$  is missing for several days at the end of November 2007.



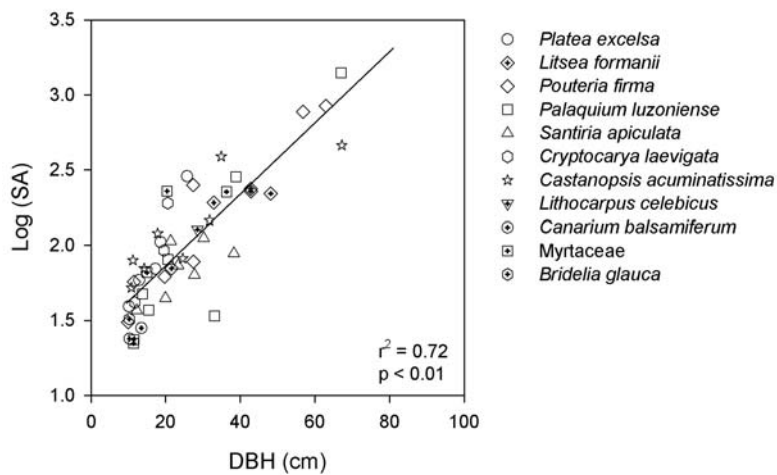
**Tab. 5.1:** Biometric characteristics of the 7 common tree species investigated for sap flux in Pono Valley, Central Sulawesi. Stem diameter at breast height (DBH), total tree height ( $H$ ), sapwood area (SA) as estimated from dye injection experiments and the SA-DBH relationship in the species.  $J$  is the mean daily xylem flux density  $\pm$  SD measured in 2007 and 2008 in the outer 2 cm of the active xylem by means of the constant heating method after Granier (1985, 1987). The number of replicates ( $n$ ) is the number of trees monitored for xylem sap flux density.

Species	Family	n	DBH (cm)	$H$ (m)	SA (cm <sup>2</sup> )	$J_{2007}$ (kg m <sup>-2</sup> d <sup>-1</sup> )	$J_{2008}$ (kg m <sup>-2</sup> d <sup>-1</sup> )
<i>Vernonia arborea</i> Buch.-Ham.	Asteraceae	3	20.1 - 43.0	22.0 - 28.7	73.6 - 256.9	371.8 $\pm$ 153.1	462.9 $\pm$ 174.2
<i>Santiria apiculata</i> A.W. Benn.	Burseraceae	5	14.6 - 58.2	17.4 - 27.6	54.5 - 589.3	418.7 $\pm$ 69.4	343.1 $\pm$ 192.4
<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	Sapotaceae	6	10.4 - 95.0	17.6 - 44.7	43.3 - 4394.9	489.6 $\pm$ 294.7	516.2 $\pm$ 307.0
<i>Cryptocarya laevigata</i> Blume	Lauraceae	6	11.2 - 27.9	15.4 - 33.2	45.2 - 112.7	373.2 $\pm$ 99.1	350.4 $\pm$ 200.0
<i>Pouteria firma</i> (Miq.) Baelni	Sapotaceae	5	14.7 - 27.9	14.7 - 44.3	54.8 - 745.2	731.9 $\pm$ 295.7	642.8 $\pm$ 359.7
<i>Platanus excelsa</i> Bl. var. <i>borneensis</i> (Heine) Sleum.	Icacinaceae	6	11.7 - 45.7	12.3 - 24.7	46.5 - 297.8	568.9 $\pm$ 295.8	502.1 $\pm$ 284.1
<i>Castanopsis acuminatissima</i> (Blume) Rheder	Fagaceae	8	11.8 - 71.4	17.6 - 43.9	46.8 - 1211.5	978.5 $\pm$ 347.5	1129.0 $\pm$ 441.3

### 5.3.2 Sapwood area and tree size

The 39 investigated trees varied considerably in size. *S. apiculata*, *V. arborea*, *C. laevigata*, and *P. excelsa* were mainly represented by mid to lower canopy individuals while *P. luzoniense*, *P. firma* and *C. acuminatissima* were present with trees of all size classes, including emergent trees of the uppermost canopy (Tab. 5.1).

We found a significant positive correlation ( $p > 0.01$ ,  $r^2 = 0.72$ ) between DBH and estimated sapwood area across 57 trees from at least 13 species (Fig. 5.2). Five individuals from the Myrtaceae family could not be identified to the species level but three morpho-species were distinguished.



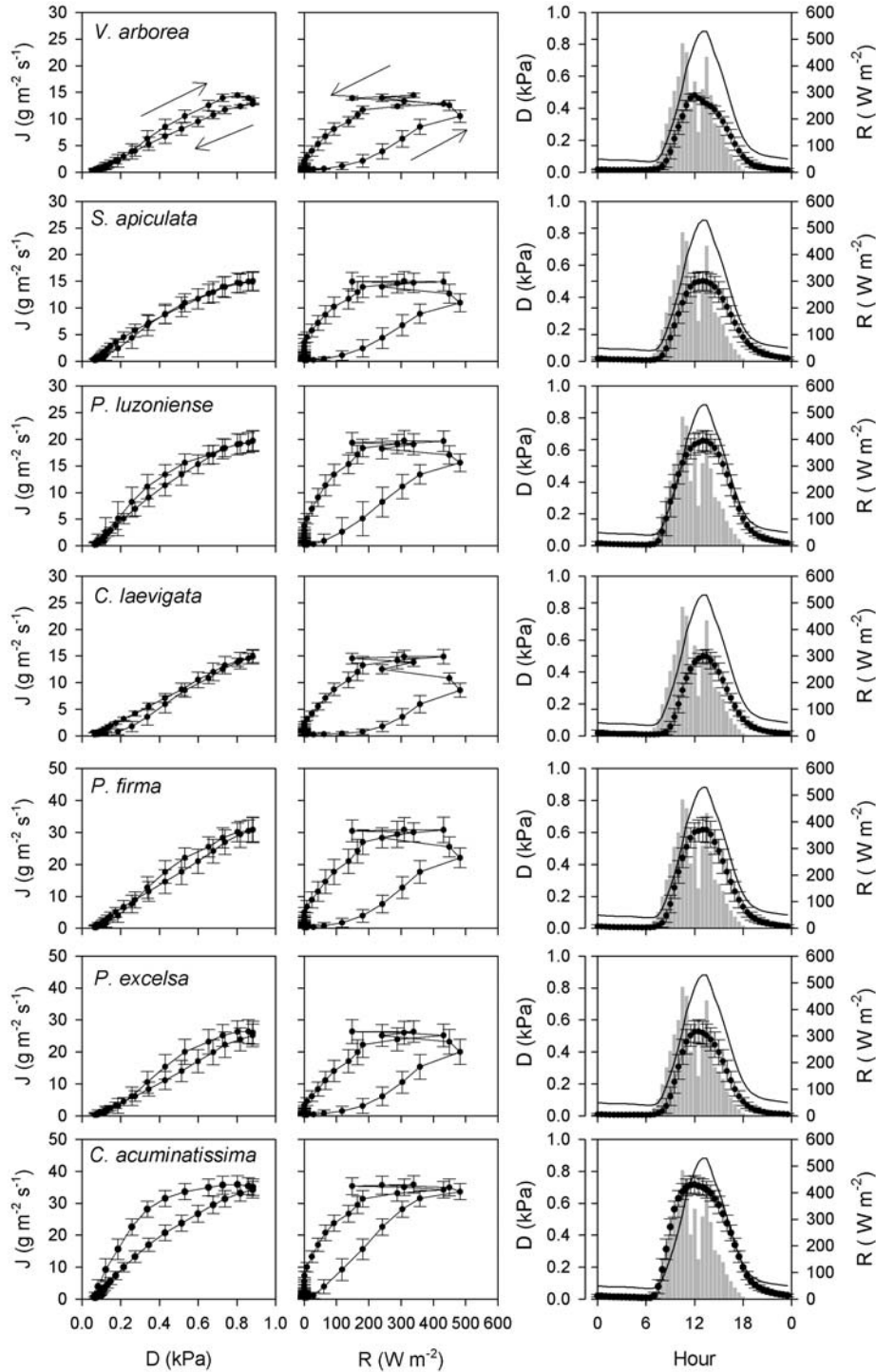
**Fig. 5.2:** Relationship between stem DBH and sapwood area (SA) across 57 trees of the perhumid forest of Pono Valley, Central Sulawesi, Indonesia. The trees belong to 10 species and at least three morpho-species from the Myrtaceae family. The solid line is the line of the regression described by a polynomial function of the form:  $\log(\text{SA}) = b_0 + b_1 \text{DBH}$ .

### 5.3.3 Sap flow of the seven tree species: response to climatic factors and tree size

Mean xylem flow was largest in *C. acuminatissima* ( $978.5 \text{ kg m}^{-2} \text{ d}^{-1}$  in 2007 and  $1129.8 \text{ kg m}^{-2} \text{ d}^{-1}$  in 2008) and lowest in *V. arborea* ( $371.8 \text{ kg m}^{-2} \text{ d}^{-1}$ ) during 2007 and in *S. apiculata* ( $343.1 \text{ kg m}^{-2} \text{ d}^{-1}$ ) during 2008 (Tab. 5.1). The mean xylem flow measured between July and December 2007 was larger than the mean value for all 12 months in 2008 for *S. apiculata*, *P. firma*, and *P. excelsa*, but lower for the other four species. However, the differences between mean xylem flow rates of 2007 and 2008 were not significant.

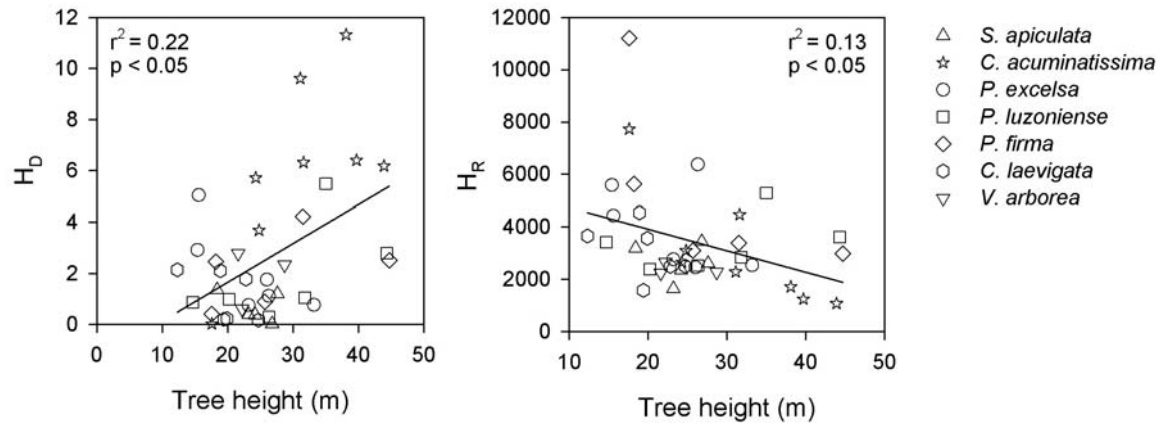
Maximum  $J$  coincided with or occurred after the daily maximum of irradiance but earlier than the maximum of  $D$  in all species (Fig. 5.3: left panels). The hysteresis loop of the relationship between sap flow and  $D$  showed a clockwise rotation for all species (Fig. 5.3), that is, xylem

flow increased rapidly with  $D$  in the morning, while in the afternoon, the  $D$  decrease preceded the decline in xylem flow. The relationship between xylem flow and solar radiation showed an opposite direction (counterclockwise rotation) for all species (Fig. 5.3: right panels).



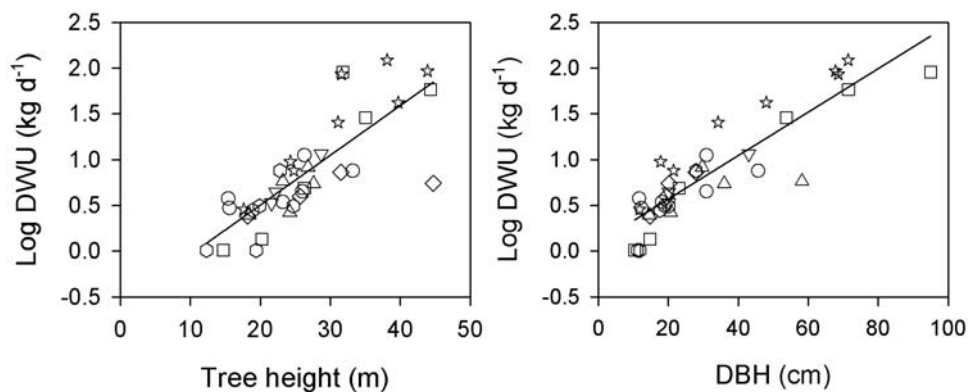
**Fig. 5.3:** Diurnal relationship between xylem flux density ( $\text{g m}^{-2} \text{s}^{-1}$ ) and vapor pressure deficit (kPa) or solar radiation ( $\text{W m}^{-2}$ ) for the 7 species. Data are mean values for half-hour periods of xylem flux density during 2007 (from July to December). Bars indicate the standard deviation. Arrows give the direction of the course of the day from morning to afternoon. In the right panels:  $D$  (solid line),  $R$  (grey bars), and mean  $J \pm \text{SE}$  (black points with bars). Note the different scaling for  $J$  between the upper 4 and the lower 3 species. This is the same for the right panels.

Rates of xylem flow in the afternoon were larger than morning values at a given  $R$  value. Plotting the estimated area of the hysteresis loop from the relationship of xylem flow with  $D$  and  $R$  against tree height yielded a significant positive relationship in both cases (Fig. 5.4), whereas no significant relation was found with DBH (data not shown).



**Fig. 5.4:** Relationship between tree height and the estimated mean area of the hysteresis from the relationship between daily xylem flow and vapor pressure deficit ( $H_D$ ) and solar radiation ( $H_R$ ). Data correspond to the study period between July and December 2007. Symbols stand for the 7 species investigated. Refer to Tab. 5.1 for information about tree species and number of trees measured. The solid line is the line of the linear regression.

Across species, we found a significant, positive linear correlation between tree daily water uptake (DWU, in  $\text{kg d}^{-1}$ ) and DBH and the height (Fig. 5.5). During both years, the correlation with DBH was slightly better than that with tree height (Tab. 5.2).



**Fig. 5.5:** Relationship between tree size, expressed in terms of tree height and DBH and mean tree daily water uptake per tree ( $\text{kg d}^{-1}$ ), across 39 trees from 7 species in the studied stand. For information about trees refer to Tab. 5.1. Data correspond to the study period between July and December 2007. The solid line is the linear regression line. The correlation coefficients and parameter estimates are listed in Tab. 5.2 (separately for 2007 and 2008).

The results of the multiple regression analysis showed that the daily xylem flow rates of the seven species was explicable to a high degree by a combination of tree size (DBH and  $H$ ) and environmental factors ( $D$ ,  $R$  and SWC) with the models reaching correlation coefficients between  $r^2 = 0.39$  for *C. acuminatissima* and  $r^2 = 0.84$  for *P. firma* (Tab. 5.3).

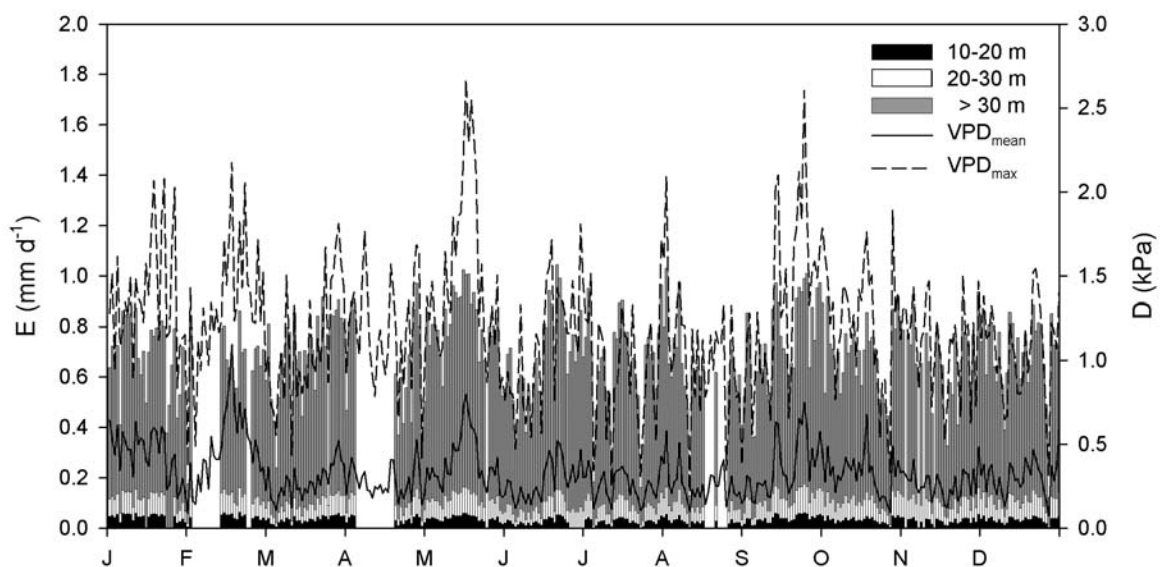
**Tab. 5.2:** Parameter estimates and coefficients of determination ( $r^2$ ) of the relationship between mean daily water uptake per tree (DWU, kg d<sup>-1</sup>) and tree DBH (cm) or height (m) during 2007 and 2008. All 39 trees belonging to 7 species were included in the analysis. Tree DWU was estimated from mean tree xylem flux density (g cm<sup>-2</sup> d<sup>-1</sup>) and the corresponding sapwood area (SA, m<sup>2</sup>). Xylem flux data from 2007 cover the period between July and December. During 2008, measurements of xylem flow were conducted through the year.

Year	DWU vs. DBH				DWU vs. H			
	Log(DWU)= $b_0+b_1$ DBH				Log(DWU)= $b_0+b_1$ H			
	$b_0$	$b_1$	$r^2$	p	$b_0$	$b_1$	$r^2$	p
2007	0.2171	0.0201	0.84	0.0001	-0.3481	0.0458	0.57	0.0001
2008	0.0948	0.0237	0.79	0.0001	-0.5815	0.0543	0.64	0.0001

In the backward selection procedure, the variable tree height was removed in the case of *C. acuminatissima* and soil water content for *P. luzoniense*. Mean vapor pressure deficit and stem DBH were the variables that explained most of the variation in daily xylem flux, but that varied in their importance among the seven species.

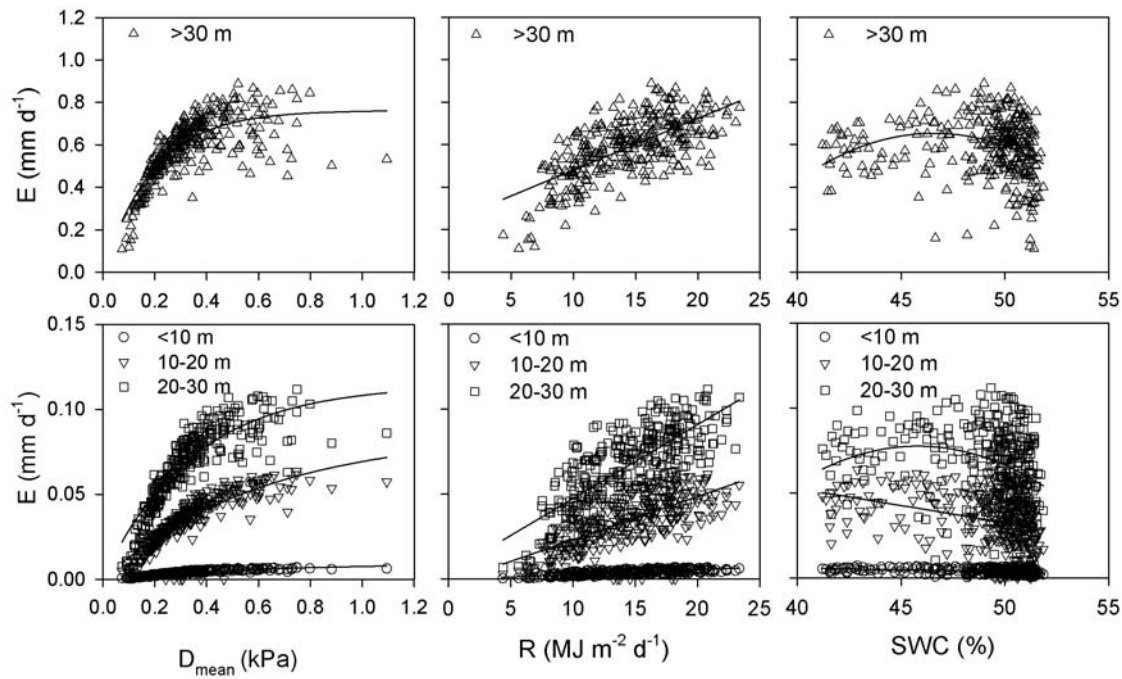
#### 5.3.4 Stand transpiration

Total mean stand sapwood area for all trees with DBH > 10 cm was  $8.6 \pm 2.1$  m<sup>2</sup> ha<sup>-1</sup>. The mean sapwood area of large trees ( $H > 30$  m) was  $6.2 \pm 1.4$  m<sup>2</sup> ha<sup>-1</sup>. Correspondingly, the up-scaled stand transpiration rates per tree height class demonstrated a major contribution of large trees (Fig. 5.6), that transpired with up to 10 times higher the estimated rates than all other tree height classes.



**Fig. 5.6:** Annual course of estimated daily transpiration rates (mm d<sup>-1</sup>) per tree height class in the perhumid forest of Pono Valley, Central Sulawesi, Indonesia. The black, white and grey bars stand for three tree height classes: the stand total of E is the top of the grey bars. Transpiration rates of trees with a diameter smaller than 10 cm were very low and not visible at the scale of this figure, for this reason, they are not included. The solid line indicates mean values of vapor pressure deficit (kPa) and the broken line gives the daily maximum vapor pressure deficit (kPa).

Estimated stand transpiration during 2008 varied from 0.09 to 1.05 mm d<sup>-1</sup>. Across all tree height classes, transpiration rates showed a strong and highly significant correlation with the atmospheric variables  $D_{\text{mean}}$  and  $R$  and a less tight, and in some cases negative, correlation with SWC (Fig. 5.7, Tab. 5.4). The correlation between transpiration rates and mean vapor pressure revealed highest correlation coefficients for the smaller trees ( $r^2 = 0.86$  for the tree height class < 10 m), and the smallest for the tallest trees ( $r^2 = 0.69$  for trees > 30 m). The relationship between  $E$  and maximum values of  $D$  resulted in much lower  $r^2$  values than with  $D_{\text{mean}}$  (data not shown).



**Fig. 5.7:** Relationship between daily transpiration rate (mm d<sup>-1</sup>) per tree height class and the ambient variables: vapor pressure deficit ( $D$  in kPa, left), solar radiation ( $R$  in W m<sup>-2</sup>, center), and volumetric soil water content (SWC in %, right). The correlation coefficients and parameter estimates are listed in Tab. 5.4.

**Tab. 5.3:** Equation parameters and explained variances due to environmental and tree size variables for the seven tree species investigated according to multiple regression analyses using the general model:  $J = b_0 + b_1DBH + b_2H + b_3D + b_4R + b_5SWC$ . Data used in the analysis are from 2008. The coefficient of determination ( $r^2$ ) for the general regression model is also presented. Non-significant variables (n.s.) were removed from the initial model. Only variables significant at the 0.05 level were left in the model.

Species	r <sup>2</sup>					Parameter estimates						
	model	DBH	H	D <sub>mean</sub>	R	SWC	b <sub>0</sub>	b <sub>1</sub>	b <sub>2</sub>	b <sub>3</sub>	b <sub>4</sub>	b <sub>5</sub>
<i>V. arborea</i>	0.59	0.13	0.008	0.32	0.13	0.004	-22.57	-0.45	0.59	40.97	0.003	0.52
<i>S. apiculata</i>	0.53	0.12	0.008	0.34	0.04	0.013	51.47	-0.51	0.60	44.55	0.003	-1.03
<i>P. luzoniense</i>	0.64	0.34	0.13	0.16	0.01	n.s.	-42.13	0.14	1.77	66.29	0.002	n.s.
<i>C. laevigata</i>	0.82	0.39	0.013	0.36	0.04	0.007	-74.93	2.65	-0.83	68.28	0.002	0.79
<i>P. firma</i>	0.84	0.59	0.013	0.18	0.05	0.001	-52.09	2.25	-1.35	72.61	0.004	0.63
<i>P. excelsa</i>	0.54	0.19	0.032	0.28	0.02	0.006	15.30	0.61	-3.29	89.33	0.002	0.99
<i>C. acuminatissima</i>	0.39	0.18	n.s.	0.13	0.05	0.022	-142.43	0.81	n.s.	91.03	0.005	3.07

**Tab. 5.4:** Parameter estimates and coefficients of determination ( $r^2$ ) of the relationship between environmental variables and daily transpiration rate ( $E$ ) per tree height class during 2008. The relationship between  $E$  and vapor pressure deficit ( $D_{mean}$ ) followed an exponential form for all tree height classes. The relationship between  $E$  and solar radiation ( $R$ ) was better fitted to a first order polynomial in all tree height classes. The relationship between  $E$  and soil water content (SWC) was better explained by a first order polynomial in the smaller tree height classes and by a second order polynomial in the taller trees. The level of significance is indicated by the asterisks with \*\*\*, standing for  $p < 0.001$ .

Tree height class	$E$ vs. $D_{mean}$					$E$ vs. $R$					$E$ vs. SWC				
	$E = a \cdot (1 - \exp(-bD_{mean}))$					$E = b_0 + b_1R$					$E = b_0 + b_1SWC + b_2SWC^2$				
	a	b	$r^2$	p		$b_0$	$b_1$	$r^2$	p		$b_0$	$b_1$	$b_2$	$r^2$	p
< 10m	0.009	1.762	0.86	***		-0.0003	0.0003	0.55	***		0.014	-0.0002	--	0.12	***
10 - 20m	0.086	1.629	0.75	***		-0.0024	0.0025	0.47	***		0.133	-0.0002	--	0.12	***
20 - 30m	0.114	2.894	0.8	***		0.0039	0.0043	0.59	***		-1.265	0.0586	-0.0006	0.07	***
> 30m	0.763	5.159	0.69	***		0.2364	0.0243	0.45	***		-10.543	0.4807	-0.0052	0.07	***

## 5.4 DISCUSSION

Among the seven species studied, xylem flux density rates in the outermost xylem varied up to 3-fold in 2007 and 2008. The significantly higher xylem flux in *C. acuminatissima* than in all other species is explained by the large hydraulic conductivity associated with the very large vessel diameters that were reported for this species (Zach *et al.* 2010). Slight differences in mean xylem flux densities between 2007 and 2008 may be due to the differences in mean saturation deficit or in the extension of the analyzed period. Effects of decreasing contact between the sensor and the xylem tissue can be excluded because most sensors were replaced when significant changes in the sensor signal were observed. The upscaled mean daily water consumption per tree revealed a large range of variation among the 39 individuals of the seven species studied. The maximum rate of water use ( $132 \text{ kg d}^{-1}$ ) was calculated for a large *C. acuminatissima* tree (DBH = 71.4 cm), the smallest rate was recorded with  $1 \text{ kg d}^{-1}$  in a small sub-canopy *C. laevigata* individual with a DBH of 11.9 cm. Jordan and Kline (1977) reported a much higher maximum daily water use of  $1180 \text{ kg d}^{-1}$  in a large tree of the Amazonian species *Eperua purpurea*. Maximum rates of daily water consumption for other tropical moist forest species varied between  $40 \text{ kg d}^{-1}$  for *Aspidosperma cruentum* (Goldstein *et al.* 1998) and  $396 \text{ kg d}^{-1}$  for *Ocotea sp.* (Jordan and Kline 1977). Maximum rates for boreal or for temperate broad-leaved and coniferous trees were reported for *Pseudotsuga menziesii* ( $530 \text{ kg d}^{-1}$ , Fritschen *et al.* 1973) and for *Quercus robur* ( $400 \text{ kg d}^{-1}$ , Čermák *et al.* 1982). Similarly, daily means of xylem flux density for the seven tree species from the tropical rain forest in Sulawesi were lower than corresponding values reported for broadleaved temperate tree species during mid summer. Hölscher *et al.* (2005) measured a mean daily sap flux density of  $1520 \text{ kg m}^{-2} \text{ day}^{-1}$  for mature beech trees in Central Germany. In comparison, in this study we measured a mean xylem flux rate of  $1129 \text{ kg m}^{-2} \text{ day}^{-1}$  in the large *C. acuminatissima* trees. All other species had smaller mean fluxes.

In our study, it is possible that the upscaled transpiration rates were underestimated because the size of the sapwood area in the stem cross-section, as calculated from the relationship to DBH, was relatively small in this forest. Motzer *et al.* (2005) reported much larger sapwood areas for tropical montane forests in Ecuador as did Meinzer *et al.* (2001) for tropical lowland forests in Panama, but Becker (1996) found also relatively small sapwood depths in Bornean tree species which are comparable to our data. Becker (1996) estimated a stand water use of 43 and  $35 \text{ mm month}^{-1}$  for dipterocarp and heath forest, respectively. These values were calculated from the relationship between daytime sap flow, measured on trees with diameters



of at least 20 cm, and basal area. In our study, estimated monthly stand water use was 31.5 mm. When comparing our site to the tall dipterocarp and heath forest sites of Becker, large differences in tree size and stem density become visible. While the trees at our site reached a maximum height of 45 m and mean stem density was 867 trees ha<sup>-1</sup> (including all trees  $\geq 0.02$  m DBH), the two sites of Becker were denser (1484 and 1341 trees ha<sup>-1</sup> of trees  $\geq 0.05$  m DBH) and composed by taller trees (maximum heights of 50 to 60 m). These differences in forest composition in combination with the continuously low  $D$  may account for the relatively low estimates of stand water use derived from our xylem flow measurements. Additionally, the ignorance of transpiration from the understory vegetation must be taken into account even though this flux is expected to be very small given the low evaporative demand at canopy height and the even lower  $D$  values at lower strata. In addition, the understory contributes only marginally to total stand sapwood area.

We found a positive correlation between tree height and tree daily water uptake across the seven common tree species of this perhumid tropical rainforests. Various other authors have also reported a positive tree-size water consumption relationship for tropical species referring either to tree height or DBH (e.g. Andrade *et al.* 1998, with tree height, Meinzer *et al.* 2005, with DBH). Tall trees are typically exposed to a higher  $D$  and often have a more extended sun crown than smaller trees which should increase water consumption. However, a certain methodological bias in estimating the water consumption of large trees cannot be excluded because tall trees have larger stem diameters and this parameter is also used for upscaling of sap flux density to the stand level in this study.

The analysis of stand transpiration partitioned into tree height classes showed the prevalence of transpiration rates from tall trees for the total stand balance. Tall trees have larger sapwood and leaf areas, the latter exposed to higher  $D$  values as explained above. Several authors have pointed to tree age as an important biotic factor driving transpiration (Vertessy *et al.* 1994, 1995, Mencuccini and Grace 1996, Vertessy *et al.* 1997, Köstner *et al.* 1998, Roberts 2000, Ryan *et al.* 2000, Schäfer *et al.* 2000, Köstner 2001, Köstner *et al.* 2002). Moreover, according to White *et al.* (1998), forests exposed to high precipitation or high soil moisture, like in the study area, typically maintain a larger leaf area per unit sapwood area. This strategy supports tree growth in environments with high humidity and hence low evaporative demand by maintaining sufficient water flow despite a comparatively small soil-to-leaf water potential difference (Tyree and Ewers 1991).

According to Meinzer (2003), the relationship between water consumption and tree size depends strongly on the temporal and spatial scale considered. In our study, the measured trees were selected in a rather homogeneous forest area (no gaps, gentle and uniform slope) and the tree species, in most cases, were represented by all tree size classes. We monitored sap flux for eighteen months with environmental conditions in this period being typical for the site. Because of the continuously high precipitation in the area, the soil water content measured in the upper 10 cm was all the time close to field capacity (van Straaten and Veldkamp, unpubl. data), even during January and February 2008, when the lowest soil moisture values were recorded. The dominant role of atmospheric vapor pressure deficit in controlling sap flux of the tree species in the perhumid forest of Sulawesi confirms the general finding that  $D$  is the main climatic factor determining the intensity of tree transpiration on a daily basis.

Wullschleger *et al.* (2001) reported that  $D$  and  $R$  accounted for up to 84 % of the variation in  $J$  in a deciduous temperate broad-leaved forest, and Zeppel *et al.* (2004) gave values of up to 75 % for an Australian woodland dominated by *Eucalyptus crebra* and *Callitris glaucophylla*. In the perhumid forest of Sulawesi, the influence of vapor pressure deficit and radiation was much less important at the species level with 17 to 45 % of the variation in  $J$  explained by a combination of  $D$  and  $R$ . In contrast, at the stand level and across tree height classes, the relationship between daily transpiration and the atmospheric evaporative demand was much tighter with correlation coefficients of 0.86 for the lower tree height class.

Tree species present with individuals mainly in the lower to middle canopy exhibited a higher correlation coefficient with  $D$  than species with trees reaching more than 40 m in height where the correlation coefficient for the relation to tree size (DBH) was particularly high. The phenomenon of remarkably small correlation coefficients of  $J$  with  $D$  in tall trees (*C. acuminatissima*, *P. firma*, *P. luzoniense*) as compared to smaller trees in lower canopy strata may have its explanation in greater water storage in stems and large roots of the taller trees, or in a stomatal control of transpiration that is more sensitive to  $D$  in trees of the upper canopy.

The variation in xylem flux density between morning and afternoon at a given  $D$  was much smaller than for  $R$ . In other words, the degree of hysteresis was larger in the relationship between xylem flux density and solar radiation than with  $D$ , indicating a closer coupling between  $J$  and the atmospheric evaporative demand in all species. According to Zeppel *et al.* (2004), who discussed several causes of this hysteresis, a possible increase in stomatal sensitivity to  $D$  or a decrease in leaf water potential could cause reduced transpiration rates due to partial stomatal closure in the afternoon. Among the species investigated in Sulawesi,

*C. acuminatissima* showed the largest hysteresis area for  $D$ . In this species, the assumption of a higher stomatal sensitivity could explain the large hysteresis. Trees of *C. acuminatissima* are reaching more than 50 m in height in the study region and they have a very efficient conducting system with extremely large vessels (more than 300  $\mu\text{m}$  in diameter, Lemmens *et al.* 1995, Pande *et al.* 1995, Zach *et al.* 2010) and high xylem flux rates. The combination of an exposed canopy and high hydraulic conductivities must translate into high transpiration rates if stomatal control is not sensitive. The clockwise rotation in the response curve to  $D$  and counterclockwise rotation in the case of  $R$  has been previously observed by O'Brien *et al.* (2004) for tropical trees in Costa Rica, and by Kelliher *et al.* (1992), Meinzer *et al.* (1997) and Zeppel *et al.* (2004) for temperate tree species. This reverse pattern has been explained by Zeppel *et al.* (2004) by differences in the timing of maximum  $D$  and  $R$ . Because  $D$  peaks later than  $R$ , the vapor pressure deficit is at a given value of  $R$  in the morning smaller than in the afternoon. The larger hysteresis loop for the radiation curve than for the  $D$  curve may be explained by the larger relative difference in  $R$  between morning and afternoon hours while the diel changes in  $D$  were smaller due to the prevailing humid conditions in the study area. An opposite result has been reported by Zeppel *et al.* (2004) for Eucalyptus trees in Australia, where the proportional variation between morning and afternoon  $D$  values was larger than the variation in radiation. Consequently the hysteresis loop area for  $D$  was larger than for  $R$ .

With coefficients of determination mostly below 0.1, the influence of soil moisture on the variation in sap flux was the smallest of all three environmental variables. We believe that this is mainly a consequence of the high soil water content that prevailed throughout the period of investigation, and the overall perhumid climate of the study area. However, analyses on the role of soil water in controlling tree sap flux showed that  $D$  and  $R$  may be more influential than soil moisture even in climates with seasonal drought, as in parts of temperate Central Europe (Gebauer *et al.*, submitted), when time scales of days to weeks are considered.

## 5.5 CONCLUSION

This study in a species-rich tropical forest of Central Sulawesi, Indonesia shows that species-specific measurements of xylem sap flow can provide insights into the role of tree size and environmental factors controlling tree water consumption in this perhumid climate. All seven tree species studied revealed convergent patterns in the regulation of sap flow in that atmospheric saturation deficit was the principal environmental factor and DBH the dominant size attribute when the fluxes were analyzed on a daily basis. This convergence in sap flow regulation is associated with a considerable functional diversity in the tree hydraulic

architectures of the tree species present in this stand. The Fagaceae *C. acuminatissima* diverges from the other species with respect to the less tight coupling of daily xylem flux to the vapor pressure deficit increase in the course of the day. Moreover, this species, that is abundant in the study area with phylogenetic relationships to extra-tropical genera, showed significantly higher sap flow and daily water uptake rates than the other coexisting species which is partly a consequence of a very high hydraulic conductivity in the root-stem-twigh flow path.

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## **6 SIXTH CHAPTER**

**CHANGE IN HYDRAULIC PROPERTIES AND LEAF TRAITS OF A TALL  
RAINFOREST TREE SPECIES SUBJECTED TO LONG-TERM THROUGHFALL  
EXCLUSION IN THE PERHUMID TROPICS**

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## Change in hydraulic properties and leaf traits of a tall rainforest tree species subjected to long-term throughfall exclusion in the perhumid tropics

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### Abstract

In a throughfall displacement experiment on Sulawesi, Indonesia, three 0.16 ha stands of a premontane perhumid rainforest were exposed to a two-year soil desiccation period that reduced the soil moisture in the upper soil layers beyond the conventional wilting point. About 25 variables, including leaf morphological and chemical traits, stem diameter growth and hydraulic properties of the xylem in the trunk and terminal twigs, were investigated in trees of the tall-growing tree species *Castanopsis acuminatissima* (Fagaceae) by comparing desiccated roof plots with nearby control plots. We tested the hypotheses that this tall and productive species is particularly sensitive to drought, and the exposed upper sun canopy is more affected than the shade canopy. Hydraulic conductivity in the xylem of terminal twigs normalised to vessel lumen area was reduced by 25 %, leaf area-specific conductivity by 10–33 % during the desiccation treatment. Surprisingly, the leaves present at the end of the drought treatment were significantly larger, but not smaller in the roof plots, though reduced in number (about 30 % less leaves per unit of twig sapwood area), which points to a drought effect on the leaf bud formation while the remaining leaves may have profited from a surplus of water. Mean vessel diameter and axial conductivity in the outermost xylem of the trunk were significantly reduced and wood density increased, while annual stem diameter increment decreased by 26 %. In contradiction to our hypotheses, (i) we found no signs of major damage to the *C. acuminatissima* trees nor to any other tree species in this stand, and (ii) the exposed upper canopy was not more drought susceptible than the shade canopy.

**Key words:** Tree height, vertical gradient, drought stress, leaf morphology, leaf nutrient content, isotope signature,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , hydraulic conductivity, stem increment, wood density, vessel anatomy.

## 6.1 INTRODUCTION

The remaining tropical moist forests may be threatened by more frequent and more severe droughts in the future (e.g. Allen *et al.* 2010, Meir and Woodward 2010) that will come along with the predicted climate change in South-East Asia (Hulme and Viner 1998, Timmermann *et al.* 1999, Williams *et al.* 2007, Bates *et al.* 2008, Newbery and Lingenfelder 2008, Sheffield *et al.* 2008) and South America (Cox *et al.* 2008, Phillips *et al.* 2009, Phillips *et al.* 2010). Since the ecosystematic impact of strong drought events is hardly predictable, manipulative field experiments have been found to provide a powerful tool for identifying gradual ecosystem responses and threshold values of ecosystem functions that might result from these putative precipitation changes (Hanson and O'Hara 2003). Experiments with reduced rainfall have so far only been conducted in tropical forests with a distinct dry period in Amazonia (Nepstad *et al.* 2002, 2007, Fisher *et al.* 2007, da Costa *et al.* 2010), where the biota most likely possess specific adaptations (e.g. deep-reaching roots) to regular dry spells. However, we expect that the results of these Amazonian experiments cannot simply be extrapolated to tropical forests with a perhumid climate where the trees should be less experienced in coping with drought because rainless periods occur only irregularly (Aldrian and Susanto 2003, Aldrian *et al.* 2004, Erasmi *et al.* 2009). Experiments on the drought response of perhumid tropical forests with continuously high soil moistures and air humidity do not yet exist. To fill this gap, a replicated throughfall displacement experiment (Sulawesi Throughfall Displacement Experiment, STDE) was carried out in a premontane perhumid rainforest in Central Sulawesi, Indonesia, to investigate the response of the trees and soil biological activity to a 24-months drought period. The study region is characterized by high amounts of rainfall throughout the year and air humidity at the canopy height that rarely drops below 80 %.

Both observational studies on natural drought events and the Amazonian throughfall displacement experiments showed that under prolonged drought especially large and tall canopy trees (and species) as well as lianas experienced higher mortalities than trees of smaller size (Slik *et al.* 2004, Van Nieuwstadt and Sheil 2005, Nepstad *et al.* 2007, da Costa *et al.* 2010, Phillips *et al.* 2010). Drought may harm trees through two pathways, exposure to increase of xylem embolism and reduced assimilate supply due to stomatal closure. Besides cell dehydration and a consequently reduced leaf expansion growth, carbon starvation could be one consequence of severe drought (Farooq *et al.* 2009), but this hypothesis has been questioned (Sala 2009).

Here, we formulate the hypothesis that the higher mortality of tall rainforest trees and lianas observed in experimental or natural droughts is primarily caused by the long path length for water flow from root to leaf. The fact that conduits taper with increasing tree height (e.g. Anfodillo *et al.* 2006, Petit *et al.* 2008, 2009) and tall trees are exposed to higher atmospheric saturation deficits than smaller ones, results in particularly wide vessels at the base of the trunk of tall trees (Zach *et al.* 2010). Tree size and vessel diameter at the stem base should be directly linked to each other, because tall trees are normally more productive than smaller trees, and a high hydraulic conductance in the soil-plant-atmosphere path seems to be an essential prerequisite for a high productivity of forests (Tyree 2003).

However, increasing vessel diameters for improving the water transport carry the burden of a higher vulnerability to cavitation (e.g. Zhu and Cao 2009, Awad *et al.* 2010, Cai and Tyree 2010, Hacke *et al.* 2010). In addition, plant communities growing under high precipitation rates typically have more shallow root systems (Schenk and Jackson 2002, Hertel *et al.* 2003, Jimenez *et al.* 2009), which may further increase their vulnerability to drought-induced cavitation.

For analyzing the effects of a two-year experimental desiccation period on tall tropical canopy trees, we selected one of the tallest and also most abundant upper canopy tree species in the premontane forest of Sulawesi, *Castanopsis acuminatissima* (Blume) Rheder. This species is a member of the Fagaceae family and has been found to be the most prominent species in terms of biomass in this forest stand (Culmsee *et al.* 2010). We assumed that cavitation caused by soil moisture deficits is a serious threat for large trees of this species. Furthermore, we expected the upper crown to be more susceptible to drought stress than the lower crown due to the growing cavitation risk with increasing path length (Ryan and Yoder 1997) and the exposure to higher vapor pressure deficits.

This study is part of the Sulawesi Throughfall Displacement Experiment and focussed on the drought response of one prominent tree species in a species-rich forest, the tall-growing and abundant Fagaceae *Castanopsis acuminatissima*. Study aims were to monitor a large number of morphological, anatomical, hydraulic and chemical traits at the leaf, branch and stem levels in drought-exposed (roof) and unaffected control trees over a desiccation period of 24 months and to identify traits that respond sensitively to soil water shortage. Among the investigated parameters were several variables related to xylem dysfunction and carbon starvation hypotheses proposed to explain drought damage to trees. We used tree climbing equipment in each of the seven mature *C. acuminatissima* in the roof and control plots in order to study the

response of sun-lit upper canopy leaves and branches. Because leaf exposure and canopy position is known to exert a great influence on leaf morphology and physiology in trees, we investigated leaves and branches of both the sun and shade canopy and compared their response to the two-year desiccation. We further hypothesized that sun canopy leaves and branches are more susceptible to desiccation than are shade canopy organs.

## 6.2 MATERIAL AND METHODS

### 6.2.1 Site description

The Sulawesi Throughfall Displacement Experiment (STDE) was established in 2006 in a premontane rainforest in the Pono Valley on the western boundary of Lore Lindu National Park in Central Sulawesi, Indonesia (S 01°29.6' E 120°03.4', elevation 1050 m). The climate of the study area is perhumid with a mean annual precipitation of 2901 mm, a mean annual temperature of 20.6 °C and a mean relative air humidity of 88.7 % (data derived from measurements in 2008). The heavily weathered soils of this old-growth forest developed on metamorphic rocks. The clayey-loamy soil texture with dominant kaolinite and hematite has been classified as Acrisol (World Reference Base for Soil Resources, Leitner 2010). The forest has a canopy height of about 45 m with a few trees reaching 55 m, a high tree species diversity with about 130 species ha<sup>-1</sup> and an average stem density of 456 ha<sup>-1</sup> (>10 cm DBH, Culmsee and Pitopang 2009, Culmsee *et al.* 2010).

### 6.2.2 Experimental design

The STDE consisted of six floristically and structurally similar plots of 0.16 ha (40 m x 40 m) that were spread in a stratified random design over an area of approximately five ha. While three plots served as control, the remaining three plots were covered by sub-canopy roofs to displace a large fraction of the rainfall. The roofs were constructed with a large number of removable transparent plastic-lined bamboo-frames placed on a wooden gutter construction to collect the throughfall water. The desiccation period started in May 2007. At the beginning, approximately 70 % of the plot area was covered by the bamboo frames. In early 2008, the roof closure was further increased to approximately 90 % by building custom-sized panels to close gaps around the tree stems and odd-sized openings. To avoid lateral soil water movement or infiltration of surface runoff into the plots and to disable trees to take up water from the surroundings of the study plots, all plots were trenched along the perimeter to 0.4 m soil depth and lined with plastic foil. Since 74.3 % of the fine root and 91.1 % of the coarse

root biomass are located in the upper 20 cm of the soil profile (Hertel *et al.* 2009), we assumed this trenching depth to be sufficient to effectively prevent root water uptake from beyond the plot edges. The litter, which had accumulated on top of the roof construction or in the runoff channels, was transferred back to the soil surface.

### 6.2.3 Microclimatic and hydrologic measurements

Above-canopy global radiation was measured with a pyranometer (CS 300, Campbell Scientific, UK). Air temperature and relative humidity were recorded with a combined temperature and humidity probe (CS 215, Campbell Scientific, U.K.). Rainfall was measured to the nearest 0.1 mm with a tipping bucket rain gauge (ARG100, Campbell Scientific, U.K.). All sensors were mounted on a 16 m tall tower located in a natural forest gap approximately 50 m away from the first study plot. Data were collected every 30 s, averaged and logged at 30 min intervals using a Campbell CR1000 data logger (Campbell Scientific, U.K.). Atmospheric vapor pressure deficit was calculated from air temperature and relative humidity according to Goff and Gratch (1946).

Volumetric soil water content was continuously measured in one main and two additional soil pits per plot. In the main soil pit, time domain reflectometry (TDR) probes (CS616, Campbell Scientific Inc., Logan, UT, USA) were installed at 10, 20, 40, 75, 150 and 250 cm soil depth. The two additional soil pits were equipped with TDR probes in 10, 40, and 75 cm soil depth. The probes were inserted horizontally in the undisturbed soil at the end of a 30 cm long hole dug into the soil pit wall. In total, 36 TDR probes were used per treatment and the data was logged hourly (CR1000, Campbell Scientific Inc., Logan, UT, USA). The TDR probes were calibrated for four soil depths following the procedure described by Veldkamp and O'Brian (2000).

The hydrological and physiological measurements began on March 27, 2007 in the roof plots and on May 31, 2007 in the control plots. For the delayed onset of the measurements in the control, a lightning strike in March 2007 was responsible that damaged both dataloggers and TDR probes.

### 6.2.4 Relative extractable water and soil water potential

The soil moisture measurements were used to calculate the relative extractable water (REW) in the soil using the following equation (Breda *et al.* 2006, Granier *et al.* 2007):

$$REW = \frac{(\theta_t - \theta_{\min})}{(\theta_{\max} - \theta_{\min})} \quad (1)$$

where  $\theta_t$  is the fractional volumetric soil water content on the respective day,  $\theta_{\min}$  the soil water content at which all plant-available water is extracted (corresponding to the water content at wilting point in a given soil depth), and  $\theta_{\max}$  the maximum water content measured during the study in a given soil depth. The volumetric soil water content at the permanent wilting point was calculated from laboratory derived soil water retention curves (van Genuchten 1980) with a pressure plate apparatus (van Straaten, unpublished data). REW varies between 1 (field capacity or maximal measured soil water content) and 0 (permanent wilting point). According to Granier *et al.* (2007) temperate trees typically experience drought stress when REW drops below a threshold of 0.4.

The soil water retention curves were further used to calculate soil matric potentials from the soil moisture measurements for all soil depths in the two treatments.

#### 6.2.5 Tree selection and plant material

In June 2009, after 24 months of experimental drought, 14 tree individuals (7 in the roofed, and 7 in the control plots) of the most abundant and tallest upper-canopy tree species of the studied forest, *C. acuminatissima*, were chosen to collect branch, twig and leaf material from the upper sun-lit canopy and from the lowermost deeply shaded part of the crown using tree climbing equipment. These samples were used to obtain data on branch wood specific gravity (wood density), twig hydraulic properties, branch wood anatomy, leaf morphology and foliar nutrient status. In addition, wood cores were taken from the trunk of every tree at 1.5 m height to determine the wood density and wood anatomy of the trunk.

#### 6.2.6 Wood density and saturated water content determination

Wood density ( $\rho$ ) was determined for trunk wood cores with a diameter of 5 mm and a mean core length of  $69.5 \pm 7.2$  mm using an increment corer (Haglöf, Långsele, Sweden) and for branch wood samples from the upper and lower crown with a mean segment diameter of  $33.1 \pm 7.8$  mm and a mean segment length of  $120.0 \pm 15.3$  mm. In total, 109 branch segments were harvested in the 14 *C. acuminatissima* trees. The fresh volume of the wood cores was calculated from the diameter of the increment corer and the length of the core sample after removing bark and phloem; the fresh volume of the branch samples was determined

gravimetrically by water replacement. After volume determination, all samples were oven-dried at 105 °C for at least four days. The dry wood cores were weighed at a precision of 0.1 mg, the branch segments at a precision of 10 mg. The dry mass of each sample was then divided by its volume to obtain  $\rho$ . The trunk wood cores were further used to determine the saturated water content of the wood (SWC). The cores were submerged in deionized water and allowed to equilibrate overnight. Afterwards, the cores were lightly blotted with tissue paper and weighted at a precision of 0.1 mg.

For comparison, we also used a non-destructive Pilodyn wood tester (Pilodyn 6J, Proceq, Switzerland) prior to trunk wood core extraction in the same trunk area to obtain a second independent measure of wood density. A circle-shaped area with a diameter of 5 cm had to be removed to apply the Pilodyn tester (Hansen 2009).

#### 6.2.7 Stem diameter increment

Annual stem diameter increment was measured with increment measurement tapes (UMS, Munich, Germany) that were installed in December 2006 on 16 tree individuals of *C. acuminatissima* (7 trees in the control plots: DBH 23-150 cm and 9 in the roofed plots: DBH 22-91 cm). Stem diameter increment was documented monthly until the end of the desiccation period in May 2009. The relative annual stem increment (increment as a fraction of basal area) for the trees was calculated separately for the first and the second year of the desiccation experiment.

#### 6.2.8 Experimental determination of axial hydraulic conductivity

The technique introduced by Sperry *et al.* (1988) was applied to measure axial hydraulic conductivity in twig segments. In total, 116 measurements were analyzed (control  $n = 56$ , roof  $n = 60$ ). For each tree individual, eight twig segments of  $139.7 \pm 34.7$  mm length and  $10.6 \pm 1.5$  mm in diameter were harvested, four from the upper canopy and four from the lower crown. These segments were immediately transferred to polyethylene tubes filled with water containing a sodium-silver-chloride complex ( $16 \mu\text{g l}^{-1}$  Ag,  $8 \text{ mg l}^{-1}$  NaCl, Micropur katadyn, Wallisellen, Switzerland) to prevent microbial growth. The samples were kept cool and transported to a nearby field laboratory. Additionally, all leaves distal to the twig segment were harvested. In the laboratory, each twig segment was recut under water with a razor blade and mounted on the tubing system. We used distilled water containing the same sodium-silver-chloride complex as described above for the conductivity measurements. Before entering the twig segment, the solution was forced through a  $0.2 \mu\text{m}$  membrane filter (Maxi



Capsule, Pall, USA). The segments were flushed at a pressure of 0.12 MPa to achieve maximum axial hydraulic conductivity ( $k_h$ ). Subsequently, length and mean diameter of the segments were determined and the samples stored in 70 % ethanol for further anatomical analyses. Hydraulic conductivity ( $k_h$ , kg m MPa<sup>-1</sup> s<sup>-1</sup>) was calculated as:

$$k_h = J_v \frac{\Delta P}{\Delta X} \quad (2)$$

where  $J_v$  is the flow rate through the branch segment (kg s<sup>-1</sup>) and  $\Delta P/\Delta X$  is the pressure gradient across the segment (MPa m<sup>-1</sup>).  $k_h$  was used to calculate vessel lumen area-specific ( $k_s$ ) and leaf area-specific conductivity (LSC, kg m<sup>-1</sup> MPa<sup>-1</sup> s<sup>-1</sup>) by dividing the maximum conductivity by the microscopically determined lumen area of the vessels (m<sup>2</sup>) or the supported leaf area (m<sup>2</sup>) of the twig segments.

#### 6.2.9 Xylem anatomy, vessel size distribution and theoretical hydraulic conductivity

Anatomical measurements were conducted in all harvested twig segments and trunk cores. We used a stereo-microscope (SteREO V20, Carl Zeiss MicroImaging GmbH, Germany) to obtain high quality top-view images of the cross-sectional cuts of the twigs and trunk cores. Before analysis, the twig segments and trunk cores were dyed with safranin and treated with chalk. The base of every twig segment was photographed to calculate the size of the xylem (sapwood area,  $A_{\text{Xylem}}$ , m<sup>2</sup>). In the trunk core samples, only the outer-most centimetre of the core was analyzed. On average, we analyzed by this procedure an area of  $45.3 \pm 4.8$  mm<sup>2</sup>. The images were analyzed with the software ImageJ (v1.42q, <http://rsb.info.nih.gov/ij>) using the particle analysis-function to estimate idealized radii ( $r$ ) from lumen area ( $A = \pi r^2$ ), vessel density (VD, n mm<sup>-2</sup>) and cumulative vessel lumen area (m<sup>2</sup>). Additionally, we calculated the hydraulically-weighted mean vessel diameter, subsequently referred to as hydraulic mean diameter ( $d_h$ ) using the expression  $\Sigma d_i^5 / \Sigma d_i^4$  after Sperry *et al.* (1994). By applying this transformation, every vessel is weighted according to its contribution to total hydraulic conductivity. With the Hagen-Poiseuille equation, the theoretical hydraulic conductivity ( $k_h^{\text{theo}}$ , m<sup>4</sup> MPa<sup>-1</sup> s<sup>-1</sup>) was calculated as:

$$k_h^{\text{theo}} = \frac{\pi \Sigma r^4}{8\eta} \quad (3)$$

We calculated with the viscosity of water ( $\eta$ ) at 20 °C ( $1.002 \cdot 10^{-3}$  Pa s, Zwieniecki *et al.* 2001).  $k_h^{\text{theo}}$  was used to calculate the theoretical vessel lumen area-specific conductivity

( $k_s^{\text{theo}}$ ,  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) by dividing by cumulative vessel lumen area ( $A_{\text{Xylem}}$ ) and multiplying  $k_s^{\text{theo}}$  with the density of water ( $\rho$ ) at 20 °C ( $998.20 \text{ kg m}^{-3}$ , James *et al.* 2003).

$$k_s^{\text{theo}} = \frac{k_h^{\text{theo}} \cdot \rho}{A_{\text{Xylem}}} \quad (4)$$

#### 6.2.10 Leaf morphology and nutrients

All leaves distal to the analysed twig segments were stripped off and analyzed for their leaf area (WinFOLIA 2005b, Regent Instruments Inc.). On average,  $105.7 \pm 59.6$  leaves per twig segment (control  $n = 56$ , roof  $n = 60$ ) were scanned to obtain the total leaf area per twig and the mean leaf size ( $A_L$ ,  $\text{cm}^2$ ). Afterwards, the whole leaf material was oven-dried for at least 72 h at 70 °C and subsequently weighed at a precision of 10 mg to relate dry mass to the total leaf area to obtain the specific leaf area (SLA,  $\text{cm}^2 \text{g}^{-1}$ ). The Huber value (HV) was calculated as the ratio of sapwood cross-sectional area to the dependent leaf area or number of leaves distal to the measured twig segment. The specific leaf number stands for the number of leaves supported per twig which was calculated by dividing the total number of leaves distal to the twig segment by the twig cross-sectional area ( $n_L^{\text{spec}}$ ,  $\text{n mm}^{-2}$ ).

In the leaf dry mass, the concentrations of C, N, P and Ca, K, Mg, Fe and Mn were analyzed and expressed on a mass and leaf area basis (control  $n = 56$ , roof  $n = 63$ ). The foliar signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined with a Delta plus isotope mass spectrometer (Finnigan MAT, Bremen, Germany), a Conflo III interface (Thermo Electron Cooperation, Bremen, Germany) and an NA2500 element analyzer (CE-Instruments, Rodano, Milano, Italy) using standard  $\delta$  notation:

$$\delta = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000 (\text{‰}) \quad (5)$$

The concentrations of P, Ca, Fe, K, Mg and Mn were determined with an ICP spectrometer Optima 5300 DV (PerkinElmer Inc., USA).

#### 6.2.11 Statistical analyses

All data sets were tested for Gaussian distribution with a Shapiro-Wilk test. Comparisons of normally-distributed parameters were made with three-way general linear models (GLM). In case of non-Gaussian distribution, the datasets were tested with the non-parametric Mann-Whitney U test for pair-wise comparison of means. Significance was assumed at  $p \leq 0.05$  in all cases. These calculations were conducted with the SAS System for Windows 9.1 (SAS

Institute, Cary, NC, USA). Linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany). When comparing upper and lower canopy of the trees in a given treatment, the analyses are labeled with ‘canopy position’, when comparing either upper canopies or lower canopies, between the roofed and control plots, the label ‘treatment’ is used.

## 6.3 RESULTS

### 6.3.1 Microclimatic conditions

During the study period, monthly gross precipitation was  $235.4 \pm 130.4$  mm. In the first year of the experiment (May 1, 2007 to April 30, 2008), annual gross precipitation was  $3156 \text{ mm y}^{-1}$ , in the second year (May 1, 2008 to April 30, 2009)  $2309 \text{ mm y}^{-1}$ . Over the course of the experiment (March 01, 2007 to September 30, 2009), the mean daily maximum vapor pressure deficit ( $D$ ) was 1.3 kPa, mean daily air temperature ( $T$ )  $20.8^\circ\text{C}$ , and mean daily global radiation  $13.4 \text{ MJ m}^{-2} \text{ d}^{-1}$ . No seasonality in  $T$  or relative humidity ( $RH$ ) was observed during the two years (Tab. 6.1).

**Tab. 6.1:** Means of air temperature ( $T$ ), relative humidity ( $RH$ ) and vapor pressure deficit ( $D$ ) at mid-canopy height (16 m) in the two experimental years for full days and the daytime periods only in the Pono forest.

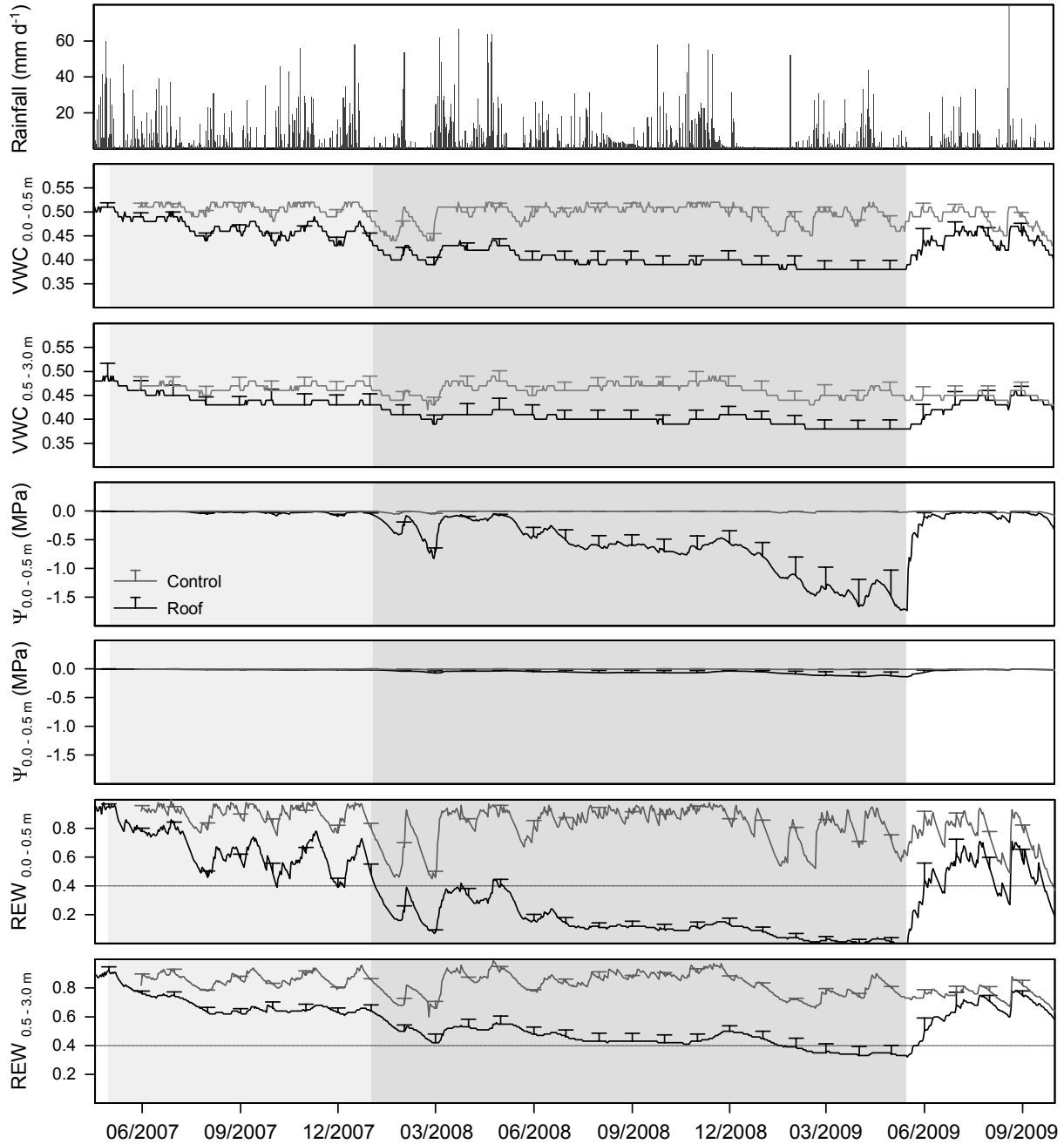
	Full day (24h)			Daylight hours (12h)		
	$T (^\circ\text{C})$	$RH (\%)$	$D (\text{kPa})$	$T (^\circ\text{C})$	$RH (\%)$	$D (\text{kPa})$
1 <sup>st</sup> year	$20.8 \pm 0.7$	$88.5 \pm 5.1$	$0.34 \pm 0.16$	$22.4 \pm 1.0$	$82.4 \pm 6.9$	$0.54 \pm 0.24$
2 <sup>nd</sup> year	$20.6 \pm 0.8$	$88.9 \pm 3.9$	$0.32 \pm 0.13$	$22.3 \pm 1.1$	$82.9 \pm 6.0$	$0.53 \pm 0.22$

### 6.3.2 Soil moisture status during the desiccation

Due to installation delays for the TDR probes caused by a lightning strike, no pre-treatment comparison between control and roof plots could be established. However, soil moisture content (volumetric soil water content,  $\theta$ ) in the roof plots at 0.1 m depth before roof closure was similar to later measured values from the control plots, indicating no differences between the treatments.

The drying of the soil proceeded in two steps that reflected the roof closure by 70 % (May 2007 – January 2008) and subsequently by 90 % (February 2008 – May 2009). While volumetric soil moisture was on average by about 5 percent points lower in the roofed plots than in the control in this first phase of the experiment (0.0-0.5 m and 0.5-3.0 m soil depth),  $\theta$  was reduced by more than 10 percent points in the upper soil and by about 7 percent points in

the lower soil in the period February 2008 – May 2009 (Fig. 6.1). While heavy rainfall resulted in a certain recharge of soil water reserves in the upper soil in the first phase due to incomplete roof closure, volumetric soil moisture remained fairly constant at 0.0-0.5 m and 0.5-3.0 m soil



**Fig. 6.1:** Volumetric soil water content ( $\theta$ ), soil water potential ( $\Psi$ , MPa) and relative extractable water (REW) of the control (grey line) and the roof (black line) plots during the 2-year experimental period (in both soil layers depicted each three measuring depths were instrumented and averaged). For the upper layer (0.0 – 0.5 m), measurements corresponded to 0.1, 0.2 and 0.4 m. For the lower layer (0.5 – 3.0 m), measurements were conducted at 0.75, 1.5, 2.5 m. Values are daily means  $\pm$  SE. The light grey area indicates the first part of the experiment, when 70 % of the roof was closed. The dark grey area indicates the second part of the experiment with a roof closure of 90 %. The roof was opened again in May 2009.

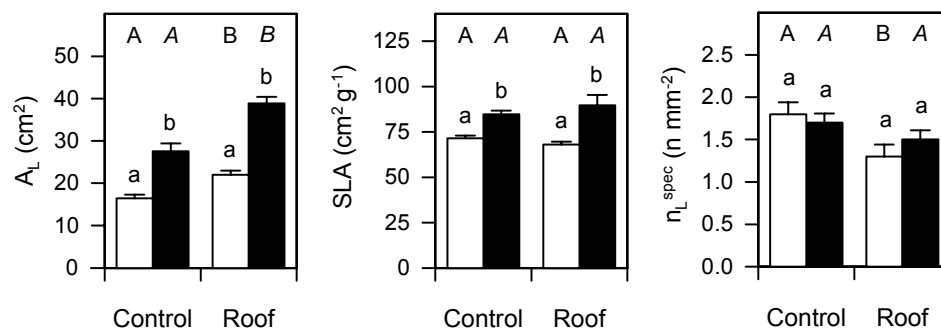
depth under the more efficient roof in the experiment's second phase. The lowest  $\theta$  values were reached shortly before the re-opening of the roof in May 2009. When expressed in relation to the control plots,  $\theta$  was on average by 30 % lower in the upper soil and by 15 % lower in the lower profile in the period June 2008 – May 2009.

According to the soil water retention curves established in the laboratory, the calculated soil matric potential ( $\Psi_{\text{soil}}$ ) decreased in the topsoil (0.1 m) up to -3 MPa during the driest phase from March 2009 until roof opening. As an average for the three investigated upper soil layers (0.1, 0.2 and 0.4 m),  $\Psi_{\text{soil}}$  dropped to -1.5 MPa at the end of the desiccation (Fig. 6.1). In contrast, no significant differences in  $\Psi_{\text{soil}}$  were detected in the lower soil layers (0.5-3.0 m) between roofed and control plots, even though  $\theta$  differed by about 15 %.

The calculated relative extractable water for the upper soil layers ( $\text{REW}_{\text{top}}$ ) dropped in the roof plots below the threshold value of 0.4 immediately after the beginning of the second phase of the desiccation in early 2008, enhanced by rather low rainfall in this period (Fig. 6.1). Interrupted by a short recovery due to strong rainfall in March/April 2008,  $\text{REW}_{\text{top}}$  decreased further in the roofed plots, leading to a 90 % smaller amount of available water in the roofed plots compared to the control. On the other hand, the relative extractable water of the lower soil layers ( $\text{REW}_{\text{low}}$ ) only dropped below the threshold of 0.4 in the driest phase of the experiment from February 2009 onwards. Nevertheless,  $\text{REW}_{\text{low}}$  was by 50 % smaller in the roofed than in the control plots from June 2008 until May 2009.

### 6.3.3 Desiccation effects on hydraulic properties and leaf traits

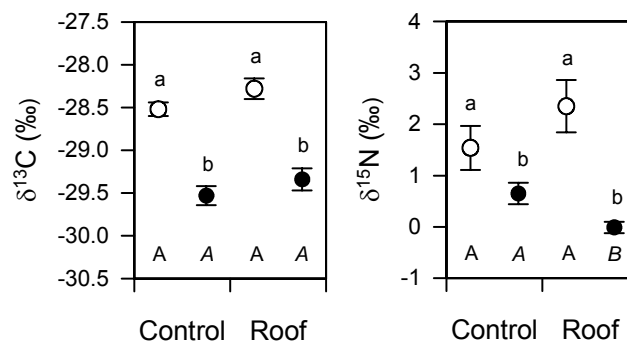
Branches of *C. acuminatissima* harvested after the two-year desiccation period had significantly lower axial hydraulic conductivities in the xylem than samples from the control trees (Fig. 6.4).



**Fig. 6.2:** Mean leaf size ( $A_L$ , cm²), specific leaf area (SLA, cm² g⁻¹), specific leaf number ( $n_L^{\text{spec}}$ , n mm⁻²) in the upper sun-lit (□) and the lower shade crown (■) of *C. acuminatissima* in the control and the roofs plots. Lower-case letters indicate significant differences between crown positions within a given treatment and upper-case

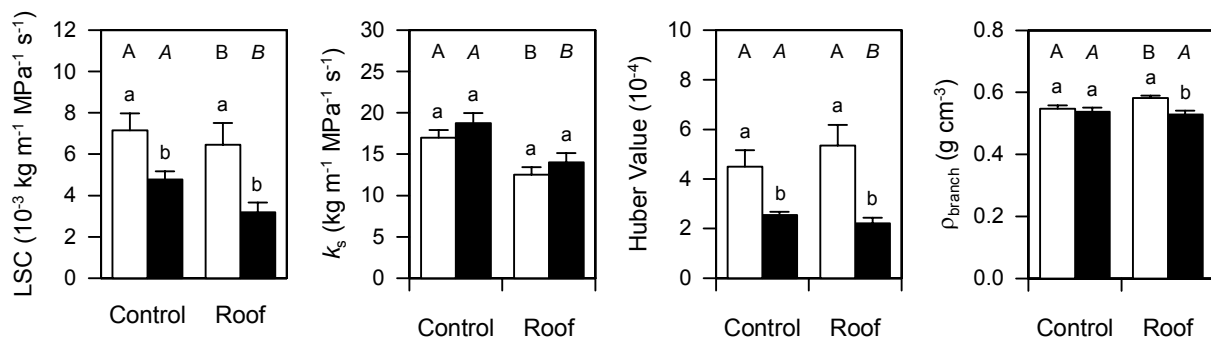
letters stand for significant differences between roof and control. Values are means  $\pm$  SE. Number of replicates were: n control = 56, n roof = 60 (number of leaves measured: n control = 7987, n roof = 5015).

This was found for leaf-specific hydraulic conductivity (LSC) and for axial conductivity normalized by vessel lumen area ( $k_s$ ) and was valid for both branches of the sun and shade canopies. While the ratio branch sapwood area : dependent leaf area (Huber value) did not alter, we recorded a significantly reduced number of leaves of about 30 % that depend in a unit branch sapwood area (leaf number-based Huber value, Fig. 6.2, Tab. 6.4). The droughted trees also showed a higher wood density in the branches of the sun canopy, but not of the shade canopy, which is consistent with the reduced hydraulic conductivity. Probably linked to the reduced leaf number per branch sapwood, we found a significant increase in mean leaf size after two years of desiccation in the roofed plots both in sun and shade canopy branches.



**Fig. 6.3:** Isotope signatures of carbon ( $\delta^{13}\text{C}$ , left) and nitrogen ( $\delta^{15}\text{N}$ , right) in leaf biomass harvested distal to the twig segments used for hydraulic investigations from the upper sun-lit crown (○) and lower shade crown (●) of *C. acuminatissima*. Values are means  $\pm$  SE. For the number of replicates see Tab. 6.3.

Analysis of isotope composition in leaf dry mass indicated no drought effects on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Fig. 6.3). The  $\delta^{13}\text{C}$ - $\text{N}_\text{A}$  relationship was not different between roof and control plots (Fig. 6.5). Leaves harvested at the end of the experiment contained in the roof plots significantly less Ca, Mg and Fe (sun and shade canopy) and N (shade canopy) per dry mass than the control (Tab. 6.3 and Tab. 6.4).



**Fig. 6.4:** Leaf-specific conductivity (LSC), vessel-lumen specific conductivity ( $k_s$ ), Huber value and branch wood density ( $\rho_{\text{branch}}$ ) of the upper sun-lit crown (□) and lower shade crown (■) of *C. acuminatissima* trees in the control and roof plots. Lower-case letters indicate significant differences between the crown positions of a given

treatment, and upper-case letters stand for significant differences between the two treatments. Values are means  $\pm$  SE. Number of replicates for LSC,  $k_s$  and HV were: n control = 56, n roof = 60; for  $\rho_{\text{branch}}$ : n control = 52, n roof = 57.

**Tab. 6.2:** Morphological, anatomical and hydraulic characteristics of the trunks at 1.5 m height in 14 tree individuals of *C. acuminatissima*. Diameter at breast height (DBH, cm), tree height (H, m), Pilodyn hardness, stem wood density ( $\rho_{\text{stem}}$ , g cm<sup>-3</sup>), saturated water content (SWC, %), vessel lumen area ( $A_{\text{lumen}}$ , %), vessel density (VD, n mm<sup>-2</sup>), mean vessel diameter ( $d$ ,  $\mu$ m, mean  $\pm$  SE), hydraulic mean diameter ( $d_h$ ,  $\mu$ m), theoretical lumen-specific conductivity ( $k_s^{\text{theo}}$ , kg m<sup>-1</sup> MPa<sup>-1</sup> s<sup>-1</sup>) and level of significance (p) between the treatments (control: C1-C7, roof: R1-R7).

Tree	DBH	H	Pilodyn	$\rho_{\text{stem}}$	SWC	$A_{\text{lumen}}$	VD	$d$	$d_h$	$k_s^{\text{theo}}$
C1	68.6	31.6	20.0	491.4	117.8	21.4	4.2	250.3 $\pm$ 5.8	291.4	554.6
C2	35.6	49.9	18.0	541.8	105.5	19.8	3.1	279.7 $\pm$ 6.1	320.8	615.4
C3	56.2	35.6	17.0	511.0	112.0	9.9	2.0	248.0 $\pm$ 6.1	284.2	246.5
C4	48.0	39.7	15.0	480.1	130.6	11.2	2.8	215.9 $\pm$ 6.8	267.9	240.2
C5	44.7	29.6	12.0	545.3	110.9					
C6	71.4	38.1	14.5	535.8	105.2	12.9	2.8	238.2 $\pm$ 5.2	275.6	291.2
C7	67.8	43.9	18.0	490.8	113.9	18.0	3.4	249.5 $\pm$ 6.3	309.8	505.5
<b>Control</b>	<b>56.0 <math>\pm</math> 5.2</b>	<b>38.2 <math>\pm</math> 2.7</b>	<b>16.4 <math>\pm</math> 1.0</b>	<b>513.0 <math>\pm</math> 10.3</b>	<b>113.7 <math>\pm</math> 3.3</b>	<b>15.6 <math>\pm</math> 2.0</b>	<b>3.1 <math>\pm</math> 0.3</b>	<b>247.4 <math>\pm</math> 2.6</b>	<b>291.6 <math>\pm</math> 8.3</b>	<b>408.9 <math>\pm</math> 68.8</b>
R1	63.8	40.5	15.0	555.0	95.9	13.6	3.2	226.9 $\pm$ 5.8	277.1	311.4
R2	49.8	41.0	15.0	545.4	100.4	13.2	2.9	234.7 $\pm$ 5.3	272.8	292.3
R3	56.9	48.8	15.0	525.4	99.9	18.6	3.8	248.1 $\pm$ 4.0	276.6	435.3
R4	81.0	34.8	17.0	496.8	124.5	12.8	2.8	232.0 $\pm$ 6.5	291.3	317.0
R5	52.7	37.0	13.5	533.0	105.8	14.1	3.3	231.5 $\pm$ 4.2	257.4	283.1
R6	59.4	39.6	14.0	540.5	102.5	13.9	2.9	237.7 $\pm$ 6.1	289.6	346.5
R7	44.7	40.5	15.0	575.6	90.5	20.1	3.4	267.4 $\pm$ 6.1	315.2	594.8
<b>Roof</b>	<b>58.3 <math>\pm</math> 4.5</b>	<b>40.3 <math>\pm</math> 1.7</b>	<b>14.9 <math>\pm</math> 0.4</b>	<b>538.8 <math>\pm</math> 9.3</b>	<b>102.8 <math>\pm</math> 4.1</b>	<b>15.2 <math>\pm</math> 1.1</b>	<b>3.2 <math>\pm</math> 0.1</b>	<b>240.1 <math>\pm</math> 2.1</b>	<b>282.9 <math>\pm</math> 6.9</b>	<b>368.6 <math>\pm</math> 42.3</b>

### 6.3.4 Stem increment, wood anatomy and wood density as affected by the desiccation

In the roof plots, the annual stem diameter increment was by 10 % lower in the first year of the experiment, and by 26 % in the second year than in the control plots in the *C. acuminatissima* trees. However, the differences were not significant ( $p = 0.12$  for the second year). Drought-induced alterations in the outermost xylem of the trunk are further documented by a significant decrease in mean vessel diameter and consequently also in theoretical hydraulic conductivity, and a significant increase in the wood density of the peripheral xylem sections (by 5 %) and an associated reduction in saturated water content (SWC) of the xylem by 10 % when comparing roof and control plots (Tab. 6.2).

**Tab. 6.3:** Foliar contents of C, N, P and cations per mass and per leaf area in leaves that were harvested distal to the twig segments used for hydraulic measurements in the control and roof plots for upper (sun) and lower (shadow) crown. The given unit is  $\text{g kg}^{-1}$  or  $\text{g m}^{-2}$ . Lower-case letters indicate significant differences between the two crown positions, and upper-case letters between the two treatments. All values are means  $\pm 1$  SE. The number of replicates for the control are  $n = 56$ , for the roof  $n = 63$ .

	Control		Roof	
	Sun	Shade	Sun	Shade
<b>Mass-related</b>				
C	503.7 $\pm$ 5.3 a A	508.4 $\pm$ 3.3 a A	494.4 $\pm$ 1.8 a A	488.9 $\pm$ 1.8 b B
N	18.11 $\pm$ 0.41 a A	18.16 $\pm$ 0.25 a A	17.63 $\pm$ 0.23 a A	16.80 $\pm$ 0.27 b B
P	1.54 $\pm$ 0.03 a A	1.54 $\pm$ 0.02 a A	1.57 $\pm$ 0.05 a A	1.61 $\pm$ 0.04 a A
Ca	9.96 $\pm$ 0.42 a A	9.73 $\pm$ 0.37 a A	7.11 $\pm$ 0.33 a B	6.93 $\pm$ 0.35 a B
Fe	0.08 $\pm$ 0.01 a A	0.09 $\pm$ 0.01 a A	0.06 $\pm$ 0.01 a B	0.07 $\pm$ 0.01 a B
K	9.75 $\pm$ 0.22 a A	10.00 $\pm$ 0.32 a A	9.47 $\pm$ 0.23 a A	9.84 $\pm$ 0.32 a A
Mg	3.60 $\pm$ 0.09 a A	4.24 $\pm$ 0.13 b A	2.82 $\pm$ 0.11 a B	3.66 $\pm$ 0.09 b B
Mn	1.26 $\pm$ 0.07 a A	1.04 $\pm$ 0.05 b A	1.32 $\pm$ 0.10 a A	1.20 $\pm$ 0.08 a A
<b>Area-related</b>				
C	71.30 $\pm$ 1.50 a A	60.85 $\pm$ 1.45 b A	74.57 $\pm$ 1.46 a B	57.10 $\pm$ 2.20 b A
N	2.57 $\pm$ 0.40 a A	2.17 $\pm$ 0.29 b A	2.65 $\pm$ 0.28 a A	1.94 $\pm$ 0.40 b B
P	0.22 $\pm$ 0.01 a A	0.18 $\pm$ 0.00 b A	0.23 $\pm$ 0.01 a B	0.19 $\pm$ 0.01 b A
Ca	1.42 $\pm$ 0.07 a A	1.16 $\pm$ 0.05 b A	1.05 $\pm$ 0.05 a B	0.83 $\pm$ 0.05 b B
Fe	0.012 $\pm$ 0.002 a A	0.011 $\pm$ 0.002 a A	0.010 $\pm$ 0.001 a A	0.008 $\pm$ 0.001 a B
K	1.37 $\pm$ 0.03 a A	1.18 $\pm$ 0.03 b A	1.41 $\pm$ 0.02 a A	1.16 $\pm$ 0.06 b A
Mg	0.50 $\pm$ 0.01 a A	0.50 $\pm$ 0.01 a A	0.42 $\pm$ 0.02 a B	0.44 $\pm$ 0.02 a A
Mn	0.18 $\pm$ 0.01 a A	0.12 $\pm$ 0.01 b A	0.19 $\pm$ 0.02 a A	0.14 $\pm$ 0.01 b A

### 6.3.5 The factor ‘canopy position’: Differences between sun and shade canopy

The large majority of leaf morphological, chemical and branch hydraulic traits differed significantly between sun-lit upper canopy and lower shade canopy of *C. acuminatissima*. Sun leaves were smaller with a lower SLA, had a less negative  $\delta^{13}\text{C}$  and a more positive  $\delta^{15}\text{N}$  signature, and generally showed higher foliar nutrient concentrations per leaf area (except for



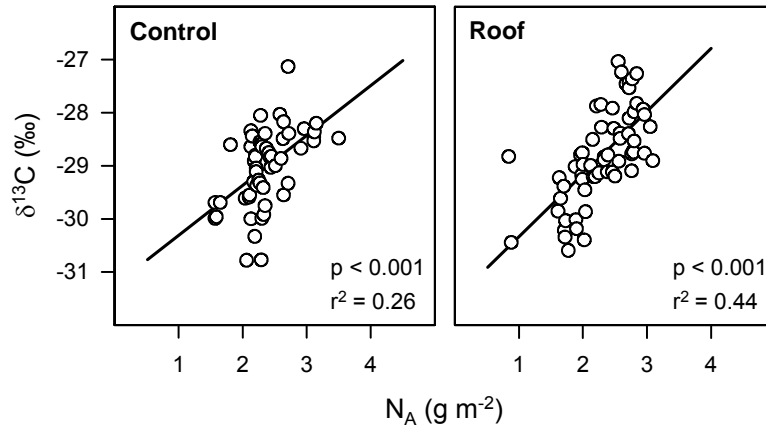
Mg and Fe) than shade leaves, while the nutrient concentrations per mass were not different (except for higher Mg and lower Mn concentrations in sun leaves, Tab. 6.3 and Tab. 6.4).

**Tab. 6.4:** P values for the comparison between means of control and roof plots or sun and shade crown of 27 parameters measured in *C. acuminatissima* trees. The first column gives the ratio of the means (for canopy position: shade over sun canopy; for the treatment: roof over control treatment), the second column indicates the significance of the difference (parametric or non-parametric traits). The levels of significance are presented as  $p \geq 0.05 = *$ ,  $p > 0.01 = **$  and  $p > 0.001 = ***$ . Not significant relations = n.s.

	Treatment effects				Canopy position effects			
	Sun leaves		Shade leaves		Control		Roof	
<i>Hydraulic traits</i>								
LSC	0.90	*	0.67	**	0.67	**	0.49	*
k <sub>s</sub>	0.74	***	0.75	**	1.10	n.s.	1.12	n.s.
HV	1.19	n.s.	0.87	**	0.56	***	0.41	***
n <sub>L</sub> <sup>spec</sup>	0.72	**	0.88	n.s.	0.94	n.s.	1.14	n.s.
<i>Leaf morphology</i>								
Leaf area	1.29	***	1.39	***	1.60	***	1.72	***
SLA	0.95	n.s.	1.06	n.s.	1.19	***	1.32	***
<i>Wood density</i>								
ρ <sub>branch</sub>	1.06	**	0.98	n.s.	0.98	n.s.	0.91	***
<i>Isotope composition</i>								
δ <sup>13</sup> C	0.99	n.s.	0.99	n.s.	1.04	***	1.04	***
δ <sup>15</sup> N	1.53	n.s.	—	*	0.43	*	—	***
<i>Nutrient concentrations</i>								
<i>Mass-specific</i>								
C	0.98	n.s.	0.96	***	1.01	n.s.	0.99	**
N	0.97	n.s.	0.93	**	1.00	n.s.	0.95	*
P	1.01	n.s.	1.05	n.s.	1.00	n.s.	1.03	n.s.
Ca	0.71	***	0.71	***	0.98	n.s.	0.98	n.s.
Fe	0.76	*	0.71	**	1.11	n.s.	1.04	n.s.
K	0.97	n.s.	0.98	n.s.	1.03	n.s.	1.04	n.s.
Mg	0.78	***	0.86	***	1.18	***	1.30	***
Mn	1.05	n.s.	1.16	n.s.	0.83	**	0.91	n.s.
<i>Area-specific</i>								
C	1.05	*	0.94	n.s.	0.85	***	0.77	***
N	1.03	n.s.	0.90	**	0.85	***	0.73	***
P	1.07	*	1.03	n.s.	0.84	***	0.81	***
Ca	0.74	***	0.72	***	0.82	**	0.79	**
Fe	0.81	n.s.	0.67	**	0.95	n.s.	0.78	n.s.
K	1.03	n.s.	0.98	n.s.	0.86	***	0.82	***
Mg	0.84	**	0.88	n.s.	1.00	n.s.	1.05	n.s.
Mn	1.11	n.s.	1.16	n.s.	0.70	***	0.74	*

Shade leaves with lower N per leaf area discriminated stronger against  $\delta^{13}C$  (more negative  $\delta^{13}C$ ) than sun leaves; the  $\delta^{13}C$ - $N_A$  relationship was not different between drought-exposed and control trees (Fig. 6.5). Sun canopy branches had a much higher sapwood area : leaf area

ratio (Huber value), and thus leaf-specific conductivities (LSC) than shade canopy branches. Vessel density and wood density in the branches differed between sun and shade canopy only in the drought-exposed roofed plots, while lumen area-specific conductivity was the same (Tab. 6.4).



**Fig. 6.5:** Relation between area-specific nitrogen content ( $N_A$ ) and  $\delta^{13}C$  in *C. acuminatissima* from the lower and upper crown in the control and roof plots. Slope  $b = 0.80$  (control),  $1.18$  (roof). For number of replicates see Tab. 6.3.

## 6.4 DISCUSSION

### 6.4.1 Desiccation effects on leaf traits and twig hydraulic properties

After 24 months of throughfall reduction, the topsoil layers of the Pono forest were strongly desiccated, exceeding conventional thresholds of critical soil water availability for plant growth ( $\Psi_{\text{soil}} < -1.5$  MPa,  $\text{REW} < 0.4$ ). In accordance with other root system studies in perhumid environments (Schenk and Jackson 2002, Hertel *et al.* 2003, Jimenez *et al.* 2009) the trees of the Pono forest most likely did not develop deep-reaching roots that could tap water reserves in deeper soil layers. In support of this assumption, Hertel *et al.* (2009) observed that 74.3 % of the fine root biomass ( $\varnothing \leq 2$  mm) in the soil of the study plots was located within the top 20 cm and only 4.4 % reached 40-60 cm soil depth. The coarse roots ( $\varnothing > 2$  mm) showed a similar depth distribution (91.1 % in the top 20 cm, 1.2 % in 40-60 cm soil depth) with an exponential biomass depth distribution decrease with depth and only extremely small fine root densities ( $0.12 \text{ g L}^{-1}$ ) at 100-300 cm depth. Our data on the depth distribution of tree roots strongly indicate that deep-reaching roots are far less important in this tropical perhumid forest than in the Amazonian forest with short dry periods studied by Nepstad *et al.* (2002). More than three months of exposure to water availabilities in the

topsoil below the conventional ‘wilting point’ of crop plants must have represented drought stress of considerable intensity for the trees of this stand.

Anatomical investigations of the conducting system and hydraulic measurements in a rather large number of sun-canopy and shade branches of *C. acuminatissima* showed that the terminal twigs, which must have been grown during the two-year experimental period, had a significantly reduced axial conductivity in their xylem when expressed per vessel lumen cross-sectional area ( $k_s$ ; 25 % reduction) or leaf area distal to the measuring point (LSC; 10-33 % reduction). The reason may be a smaller mean vessel diameter or decreased vessel densities in the twig xylem, and hence a higher wood density in the branches of the desiccation treatment. Several authors have reported that trees adjust the shape of their vessels when exposed to drought (e.g. Sass and Eckstein 1995, Eilmann *et al.* 2006), reflecting plant water status at the time of cell differentiation (García-González and Eckstein 2003).

Remarkably, we found an impaired hydraulic performance of the terminal twigs. The comparative investigation of about 60 twigs each in the roof and control plots produced evidence that drought may also have affected processes of leaf bud initiation and leaf expansion because our data show a significant reduction in the number of leaves per twig sapwood area (lower Huber-value normalized to leaf number) in the sun crown, and an increase in mean leaf size by 30-40 % in twigs in the sun and shade crown of the desiccation plots at the end of the treatment. Since we found no scars of abscised leaves on the investigated twigs, we assume that twigs grown during the desiccation treatment have formed a smaller number of new leaf buds, thereby reducing the leaf area to be supplied with water, thus improving the water status of the remaining leaf buds and allowing them to unfold larger leaves. A similar effect has been observed in saplings of silver birch (*Betula pendula*) that produced fewer but larger under drought (Aspelmeier and Leuschner 2006). The same was found along a precipitation gradient in Central Germany for beech (*Fagus sylvatica*, Meier and Leuschner 2008). This reasoning could also explain why we did not find a decrease in  $\delta^{13}\text{C}$  signatures in the drought-exposed leaves, as would be expected when leaf conductance and leaf expansion growth were reduced during periods of water shortage (Lambers *et al.* 1998, Lösch 2001). However, an alternative strategy is to reduce the number of leaves in order to maintain, or even improve, the water status of the remaining leaves, which may have happened in *C. acuminatissima* in our experiment.

Foliar nutrient analyses did not provoke evidence for the hypothesis that soil desiccation considerably influences the metabolism of trees through nutrient, mainly N, shortage (e.g.

Gessler *et al.* 2004, Beier *et al.* 2008, Fotelli *et al.* 2009, Kreuzwieser and Gessler 2010). Neither foliar N nor P were significantly altered after 24 months of desiccation treatment. However, significant smaller leaf Ca contents per dry mass and also per leaf area may indicate either reduced transpiration rates or smaller Ca concentrations in the soil solution of the roofed plots, because the element mostly is transported passively with the mass-flow of water in soil and xylem (Gollan *et al.* 1992, McDonald and Davis 1996). We speculate that the droughted trees extracted water from deeper soil layers where the concentrations of Ca and other nutrients were lower.

Reduced stomatal conductance in periods of high atmospheric saturation deficits and low soil moisture often have been found to result in less discrimination against  $\delta^{13}\text{C}$  in the course of  $\text{CO}_2$  assimilation (e.g. Saurer *et al.* 1997, Handley *et al.* 1999, Jäggi *et al.* 2003, Sala and Hoch 2009, Fichtler *et al.* 2010), while the  $\delta^{15}\text{N}$  signature of leaves typically shows no strong drought signal (Peuke *et al.* 2006, Hartman and Danin 2010). Thus, the lack of differences in  $\delta^{15}\text{N}$  between roof and control trees fits to the expectation, while the absence of  $\delta^{13}\text{C}$  differences comes as a surprise. It appears that leaf conductance was not significantly reduced in response to the 24-months desiccation. Further, the foliar nitrogen-leaf area relationship was similar in roofed and control trees (see Fig. 6.5) which suggests that stomatal and biochemical photosynthesis were not larger in the drought-exposed trees than in the control. The  $\delta^{13}\text{C}$  signal is viewed as support of the assumption, that soil desiccation led to a reduction in leaf numbers, while the water status of the remaining leaves was not deteriorated.

#### 6.4.2 Desiccation effects on the hydraulic system of the stem

In concert with the alterations observed in the xylem of sun canopy and also shade canopy twigs, we detected reductions in mean vessel diameter and axial conductivity in the outermost xylem of the trunks of the roofed plots which also showed up in a higher wood density and a reduced saturated water content of this recently developed section of the xylem. These anatomical responses may also partly explain the 26 % reduction in stem diameter growth observed in the drought-exposed *C. acuminatissima* trees during the second year of the experiment, even though stem shrinking most likely has also contributed to the relatively small diameter increase in these trees. It has to be mentioned that the difference in stem increment between roofed and control plots despite its absolute size was not significant ( $p = 0.12$  for the second year) which was mainly caused by the relatively small number of large *C. acuminatissima* trees (9 or 7) that grew in the roofed and control plots.

In contrast to our expectations of a sensible drought-response of the tree of this perhumid forest, we found no signs of major damage in the adult trees after 24-months desiccation, while most of the tree saplings and herb layer plants had already died. Rather, our data indicate adaptive responses in the hydraulic system and canopy leaf area of the tall *C. acuminatissima* trees that are suited to lower the risk of cavitation and reduce canopy transpiration. One might conclude that *C. acuminatissima* is not as drought-sensitive as we assumed due to its frequent occurrence in this perhumid forest with only exceptionally occurring droughts.

However, several facts make it likely that this conclusion is premature. First, other desiccation experiments in forests showed that severe damage to the trees may occur only after two or more years of soil desiccation. For example, Nepstad *et al.* (2007) observed increased mortality of large trees in the Tapajós throughfall displacement experiment only after four years of desiccation, and da Costa *et al.* (2010) after seven years for the ‘Caxiuanã’ throughfall displacement experiment. Thus, a considerable lag phase in the response of tall trees seems to be characterized and our two-year experiment may have lasted not long enough to damage the trees critically. Second, all throughfall displacement experiments have the disadvantage that they can reduce soil moisture to a critical level, but they leave the air humidity at canopy height unchanged. Clearly, the trees would be exposed to a much higher evaporative demand during a natural ENSO-related drought than it was simulated in our experiment where relative humidity did not drop below 88 % in the experimental period (see Tab. 6.1) despite the long-lasting and marked soil desiccation.

There is also the possibility that the trees were profiting from the high rainfall in the area by foliar uptake of water, thereby mitigating the effects of soil water shortage. For example, some studies obtained evidence for water absorption through the leaf cuticle of tropical trees (Yates and Hutley 1995, Diaz and Granadillo 2005, Oliveira *et al.* 2005). Thus, it is likely that soil desiccation in a natural dry spell will have a much stronger effect on the studied tree individuals of *C. acuminatissima* than it was simulated in our experiment.

#### 6.4.3 *Is the sun canopy more drought sensitive than the shade canopy?*

Our second hypothesis postulated that the sun canopy of tall trees is more susceptible to drought than lower crown parts in the deep shade where air humidity is higher. Except for wood density in the twigs, all hydraulic and leaf parameters that showed responses to the desiccation treatment for sun canopy twigs, reacted in a similar way in shade twigs as well.

Indeed, the decrease in twig axial hydraulic conductivity, in the number of leaves per sapwood area (modified Huber value) and the increase in leaf size upon drought were observed in the shade canopy in a similar manner as in the tree top. Moreover, the reduction in LSC was even greater than in the sun canopy. Thus, a stress-mitigating effect of the humid forest interior did not occur; the physiological consequences of soil desiccation seem to develop in tall *C. acuminatissima* trees rather independently of height in the tree and the specific microclimate.

This is astonishing given the large differences in leaf and hydraulic traits between the sun and shade canopy. Shade leaves of *C. acuminatissima* were on average 60-70 % larger and had 20-30 % higher SLA than sun leaves, while leaf-specific conductivity in the twig xylem and the Huber value were about 40-60 % smaller in the shade canopy due to lower evaporative demand. On the other hand, lumen area-specific conductivity was about 10 % higher in the xylem of the shade branches than in the sun canopy (differences not significant) which is associated with a smaller wood density in the twig xylem. Thus, despite a greater exposure to atmospheric drought, sun leaves and twigs did not differ from shade leaves and twigs in their response to soil desiccation.

## 6.5 CONCLUSIONS

The Sulawesi Throughfall Displacement Experiment is the first experimental study about the effects of an extended soil desiccation period on the trees of a perhumid tropical rainforest where natural droughts occur only exceptionally. The very shallow depth distribution patterns of fine and coarse roots are interpreted as resulting from the continuously high rainfall and permanently low atmospheric saturation deficit; these hydrologic characteristics allow to contrast the Sulawesi experiment with the two throughfall displacement experiments in Eastern Amazonia where regular dry periods occur and certain trees may have deep-reaching roots (e.g. Markewitz *et al.* 2010 and references therein). While no signs of canopy dieback or other critical damage were observed in the tall *Castanopsis acuminatissima* trees or the other trees in the stand, the long and severe desiccation of the upper soil caused marked reductions in the hydraulic conductivity of the xylem of the trunk and of the terminal twigs, a reduction in leaf number per conducting sapwood in the twigs (but no reduction in leaf size), and a tendency for reduced stem diameter growth. We conclude that the tall *C. acuminatissima* trees in this perhumid forest were – in contrast to our second hypothesis – not more drought-susceptible in the upper sun canopy than in the shade crown. Neither the *C. acuminatissima*

trees nor other less tall-growing tree species showed signs of critical damage which rejects our first hypothesis. We assume that the constantly high air humidity in this environment, which was not reduced by the throughfall displacement, plays an important role for the vigor of these trees and may have buffered against critical drought-induced damages as they were expected from the soil water status data.

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**7 SEVENTH CHAPTER**  
**SYNTHESIS**

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## 7.1 SUMMARY OF PRESENT FINDINGS AND DISCUSSION

### 7.1.1 Microclimatic conditions and xylem sap flux density in the old-growth perhumid rainforest of Central Sulawesi

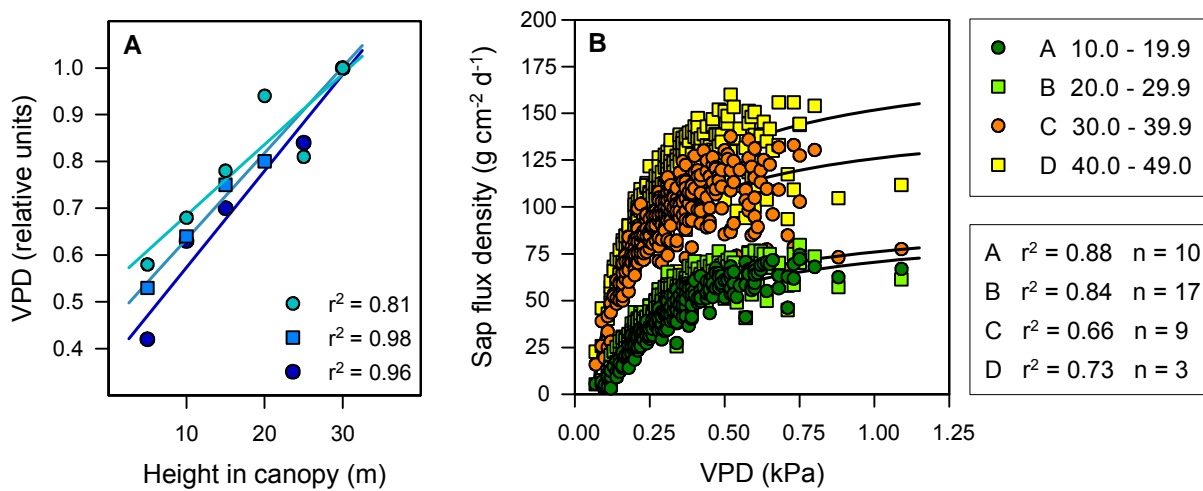
In the premontane perhumid rainforest of Central Sulawesi, Indonesia, with annual precipitation rates of more than 2500 mm, abiotic factors such as temperature and relative air humidity (RH) vary only slightly diurnally as well as throughout the year (Tab. 2.1). Hence, average atmospheric vapor pressure deficit (VPD) was continuously low with an annual mean of 0.54 kPa. Comparing the evaporative demand of this perhumid environment with an old-growth forest stand in Central Germany (Hainich National Park) showed, that during the normal vegetation period (April to September 2008), the temperate deciduous forest is on average exposed to a 35 % higher VPD despite much lower temperatures.

In the present study, the highest recorded mean daily water use in the year 2008 was reached by a tall *C. acuminatissima* individual, a member of the family Fagaceae. With 132 kg d<sup>-1</sup> this is a remarkably low daily total for a tropical climate, and comparable to the water consumption of *Fagus sylvatica* trees, a temperate member of this family. Hölscher *et al.* (2005) reported a mean daily water use of 152 kg d<sup>-1</sup> in a Central German forest for this tree species. It can be assumed that only tropical trees from seasonal dry forests, or other forests with a higher evaporative demand, reach extraordinary high amounts of tree water consumption as commonly assumed for tropical forests. Meinzer *et al.* (2004), for instance, reported a water use of 800 kg d<sup>-1</sup> for a tall *Anacardium excelsium* individual in the seasonal dry tropical forest of Panama.

The importance of atmospheric factors for the regulation of water flux in the trees is also reflected in the results on xylem sap flux density and root water uptake. The xylem sap flux density (XFD) of the trees in this perhumid forest showed a more tight correlation with VPD than with global radiation (Tab. 5.4), despite the prevailing high relative air humidity. This is in agreement with results from a comparable study in French Guiana (Granier *et al.* 1996). Coners and Leuschner (2005) found the rates of root water uptake in mature beech, oak and spruce trees to be primarily controlled by VPD as well.

In the present study, mean VPD doubled from the ground level to 30 m canopy height in the stand (Fig. 7.1, left). The increase in VPD with increasing tree height was reflected in the XFD of the eight investigated co-occurring tree species: smaller trees, independent of family

and species, reached much lower XFD values in the outermost xylem than taller trees from the upper canopy (Fig. 7.1, right).

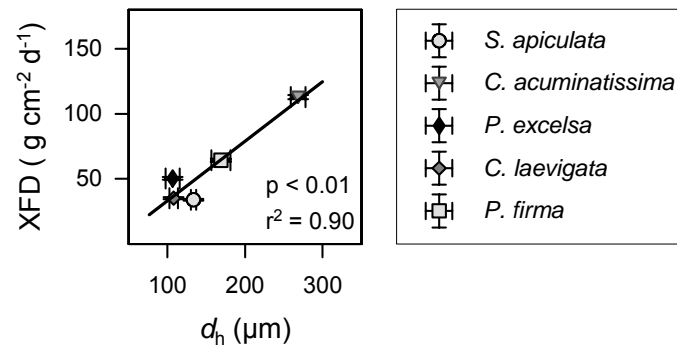


**Fig. 7.1:** (A): Increase in mean VPD (relative units, 30 m = 1.0) with height in the forest. Regression lines and symbols correspond to three different vertical profiles ( $p < 0.01$ ). Points are mean values for continuous measurements over a period of 12 days. (B): Mean rates of xylem sap flux density of different tree height classes (A to D) as related to mean daily atmospheric vapor pressure deficit (VPD). Data from 365 days are compiled. Measured tree individuals are aggregated in four tree height classes and regression analysis ( $p < 0.001$ ) is given for each height class separately. The tree individuals belong to seven tree species. For further explanations see chapter 2.3.3.

### 7.1.2 Morphological adaptations of the trees to a low evaporative demand in a perhumid climate

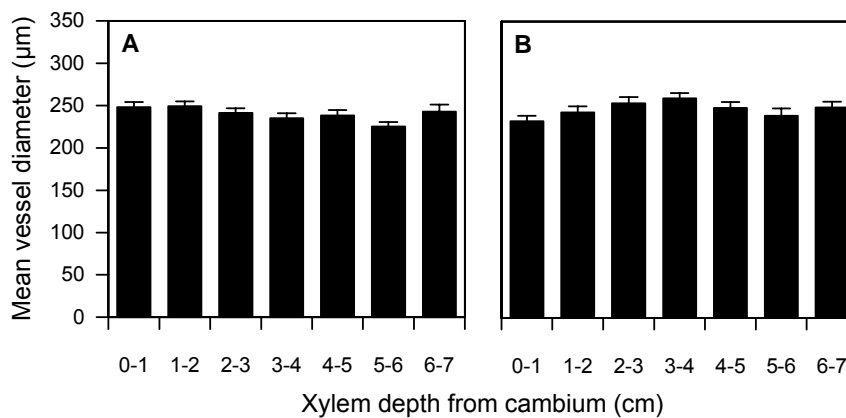
According to the model proposed by West *et al.* (1999), conduits need to taper acropetally from the trunk base towards the upper canopy, with the smallest vessel diameters occurring in the terminal branches and twigs. Consequently, the wood at the stem base should contain the largest vessels along the flow path from root to twig. This relationship should depend on tree height, with tall trees from the upper canopy being forced to taper their vessels to a higher degree due to a longer flow path than species from the understory. In support of this assumption, vessels were found to taper from the stem base towards the crown across the eight species studied (Fig. 4.3), and the tallest trees showed the largest vessels in the wood (Fig. 3.2). The vessel size distribution along the flow path from small roots over strong roots and the trunk to the distal twigs was best described by an optimum curve. Our results suggest that, under a perhumid climate, the long distance for water transport in large trees requires intrinsic adjustments of the plant hydraulic system. Large trees apparently have to compensate for the longer water flow path and for a comparatively low leaf-to-soil water potential gradient for most of the year. In support of this assumption, we found a tight relationship

between sap flux density measured at the stem base and vessel diameter size in the trunk wood for five of the eight co-occurring tree species (Fig. 7.2). In contrast, adaptations to water shortage seem to be less economic under the aseasonal conditions of perhumid tropical rainforests.



**Fig. 7.2:** Mean xylem sap flux density (XFD) averaged for 365 days in relationship to hydraulic mean vessel diameter ( $d_h$ ) in the trunk of five tree species. Values are means  $\pm$  SE for a given species. For further explanation see chapter 2.3.3 and 4.2.3.

Increasing vessel size with tree height has the implication that the vessel diameter should additionally increase with increasing tree age at the trunk base, leading to a growing cavitation risk in older and taller trees.



**Fig. 7.3:** Mean vessel diameter in the trunk wood at breast height with increasing wood age i.e. distance from cambium towards the hardwood for two tall *C. acuminatissima* tree individuals (A: BDH = 56.2 cm, H = 35.6 m; B: DBH = 81.0 cm, H = 34.8). Values are means  $\pm$  SE. Number of vessels for each 1 cm segment = 59-146.

However, we found vessel size to stay constant along the radial profile from older to younger tissue. It seems that tropical tree species increase rather the vessel number per cross-sectional area than the size while growing taller (Fig. 7.3, Fig. 7.4).

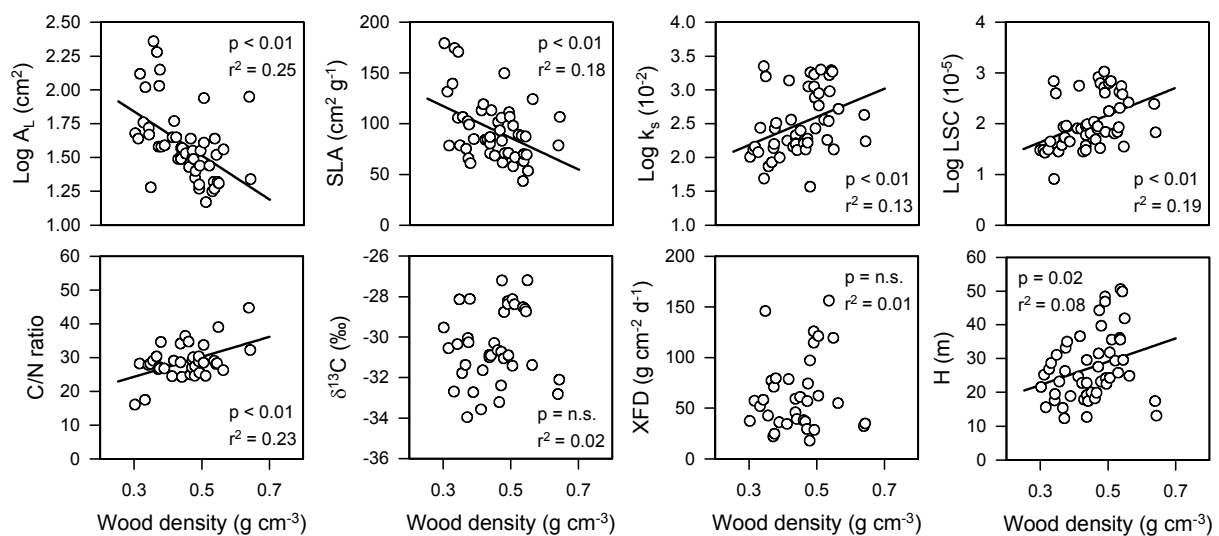


**Fig. 7.4:** Trunk wood core extracted at breast height and colored with safranin from a tall *C. acuminatissima* tree individual (Fig. 7.3 B: DBH = 81.0 cm) from the cambium (left) seven centimeters to the center (right).



### 7.1.3 Influence of wood density on tree physiological and morphological traits

Wood density is a tree trait with strong ecological implications (Falster 2006). Wood density depends on the amount of fibres and tracheids per volume tissue. It affects the physical stability of woody tissues during high negative pressures as they are caused by drought stress (Domec *et al.* 2009). While light wood is commonly associated with fast-growing and low cost strategies, a high wood density is a characteristic feature of slow-growing trees guaranteeing high biomechanical strength and hydraulic safety (Putz *et al.* 1983, Hacke *et al.* 2001, Sterck *et al.* 2006). We tested the data of the control plots (see chapter 2.3.6) to analyze relationships between wood density and hydraulic properties or leaf morphological and chemical traits among eight co-occurring tropical tree species (Fig. 7.5). We found a close negative relation between leaf morphology and wood density, i.e. the lighter the trunk wood, the larger the leaves. Further, several twig hydraulic traits were correlated with wood density. Trees with a denser wood showed a higher leaf-specific conductivity and grew taller in this stand. Xylem sap flux density and carbon isotope ratio, however, were not related to wood density. We found no significant variation in wood density among four different organs of a tree along the flow path from strong roots over the trunk to the branches and twigs. While wood density varied by less than 10 % within a species (Tab. 4.2), wood anatomical traits (total vessel lumen area, mean vessel diameter and vessel density) showed a great variability, which were closely related to important hydraulic properties.



**Fig. 7.5:** Wood density in the trunk wood at breast height in relationship to leaf morphological (mean leaf area,  $A_L$  and specific leaf size, SLA) and chemical traits (C/N ratio and carbon isotope ratio,  $\delta^{13}\text{C}$ ), twig hydraulic properties (twig specific conductivity,  $k_s$  and leaf-specific conductivity, LSC, both in  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), xylem sap flux density measured at breast height (XFD) and tree height (H).

Tall trees need sufficient mechanical strength to reach a tree height of 40 m or more, and such tree species are only exceptionally light-demanding fast-growing tree species (e.g. Poorter *et al.* 2010), though they are present in the upper canopy and are exposed to full sunlight. At least in our forest, these tallest trees are typically slower-growing species with a higher wood density. Despite the rather high wood density, it seems to be beneficial for tall trees to possess rather large vessels that have the potential for sufficient tapering all the way up to the crown, while the vessel number is reduced due to mechanical constraints. A similar pattern was observed in woody plants from a Mediterranean-type climate (Preston *et al.* 2006).

Dicotyledon wood is composed of three different tissue types that fulfill different functions: vessels for longitudinal water transport, parenchymatic cells for carbohydrate storage and radial transport, and fibres for mechanical strength. Wider vessels contribute to a larger hydraulic conductance (Sperry *et al.* 2006), whereas smaller vessels should lead to higher hydraulic safety due to a decreased risk of vessel implosion (Hacke *et al.* 2001). If cell implosion in light wood is a relevant risk in dicotyledons that possess vessels of 100  $\mu\text{m}$  or larger in the trunk, is questionable. In these large vessels, cavitation through air-seeding might be more likely. Nevertheless, the results of both processes are the same, a loss of hydraulic conductivity due to catastrophic xylem dysfunction.

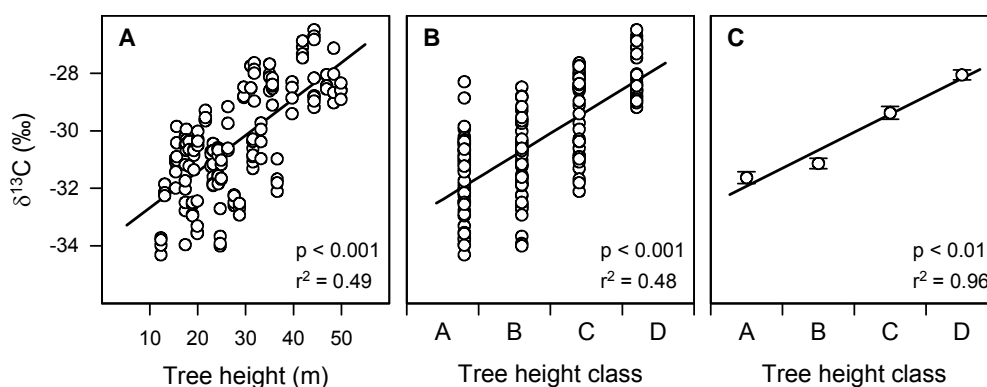
A combination of these three tissue types at varying proportions to each other can result in the same wood density, but will lead to different hydraulic properties. This implies that an assessment of the vulnerability of wood tissue to severe drought stress based on wood density measurements only must be premature. Only in combination with measurements on wood anatomy (vessel size and density) and hydraulics and plant water status (leaf water potential or vulnerability curves), this information can contribute to a better understanding of the strategies of trees with respect to drought-avoidance and drought-tolerance.

#### 7.1.4 Vertical gradients of tree physiological properties within the forest stand

In contrast to temperate forests, wet tropical forests seem to be characterized by a more continuous change of the stand microclimate with height in the forest. The great number of subcanopy and understory species results in a more complex vertical stratification of the stand and may be the main cause for their high species diversity (Niklas *et al.* 2003). In accordance with other studies, we found large trees of the upper canopy to account for the bulk of stand transpiration, while suppressed subcanopy trees contributed only to a minor extent (Granier *et al.* 1996, Phillips *et al.* 1999). Poorter *et al.* (2008) found maximum crown area to scale

closely with the maximum diameter of the species in tropical forests which relates to architecture and water consumption.

We pooled the datasets from the three control plots (see Tab. A8.1 – Tab. A8.8) to investigate patterns of physiological and morphological attributes along the height gradient in this forest. Our results showed that several parameters exhibited a tight correlation with canopy or individual tree height (Tab. 7.1, see chapter 2.3.6). Diameter at breast height (DBH) and basal area were closely related to tree height, as well as hydraulic conductivity in the xylem of terminal twigs (normalised to vessel lumen area), leaf-specific conductivity (Fig. 3.1), xylem sap flux density (XFD) in the trunk and carbon isotope ratios ( $\delta^{13}\text{C}$ ). The taller the trees were the less negative was the  $\delta^{13}\text{C}$  signature of sun-canopy leaves (Fig. 7.6), supporting the results from e.g. Duursma and Marshall (2006), Huang *et al.* (2008) and Lloyd *et al.* (2010).



**Fig. 7.6:** Carbon isotope signature of leaf dry matter in relation to tree height for the eight co-occurring tree species from the control plots expressed either for the individual trees (left, number of samples per species 6-44) or for the four tree height classes (middle and right, values are means  $\pm$  SE, A = 10.0-19.9 m, B = 20.0 – 29.9 m, C = 30.0 – 39.9 m, D = 40.0 – 49.9 m). For further explanations see Tab. 2.5, or chapter 6.2.10.

Some other parameters showed a significant, but only weak correlation on tree individual basis like stem and branch wood density, mean and specific leaf area, and some others. However, all these weak relationships with tree height became more closely related, when averaged across the four tree height classes (Tab. 7.1).

It seems that among these co-occurring tropical tree species convergent patterns exist, which distinguish tall trees from smaller ones with respect to various tree physiological and morphological attributes.

**Tab. 7.1:** Level of significance (p) and coefficient of determination ( $r^2$ ) for the Pearson correlation between tree height and a number of morphological and physiological traits calculated either for tree individuals (left, single value vs. TH,  $n = 50$ ) or for the averages of four tree height classes (right; A: 15 m, B: 25 m, C: 35 m, D: 45 m) for eight co-occurring tree species ( $n = 2-12$ ) on the control plots (see chapter 2.3.6.). The direction of the slope is indicated as b. Not significant relation = n.s.

Variable	Unit	b	Single value vs. TH		Tree height class	
			p	r <sup>2</sup>	p	r <sup>2</sup>
<i>Biometric characteristics</i>						
DBH	(cm)	+	<0.001	0.53	<0.001	1.00
Basal area	(cm <sup>2</sup> )	+	<0.001	0.62	<0.001	1.00
<i>Wood density</i>						
ρ <sub>Stem</sub>	(g cm <sup>-3</sup> )	+	0.02	0.08	0.03	0.89
ρ <sub>Branch</sub>	(g cm <sup>-3</sup> )	+	0.03	0.07	n.s.	0.52
Pilodyn		-	n.s.	0.02	n.s.	0.61
SWC	(%)		n.s.	0.00	n.s.	0.01
<i>Hydraulic traits</i>						
K <sub>S</sub> <sup>Twig</sup>	(kg m <sup>-1</sup> MPa <sup>-1</sup> s <sup>-1</sup> )	+	<0.001	0.32	0.03	0.87
LSC	(kg m <sup>-1</sup> MPa <sup>-1</sup> s <sup>-1</sup> )	+	<0.001	0.33	0.03	0.89
HV	(10 <sup>-4</sup> )	-	n.s.	0.01	n.s.	0.73
n <sub>L</sub> <sup>spec</sup>	(n mm <sup>-2</sup> )	-	<0.01	0.18	0.04	0.86
XFD	(g cm <sup>-2</sup> d <sup>-1</sup> )	+	<0.001	0.40	0.01	0.95
XFD <sub>daily max</sub>	(g cm <sup>-2</sup> d <sup>-1</sup> )	+	<0.001	0.28	0.01	0.94
DWU <sub>Sensor</sub>	(g cm <sup>-2</sup> d <sup>-1</sup> )	+	<0.001	0.68	<0.01	0.95
<i>Leaf morphology</i>						
Leaf size	(cm <sup>2</sup> )	-	0.04	0.06	<0.01	0.96
SLA	(cm <sup>2</sup> g <sup>-1</sup> )	-	<0.01	0.13	n.s.	0.69
<i>Isotope composition</i>						
δ <sup>13</sup> C	(‰)	+	<0.001	0.51	<0.01	0.97
δ <sup>15</sup> N	(‰)	+	0.03	0.09	n.s.	0.52
δ <sup>18</sup> O	(‰)	-	n.s.	0.02	n.s.	0.40
<i>Nutrient concentrations</i>						
C	(g kg <sup>-1</sup> )	+	<0.01	0.15	0.05	0.80
N	(g kg <sup>-1</sup> )		n.s.	0.00	n.s.	0.03
P	(g kg <sup>-1</sup> )		n.s.	0.00	n.s.	0.03
K	(g kg <sup>-1</sup> )		n.s.	0.01	n.s.	0.08
Ca	(g kg <sup>-1</sup> )	+	n.s.	0.01	n.s.	0.77
Fe	(g kg <sup>-1</sup> )	+	<0.01	0.22	<0.01	0.98
Mg	(g kg <sup>-1</sup> )	-	n.s.	0.02	n.s.	0.70
Mn	(g kg <sup>-1</sup> )	+	0.01	0.17	0.05	0.83

### 7.1.5 *An attempt to explain, why tall tropical trees show higher mortality rates after extended droughts than smaller ones*

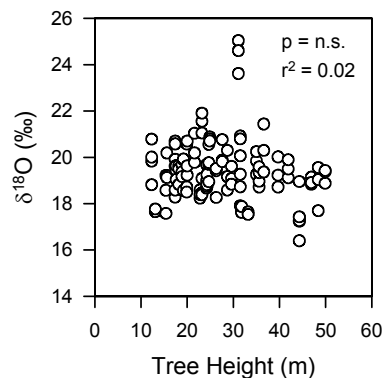
It is still uncertain how tropical moist forest trees might response to a possible higher drought frequency in a changing global climate. However, recent studies revealed the highest mortality rates in tall tropical trees under prolonged drought (Slik *et al.* 2004, Van Nieuwstadt and Sheil 2005, Nepstad *et al.* 2007, Phillips *et al.* 2009, da Costa *et al.* 2010, Phillips *et al.* 2010), but the possible physiological causes for the dying of these trees are still uncertain.

We found a large variation in the hydraulic architecture with variation in tree height. This may be a direct response to the marked changes in ambient conditions occurring in the stand microclimate from the forest understory to the canopy top. Large trees might be less susceptible to drought events in the short run due to (a) a more extensive root system, and (b) a more effective stomatal regulation of water loss due to the exposure to a higher VPD. However, in the long term, especially the higher evaporative demand during extended drought periods may make them more vulnerable than understory trees.

The tall-growing trees in this study are exposed to more than twice the vapor pressure deficits as compared to understory trees, and they have to account for increasing flow resistances and growing gravity effects with increasing xylem path length, which should reduce the water potential in the leaves of the upper crown greatly (Oldham *et al.* 2010). As trees grow taller, a deterioration of leaf-level water status may lead to reductions in stomatal aperture and to a decreased photosynthetic carbon gain (Ryan and Yoder 1997), which can show up in less negative  $\delta^{13}\text{C}$  values as they were observed in our study in tall trees.  $\delta^{13}\text{C}$  increased by approximately 4 ‰ from tree height class A (10.0-19.9 m) to tree height class D (40.0-49.9 m) in the Sulawesi forest. A vertical increase in foliar  $\delta^{13}\text{C}$  can, in theory, be caused either by an increased photosynthetic capacity (at a constant stomatal conductance), or decreased stomatal conductance (at a constant photosynthetic capacity, Huang *et al.* 2008). Other authors attributed the vertical change in  $\delta^{13}\text{C}$  to gradients in drought intensity within the canopy (Niinemets *et al.* (2004) as caused by a vertical increase in hydraulic resistance, especially during periods of soil moisture deficits. The isotope ratio of oxygen ( $\delta^{18}\text{O}$ ) was not related to increasing tree height in the present study (Fig. 7.7).

Foliar  $\delta^{18}\text{O}$  is expected to show a negative correlation with stomatal conductance for plants grown with the same source of water and under the same atmospheric conditions (Cernusak *et*

*al.* 2003, 2007). Thus, the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  patterns found with tree height seem to be partly contradictory with respect to leaf conductance.



**Fig. 7.7:** Tree height in relation to the isotope ratio of oxygen ( $\delta^{18}\text{O}$ ) in sun leaves for the eight co-occurring tree species from the control plots (number of samples per species 6–44), for further explanation see chapter 2.3.6.

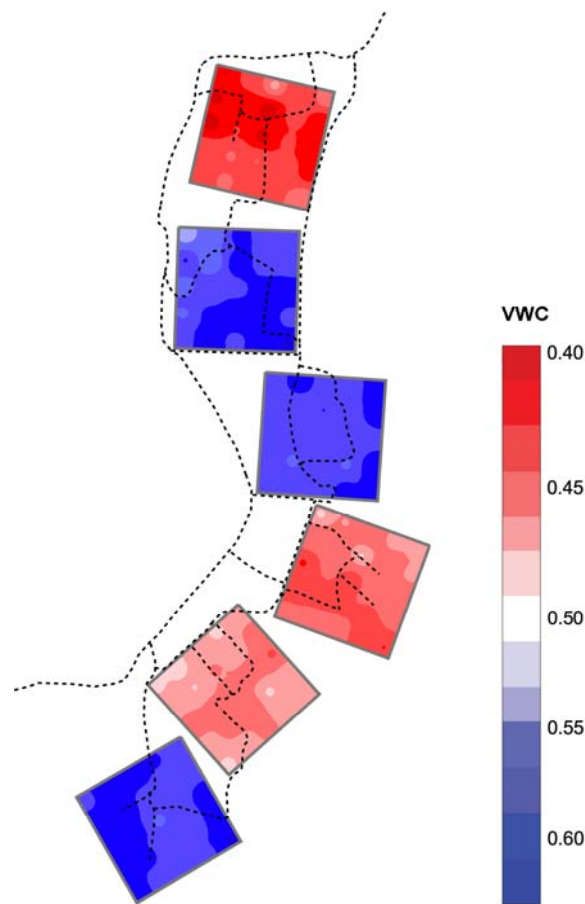
In conclusion, we assume that (a) the exposure to a higher evaporative demand in the upper canopy, (b) the inevitable increase in hydraulic resistance, and hence (c) the wider vessels at the base of the trunk are explaining the reported higher mortality rates of tall tropical trees after prolonged drought. We found evidence in support of all three mentioned phenomena in our study. The carbon starvation hypothesis (see chapter 1.2.1) is not very likely, since carbon starvation and tree height are not necessarily related to each other (Hartmann 2010). Carbon starvation might as well be attributed to catastrophic xylem dysfunction due to large vessels and a long flow path, which results in a deterioration of leaf water status. However, more empirical studies under natural drought conditions which include soil desiccation and a high evaporative demand are needed to distinguish between several possible explanations for increased tree mortality among tall tropical tree species.

#### 7.1.6 Lessons learned from a two-year throughfall displacement experiment in the perhumid tropics

The Sulawesi Throughfall Displacement Experiment was the first experimental study about the effects of an extended soil desiccation event on the trees of a perhumid tropical rainforest where natural droughts occur only exceptionally. The very shallow depth distribution patterns of fine and coarse roots reported in this forest (Hertel *et al.* 2009) are interpreted as resulting from the continuously high rainfall and permanently low atmospheric saturation deficit. After 24 months of throughfall displacement, soil moisture content in the upper soil layers was reduced beyond the conventional wilting point, whereas relative air humidity stayed unaltered throughout the experiment. According to the biweekly conducted volumetric water content

(VWC) measurements, we can exclude a strong edge effect by surface water entering the experimental plots from outside (Fig. 7.8). Because the soil moisture maps do not reveal major horizontal gradients, we assume that the trenching to a depth of 40 cm was sufficient for isolating the plots.

To test the effects of this two-year-continuous desiccation experiment on tall tropical canopy trees, one of the most abundant upper canopy tree species in this tropical perhumid forest was selected. *Castanopsis acuminatissima* (Blume) Rheder is a member of the family Fagaceae and has been reported to produce the highest above ground biomass in this forest stand (Culmsee *et al.* 2010). We assumed that cavitations caused by soil moisture deficits are a serious threat for large trees of this species (Nepstad *et al.* 2007).



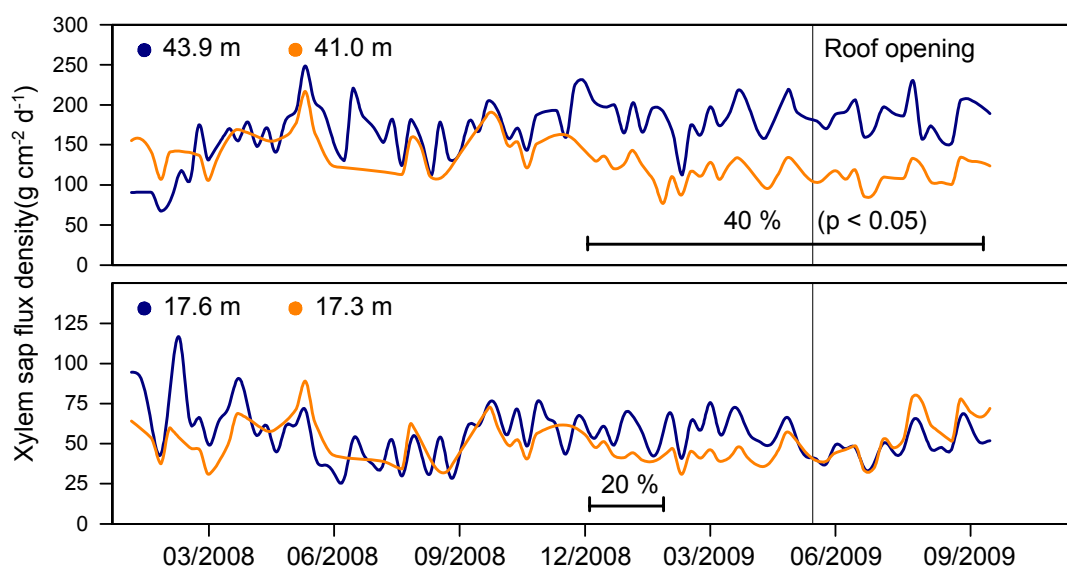
**Fig. 7.8:** Spatial distribution of volumetric soil water content (VWC) measured within the top 30 cm of the soil layer for the three experimental roof (red) and control plots (blue). The data presented here were averaged over 100 measurements per plot from January, 2009 until roof opening in May, 2009 taken biweekly. For further explanation see chapter 2.3.1.

The long and severe desiccation of the upper soil caused a marked reduction in the xylem hydraulic conductivity of terminal twigs normalised to vessel lumen area (by 25 %). Leaf area-specific conductivity was reduced by 10-33 % as well. Surprisingly, at the end of the

drought treatment, individual leaf area was significantly larger in the roof plots, but the number of leaves was reduced by about 30 % per unit of twig sapwood area. This result points to a drought effect on leaf bud formation. In parallel, the stand fine litter production (see chapter 2.3.5) was reduced by 30 % during the driest phase from March until June 2009. A similar finding was reported from a tropical throughfall exclusion experiment in the Amazon (Nepstad *et al.* 2002). Reduced soil moisture content for a prolonged period appears to inhibit the formation of new leaves rather than causing a pulse of leaf shedding.

Further drought effects after the two-year experimental desiccation were observed in the stem xylem with significant reductions in mean vessel diameter and axial conductivity and a parallel increase in wood density in the outermost xylem of the trunk of tall *C. acuminatissima* individuals located under the experimental roofs. Similarly, annual stem diameter increment decreased by 26 %, though not significant.

Even though we found no signs of major damage (e.g. strong leaf shedding, increased mortality rates etc.), there was evidence that tall *C. acuminatissima* individuals were to a higher degree more susceptible to drought than smaller ones. During drought, one of the first reactions expected is a decrease in sap flow either due to stomatal regulation responding to elevated evaporative demand, or due to decreasing soil moisture content. Four tree individuals of this species with different size were continuously monitored for xylem sap flux density (XFD, Fig. 7.9) from January, 2008 until September, 2010.



**Fig. 7.9:** Xylem sap flux density (XFD) for a tall and a small individual of the species *C. acuminatissima* from the control (blue) and the experimental roof (orange) plots, respectively. Tree height is given as well. The data presented were recorded from January, 2008 until September, 2010. For further explanation see chapter 2.3.3. Notice different scaling for XFD for the two panels.



After December, 2008, during the driest phase of the throughfall exclusion experiment (see Fig. 6.1), the two tall tree individuals differed significantly (by 40 %) in XFD between control and experimental roof plots until the end of the experiment. The two small tree individuals had more similar flux densities (only 20 % difference between treatments for December, 2008 and January, 2009). The results on xylem flux density are in agreement with other findings on drought effects on the tall *C. acuminatissima* individuals. Even though mean vessel diameter in the outermost xylem of the trunk was significantly reduced by only 3 % (788-1033 measured vessels per treatment), the resulting reduction in hydraulic conductivity was 12 % for the individual vessel according to the Hagen-Poiseuille equation. Such an adaptive response of the hydraulic system to reduced soil water contents has also been described for temperate dicotyledonous trees (Sass and Eckstein 1995) and conifers (Eilmann *et al.* 2006). According to García-González and Eckstein (2003), the effect of water availability at the time of cell differentiation is reflected in the vessel size.

All throughfall displacement experiments have the disadvantage that they can reduce soil moisture to a critical level, but they leave the air humidity at canopy height unchanged. It is likely that soil desiccation in a natural dry spell will have much stronger effects than was simulated in our experiment. Moreover, two similar throughfall exclusion experiments in Eastern Amazonia (Nepstad *et al.* 2007, da Costa *et al.* 2010) revealed that tropical seasonal dry forest stands were remarkably resistant against drought within the first two years, until a certain threshold in soil water content was reached approximately after more than three years. Even though our experiment was carried out in a perhumid climate and the occurring tree species should not possess adaptations to severe drought events, two years of throughfall displacement might still have been insufficient to provoke symptoms of critical damage.

## 7.2 FINAL CONCLUSIONS

In the first chapter, a number of hypotheses were forwarded concerning tree physiological and morphological adaptations to increasing tree height, and with respect to tree responses to prolonged and severe soil water deficits. This final chapter aims to synthesize the previously presented results and conclusions. In response to the hypotheses formulated in the present study, the following results were found:

*(i) The environmental control of sap flux density is directly related to tree height*

In support of the hypothesis, this study provided evidence that co-occurring tropical tree species differ strongly in measured xylem sap flux densities in the outermost xylem of the trunk, which is largely dependent on the canopy position within the forest stand. Despite the perhumid climate, VPD was the most important environmental factor controlling sap flow. Mean VPD increased linearly with height in the canopy. The close relation between sap flux density and tree height in this perhumid forest, irrespective of systematic position, may be interpreted as convergent patterns in the water use of tropical trees.

*(ii) Tropical trees show an adaptation of their hydraulic architecture when growing tall for counteracting the effect of increasing hydraulic resistance with increasing flow path length*

This study found evidence for several important changes in the hydraulic architecture with tree height in the eight studied species. Vessels were found to taper acropetally from the stem base towards the upper canopy in *C. acuminatissima* trees, and the smallest vessels were found in all species in the distal twigs. Tall trees generally possessed the largest vessels along the whole flow path from small roots over strong roots and the trunk to the distal twigs. The vessel diameter showed an optimum curve with maximal diameters found in the trunk and not in the roots. Leaf-specific and sapwood-area specific conductivity increased significantly with tree height; both conductivities were linked closely to the increase in vessel diameter.

*(iii) Tall trees of the premontane forest in Central Sulawesi are adapted to the prevailing perhumid conditions and thus are more vulnerable to prolonged soil water deficits than species from humid or semihumid forests*

This hypothesis cannot clearly be confirmed or rejected. According to the results obtained after 24 months of soil desiccation, the most abundant upper canopy tree species did not show

signs of critical damage, though several tree physiological and morphological variables showed adaptive responses. However, the reduction in sap flux densities during drought was more pronounced in taller trees than in smaller ones, indicating that drought-induced physiological effects should appear earlier in tall than in smaller trees, caused by the larger flow resistance and the exposure to a higher evaporative demand. Stem diameter growth, the diameter growth of xylem vessels, and leaf bud formation (and presumably increased fine root mortality) were found to be particularly sensitive growth processes in this tree species, while pre-senescent leaf shedding or canopy dieback were – contrary to expectation – not observed.

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## **8 EIGHTH CHAPTER**

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### **8.3 INDIVIDUAL TREE DATA**

The following eight tables summarize individual tree data used to analyse the influence of tree height or wood density on several tree physiological and morphological attributes (see chapter 2.3.6). These are biometric characteristics, wood density, sap flux density, twig hydraulic properties, leaf morphology, isotopic signatures and leaf nutrient concentrations for 50 tree individuals from eight common tree species of the Pono forest, all located in the control plots.

**Tab. A8.1:** 37 parameters of the 50 investigated tree individuals in the control plots of the eight common tree species from the Pono forest, Central Sulawesi (Indonesia). The following 4 tables are summarizing individual tree data on biometric characteristics, wood density, sap flux density, twig hydraulic properties, leaf morphology, isotopic signatures and leaf nutrient concentrations for the first 25 trees. Here, crown position (A) or understory (B) is given (Type), tree height class (THC), tree height (m), diameter at breast height (DBH), diameter at the insertion point for the sap flux sensors (DBH<sub>sensor</sub>), basal area (A<sub>B</sub>), conducting sap wood area for the sensor length (A<sub>S</sub><sup>Sensor</sup>), Piloodyn wood hardness, stem wood density at breast height, saturated water content and branch wood density. Number of samples = n. Values are means ± SE.

TAG	Family	Species	Biometric characteristics						Wood density					
			Type	THC	H (m)	DBH (cm)	DBH <sub>Sensor</sub> (cm)	A <sub>B</sub> (cm <sup>2</sup> )	A <sub>S</sub> <sup>Sensor</sup> (cm <sup>2</sup> )	Pilo <sub>dyn</sub>	WD <sub>stem</sub> (kg m <sup>-3</sup> )	SWC (%)	WD <sub>Branch</sub> (n)	WD <sub>Branch</sub> (kg m <sup>-3</sup> )
C1	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	B	B	24.3	17.8	22.3	390	155.4	13.5	504.8	107.3	4	479.0 ± 59.9
C2	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	D	46.9	58.8	56.8	2529	426.1	20.0	491.4	117.8		
C3	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	B	C	36.6	22.2	23.6	439	166.0	13.5	417.1	146.2	4	397.0 ± 19.2
C4	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	D	50.6	66.0	66.0	3421	498.7	14.0	536.7	107.7	6	576.6 ± 34.6
C5	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	D	49.9	35.6	35.6	996	260.0	18.0	541.8	105.5	3	544.7 ± 1.9
C6	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	C	35.6	56.2	45.7	1643	339.6	17.0	511.0	112.0		
C7	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	C	39.7	48.0	49.5	1922	368.9	15.0	480.1	130.6	4	491.3 ± 32.2
C8	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	B	29.6	44.7	44.0	1522	326.1	12.0	545.3	110.9	4	595.2 ± 5.7
C9	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	C	35.6	18.5	50.4	1993	376.0	14.5	535.8	105.2	4	611.4 ± 5.8
C10	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	C	31.1	34.2	38.5	1161	282.4	16.0	348.4	207.9	4	432.8 ± 3.0
C11	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	B	A	17.6	11.8	12.9	131	81.9	20.0	342.2	141.8	4	527.0 ± 30.8
C12	Fagaceae	<i>Castanopsis acuminatissima</i> (Blume) Rheder	A	D	48.4	59.7	60.5	2873	455.4	18.0	490.8	113.9	4	557.4 ± 23.3
C13	Lauraceae	<i>Cryptocarya laevigata</i> Blume	A	A	12.7	21.9	21.9	377	152.4	17.5	437.5	117.3	4	454.1 ± 23.4
C14	Lauraceae	<i>Cryptocarya laevigata</i> Blume	B	B	24.7	20.1	20.0	315	137.7	18.0	412.5	109.2	4	395.2 ± 32.1
C15	Lauraceae	<i>Cryptocarya laevigata</i> Blume	B	B	22.8	27.9	29.6	686	212.5	15.0	437.3	112.1	4	378.5 ± 55.0
C16	Lauraceae	<i>Cryptocarya laevigata</i> Blume	B	A	12.3	11.2	11.1	96	67.2		370.8	122.9	4	429.6 ± 81.9
C17	Lauraceae	<i>Cryptocarya laevigata</i> Blume	B	A	18.9	17.6	17.4	239	117.3	18.0	388.9	99.3	4	492.9 ± 145.5
C18	Lauraceae	<i>Cryptocarya laevigata</i> Blume	B	A	19.9	19.0	17.2	231	115.1	16.5	465.7	81.9	4	399.8 ± 26.1
C19	Lauraceae	<i>Cryptocarya laevigata</i> Blume	A	A	17.9	17.5	17.5	241	117.8	15.5	428.6	92.1	4	514.8 ± 9.6
C20	Lauraceae	<i>Cryptocarya laevigata</i> Blume	A	B	22.8	22.7	22.7	405	158.7	14.0	423.4	108.1	4	412.8 ± 10.9
C21	Myrtaceae	<i>Myrtaceae spec.</i>	B	A	17.4	14.0	14.6	168	95.3	13.0	639.3	75.8	4	598.9 ± 12.8
C22	Myrtaceae	<i>Myrtaceae spec.</i>	B	A	13.1	11.0	11.1	96	67.2	9.5	643.0	84.9	4	544.8 ± 35.0
C23	Sapotaceae	<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	A	C	35.0	53.7	41.4	1343	305.1	23.0	378.9	111.5	4	352.3 ± 20.9
C24	Sapotaceae	<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	A	D	44.3	71.5	54.4	2321	407.3	16.0	473.9	106.8	4	416.6 ± 57.1
C25	Sapotaceae	<i>Palaquium luzoniense</i> (Fern.-Vill.) Vidal	A	C	31.8	95.0	59.4	2774	447.1	13.0	504.6	101.3	4	404.6 ± 21.4

**Tab. A8.2: (continuation)** For the same tree individuals as given in Tab. A8.1 (see TAG), here are summarized individual tree data for sap flux measurements and twig hydraulic properties. These are number of days for sap flux measurements (n days), mean xylem flux density (XFD), mean daily maximal sap flux density, calculated daily water use for the conducting sap wood area for the sensor length ( $DWU_{\text{Sensor}}$ ), number of investigated twig segments, mean segment length, mean segment diameter, bark strength, vessel lumen area-specific conductivity ( $K_S$ ), leaf-specific conductivity (LSC) and Huber value (HV). Values are means  $\pm$  SE.

TAG	Sap flux density				Twig hydraulic properties							
	XFD (n days)	XFD ( $\text{g cm}^{-2} \text{d}^{-1}$ )	XFD <sub>daily Max</sub> ( $\text{g cm}^{-2} \text{d}^{-1}$ )	$DWU_{\text{Sensor}}$ ( $\text{kg d}^{-1}$ )	Twigs (n)	Segment length (mm)	Segment Ø (mm)	Bark (mm)	$K_S$ ( $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ )	LSC (n)	LSC ( $10^{-5} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ )	HV ( $10^{-4}$ )
C1	348	121.2 $\pm$ 2.3	467.2 $\pm$ 7.4	18.8	4	126.0 $\pm$ 1.9	8.9 $\pm$ 0.3	0.54 $\pm$ 0.08	5.94 $\pm$ 0.96	4	178.9 $\pm$ 45.1	17.9 $\pm$ 4.5
C2	348	114.7 $\pm$ 1.5	379.6 $\pm$ 3.0	48.9	4	131.4 $\pm$ 1.3	11.1 $\pm$ 0.4	1.12 $\pm$ 0.10	11.33 $\pm$ 1.02	4	1071.0 $\pm$ 449.6	8.8 $\pm$ 2.9
C3	348	78.7 $\pm$ 1.3	284.7 $\pm$ 3.0	13.1	4	123.5 $\pm$ 0.6	10.2 $\pm$ 0.4	0.72 $\pm$ 0.06	13.77 $\pm$ 1.49	4	563.2 $\pm$ 63.8	56.3 $\pm$ 6.4
C4					8	135.1 $\pm$ 6.9	8.3 $\pm$ 0.4	0.93 $\pm$ 0.04	9.61 $\pm$ 0.95	8	206.1 $\pm$ 23.8	2.2 $\pm$ 0.2
C5					4	182.3 $\pm$ 8.7	12.4 $\pm$ 0.4	1.03 $\pm$ 0.05	19.57 $\pm$ 1.53	4	554.8 $\pm$ 88.6	2.8 $\pm$ 0.4
C6					4	128.7 $\pm$ 1.0	11.4 $\pm$ 0.3	0.92 $\pm$ 0.09	19.86 $\pm$ 1.22	4	685.3 $\pm$ 112.4	3.4 $\pm$ 0.5
C7	335	97.1 $\pm$ 1.4	322.3 $\pm$ 2.7	35.8	4	129.6 $\pm$ 0.4	11.0 $\pm$ 0.4	1.03 $\pm$ 0.11	18.07 $\pm$ 1.79	4	638.2 $\pm$ 153.8	3.5 $\pm$ 0.9
C8					4	128.3 $\pm$ 0.8	10.2 $\pm$ 0.3	1.15 $\pm$ 0.03	18.48 $\pm$ 3.23	4	383.8 $\pm$ 65.4	2.1 $\pm$ 0.2
C9	335	156.4 $\pm$ 1.8	528.2 $\pm$ 5.1	58.8	8	129.9 $\pm$ 18.9	9.4 $\pm$ 0.5	1.09 $\pm$ 0.08	16.51 $\pm$ 1.75	12	430.1 $\pm$ 75.4	2.6 $\pm$ 0.4
C10	364	145.9 $\pm$ 1.9	459.0 $\pm$ 3.7	41.2	4	121.9 $\pm$ 0.7	11.8 $\pm$ 0.6	1.21 $\pm$ 0.21	15.96 $\pm$ 3.02	4	394.2 $\pm$ 64.3	2.5 $\pm$ 0.1
C11	364	58.3 $\pm$ 1.3	269.3 $\pm$ 4.9	4.8	4	122.1 $\pm$ 1.1	11.5 $\pm$ 0.5	1.02 $\pm$ 0.03	22.20 $\pm$ 0.88	4	691.1 $\pm$ 49.0	69.1 $\pm$ 4.9
C12	364	125.8 $\pm$ 1.7	400.9 $\pm$ 4.2	57.3	11	126.9 $\pm$ 5.3	9.0 $\pm$ 0.5	1.03 $\pm$ 0.05	17.14 $\pm$ 2.06	11	526.9 $\pm$ 135.1	2.8 $\pm$ 0.5
C13	348	45.9 $\pm$ 0.9	187.6 $\pm$ 2.6	7.0	6	127.4 $\pm$ 4.4	11.7 $\pm$ 0.5	0.75 $\pm$ 0.06	1.94 $\pm$ 0.46	6	30.3 $\pm$ 3.6	2.1 $\pm$ 0.6
C14	348	34.6 $\pm$ 0.8	147.1 $\pm$ 2.3	4.8	4	127.3 $\pm$ 0.8	11.0 $\pm$ 0.6	1.09 $\pm$ 0.09	1.77 $\pm$ 0.78	4	81.3 $\pm$ 36.5	8.1 $\pm$ 3.6
C15	348	59.4 $\pm$ 1.2	256.1 $\pm$ 3.7	12.6	4	123.0 $\pm$ 3.4	11.1 $\pm$ 0.4	0.66 $\pm$ 0.16	1.63 $\pm$ 0.19	4	92.2 $\pm$ 48.3	9.2 $\pm$ 4.8
C16	335	22.2 $\pm$ 0.6	96.1 $\pm$ 2.5	1.5	4	124.0 $\pm$ 0.4	11.1 $\pm$ 0.2	0.99 $\pm$ 0.04	1.38 $\pm$ 0.08	4	87.8 $\pm$ 34.7	8.8 $\pm$ 3.5
C17	335	36.2 $\pm$ 0.9	165.0 $\pm$ 3.1	4.2	4	122.1 $\pm$ 2.0	11.9 $\pm$ 0.5	0.89 $\pm$ 0.02	0.99 $\pm$ 0.25	4	44.4 $\pm$ 16.0	4.4 $\pm$ 1.6
C18	335	37.0 $\pm$ 0.8	170.9 $\pm$ 3.1	4.3	4	123.6 $\pm$ 1.0	11.8 $\pm$ 0.8	1.07 $\pm$ 0.04	1.30 $\pm$ 0.11	4	48.4 $\pm$ 10.4	4.8 $\pm$ 1.0
C19					7	134.1 $\pm$ 3.3	10.3 $\pm$ 0.4	0.73 $\pm$ 0.04	1.43 $\pm$ 0.17	7	28.3 $\pm$ 2.8	2.0 $\pm$ 0.2
C20					6	138.9 $\pm$ 3.0	12.0 $\pm$ 0.3	0.83 $\pm$ 0.05	3.62 $\pm$ 0.34	6	79.2 $\pm$ 3.2	2.3 $\pm$ 0.3
C21	348	32.4 $\pm$ 0.7	160.4 $\pm$ 2.8	3.1	4	121.0 $\pm$ 1.0	10.2 $\pm$ 0.7	0.54 $\pm$ 0.08	4.24 $\pm$ 1.38	4	243.9 $\pm$ 96.5	24.4 $\pm$ 9.6
C22	335	35.0 $\pm$ 1.0	150.4 $\pm$ 3.5	2.4	4	123.2 $\pm$ 1.1	9.8 $\pm$ 0.2	0.92 $\pm$ 0.02	1.75 $\pm$ 0.20	4	67.1 $\pm$ 17.9	6.7 $\pm$ 1.8
C23	335	79.5 $\pm$ 1.9	275.1 $\pm$ 5.3	24.3	4	118.2 $\pm$ 2.6	10.6 $\pm$ 0.2	1.12 $\pm$ 0.24	3.25 $\pm$ 0.42	4	90.4 $\pm$ 19.1	2.8 $\pm$ 0.4
C24	363	74.4 $\pm$ 1.2	275.5 $\pm$ 2.8	30.3	4	125.0 $\pm$ 1.3	12.6 $\pm$ 0.8	1.21 $\pm$ 0.18	11.11 $\pm$ 2.36	4	841.0 $\pm$ 550.0	6.6 $\pm$ 3.3
C25	364	62.4 $\pm$ 0.9	214.9 $\pm$ 2.2	27.9	4	127.1 $\pm$ 1.5	11.3 $\pm$ 0.6	1.31 $\pm$ 0.14	8.90 $\pm$ 1.59	4	628.1 $\pm$ 347.8	6.3 $\pm$ 2.9

**Tab. A8.3: (continuation)** For the same tree individuals as given in Tab. A8.1 (see TAG), here are summarized individual tree data for leaf morphology and isotope signatures. These were specific leaf area (SLA), total number of leaves distal to the twig segment used for hydraulic measurements, total supported leaf area distal to the twig segment ( $A_L^{\text{Total}}$ ), mean leaf size ( $A_L$ ), maximal leaf size ( $A_L^{\text{max}}$ ), carbon isotope signature ( $\delta^{13}\text{C}$ ) and nitrogen isotope signature ( $\delta^{15}\text{N}$ ). Values are means  $\pm$  SE.

TAG	Leaf morphology						Isotope signatures		
	SLA	SLA	Leaves	A <sub>L</sub> <sup>Total</sup>	A <sub>L</sub>	A <sub>L</sub> <sup>Max</sup>	δ <sup>13</sup> C	δ <sup>15</sup> N	
	(n)	(cm <sup>2</sup> g <sup>-1</sup> )	(n)	(cm <sup>2</sup> )	(cm <sup>2</sup> )	(cm <sup>2</sup> )	(n)	(‰)	(‰)
C1	4	98.29 ± 4.7	85	7487	88.1 ± 4.2	186.7	4	-31.4 ± 0.3	-0.21 ± 0.08
C2	4	71.29 ± 0.4	756	15036	19.9 ± 0.5	80.4	4	-28.4 ± 0.1	3.22 ± 0.08
C3	4	119.39 ± 7.1	102	5977	58.6 ± 2.8	118.9	4	-31.6 ± 0.2	0.83 ± 0.42
C4	8	70.19 ± 1.2	233	10157	43.6 ± 1.2	98.5			
C5	4	87.49 ± 4.9	1013	33295	32.9 ± 0.7	133.8	4	-28.6 ± 0.1	-0.22 ± 0.09
C6	4	67.09 ± 0.9	1554	23105	14.9 ± 0.2	75.5	4	-28.4 ± 0.1	0.31 ± 0.4
C7	4	70.99 ± 2.6	711	17951	25.2 ± 0.5	90.2	4	-28.8 ± 0.2	5.05 ± 1.08
C8	4	69.59 ± 1.7	1079	22339	20.7 ± 0.3	95.4	4	-28.7 ± 0.1	1.40 ± 1.55
C9	12	63.19 ± 1.2	1434	26818	18.7 ± 0.2	71.9	4	-28.5 ± 0.2	1.32 ± 0.77
C10	4	78.69 ± 1.7	974	18351	18.8 ± 0.3	67.6	4	-28.1 ± 0.2	0.14 ± 0.06
C11	4	105.99 ± 5.1	174	9211	52.9 ± 1.6	117.5	4	-30.3 ± 0.2	0.45 ± 0.12
C12	11	70.79 ± 1.4	1440	26523	18.4 ± 0.3	85.8	4	-28.2 ± 0.4	0.04 ± 0.03
C13	6	84.79 ± 2.7	976	31827	32.6 ± 0.5	91.0			
C14	4	113.29 ± 7.9	122	5402	44.3 ± 1.7	89.8	4	-33.6 ± 0.3	-0.48 ± 0.07
C15	4	80.59 ± 1.9	291	8909	30.6 ± 0.8	73.2	4	-31.0 ± 0.1	-1.40 ± 0.11
C16	4	102.69 ± 5.5	180	6917	38.4 ± 1.0	82.0	4	-34.0 ± 0.1	-1.04 ± 0.11
C17	4	84.89 ± 2.3	208	8182	39.3 ± 0.9	69.1	4	-32.7 ± 0.1	-1.27 ± 0.09
C18	4	93.69 ± 2.5	187	8245	44.1 ± 0.9	81.2	4	-33.2 ± 0.3	-0.99 ± 0.14
C19	7	84.79 ± 1.5	727	22239	30.6 ± 0.4	69.3			
C20	6	84.39 ± 2.5	513	22976	44.8 ± 0.9	117.8			
C21	4	78.69 ± 3.3	59	5289	89.6 ± 3.0	133.9	4	-32.8 ± 0.4	-1.60 ± 0.11
C22	4	106.69 ± 1.6	262	5770	22.0 ± 0.5	45.9	4	-32.1 ± 0.1	-0.64 ± 0.10
C23	4	61.09 ± 1.6	439	16829	38.3 ± 0.8	92.7	4	-28.1 ± 0.2	-1.32 ± 0.07
C24	4	61.89 ± 1.7	691	21464	31.1 ± 0.7	94.3	4	-27.2 ± 0.5	0.07 ± 0.11
C25	4	58.19 ± 2.1	280	11427	40.8 ± 1.3	120.7	4	-28.1 ± 0.3	-1.32 ± 0.06

**Tab. A8.4: (continuation)** For the same tree individuals as given in Tab. A8.1 (see TAG), here are summarized individual tree data for leaf nutrient concentrations. These were foliar contents of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn) and iron (Fe). Values are means  $\pm$  SE. For number of samples see isotope signatures (**Fehler! Verweisquelle konnte nicht gefunden werden.**).

TAG	<i>Leaf nutrient concentrations</i>							
	C (g kg <sup>-1</sup> )	N (g kg <sup>-1</sup> )	P (g kg <sup>-1</sup> )	K (g kg <sup>-1</sup> )	Ca (g kg <sup>-1</sup> )	Mg (g kg <sup>-1</sup> )	Mn (g kg <sup>-1</sup> )	Fe (g kg <sup>-1</sup> )
C1	488.0 $\pm$ 1.2	17.1 $\pm$ 0.2	1.39 $\pm$ 0.03	12.75 $\pm$ 0.27	9.63 $\pm$ 0.70	3.31 $\pm$ 0.13	1.24 $\pm$ 0.04	0.063 $\pm$ 0.007
C2	479.6 $\pm$ 0.6	15.8 $\pm$ 0.3	1.41 $\pm$ 0.05	10.94 $\pm$ 0.29	8.18 $\pm$ 0.32	3.53 $\pm$ 0.06	0.93 $\pm$ 0.04	0.142 $\pm$ 0.035
C3	487.6 $\pm$ 2.0	16.8 $\pm$ 0.4	1.62 $\pm$ 0.13	11.18 $\pm$ 0.67	13.38 $\pm$ 1.97	3.70 $\pm$ 0.18	1.09 $\pm$ 0.22	0.100 $\pm$ 0.027
C4								
C5	512.1 $\pm$ 0.8	18.2 $\pm$ 0.4	1.52 $\pm$ 0.01	10.56 $\pm$ 0.24	8.85 $\pm$ 0.61	4.39 $\pm$ 0.07	1.88 $\pm$ 0.15	0.031 $\pm$ 0.005
C6	514.6 $\pm$ 0.5	20.9 $\pm$ 0.2	1.55 $\pm$ 0.03	10.99 $\pm$ 0.11	12.56 $\pm$ 0.45	3.28 $\pm$ 0.11	0.97 $\pm$ 0.06	0.059 $\pm$ 0.009
C7	508.5 $\pm$ 14.1	18.6 $\pm$ 0.7	1.64 $\pm$ 0.12	8.90 $\pm$ 0.23	6.96 $\pm$ 0.12	3.77 $\pm$ 0.15	1.01 $\pm$ 0.06	0.094 $\pm$ 0.029
C8	511.8 $\pm$ 30.0	18.3 $\pm$ 1.9	1.66 $\pm$ 0.06	9.22 $\pm$ 0.40	12.31 $\pm$ 0.29	3.72 $\pm$ 0.07	1.16 $\pm$ 0.05	0.047 $\pm$ 0.006
C9	476.6 $\pm$ 1.0	16.4 $\pm$ 0.3	1.54 $\pm$ 0.04	8.15 $\pm$ 0.08	9.85 $\pm$ 0.21	3.19 $\pm$ 0.17	1.62 $\pm$ 0.05	0.084 $\pm$ 0.014
C10	483.4 $\pm$ 1.2	17.2 $\pm$ 0.4	1.99 $\pm$ 0.10	11.90 $\pm$ 0.42	5.25 $\pm$ 0.41	3.33 $\pm$ 0.23	0.41 $\pm$ 0.06	0.026 $\pm$ 0.004
C11	490.7 $\pm$ 0.7	17.7 $\pm$ 0.6	1.64 $\pm$ 0.05	10.24 $\pm$ 0.40	9.04 $\pm$ 0.94	3.21 $\pm$ 0.11	0.49 $\pm$ 0.06	0.039 $\pm$ 0.006
C12	516.8 $\pm$ 4.3	17.9 $\pm$ 0.6	1.65 $\pm$ 0.20	12.37 $\pm$ 2.97	14.15 $\pm$ 2.90	4.05 $\pm$ 0.84	0.94 $\pm$ 0.30	0.134 $\pm$ 0.030
C13								
C14	501.5 $\pm$ 1.4	20.5 $\pm$ 0.7	1.64 $\pm$ 0.07	12.77 $\pm$ 0.95	6.54 $\pm$ 0.71	3.13 $\pm$ 0.19	0.05 $\pm$ 0.00	0.088 $\pm$ 0.006
C15	511.2 $\pm$ 2.2	18.0 $\pm$ 0.7	1.48 $\pm$ 0.10	7.12 $\pm$ 0.32	8.25 $\pm$ 0.44	3.00 $\pm$ 0.10	0.04 $\pm$ 0.01	0.048 $\pm$ 0.009
C16	506.0 $\pm$ 2.4	19.1 $\pm$ 0.7	1.51 $\pm$ 0.16	11.66 $\pm$ 0.98	6.68 $\pm$ 0.49	2.77 $\pm$ 0.05	0.08 $\pm$ 0.01	0.072 $\pm$ 0.033
C17	499.1 $\pm$ 1.7	18.6 $\pm$ 0.4	1.45 $\pm$ 0.08	12.04 $\pm$ 0.66	8.58 $\pm$ 0.37	3.61 $\pm$ 0.18	0.08 $\pm$ 0.01	0.039 $\pm$ 0.005
C18	503.1 $\pm$ 0.9	20.1 $\pm$ 0.2	1.76 $\pm$ 0.11	13.89 $\pm$ 0.75	9.62 $\pm$ 0.67	3.14 $\pm$ 0.11	0.07 $\pm$ 0.01	0.048 $\pm$ 0.002
C19								
C20								
C21	481.5 $\pm$ 1.1	10.8 $\pm$ 0.2	1.22 $\pm$ 0.07	7.39 $\pm$ 1.01	6.53 $\pm$ 0.97	5.48 $\pm$ 0.48	0.23 $\pm$ 0.05	0.024 $\pm$ 0.009
C22	481.2 $\pm$ 3.7	14.9 $\pm$ 0.3	1.07 $\pm$ 0.04	20.03 $\pm$ 0.94	9.79 $\pm$ 0.40	10.17 $\pm$ 0.84	0.17 $\pm$ 0.01	0.026 $\pm$ 0.004
C23	518.3 $\pm$ 6.4	15.0 $\pm$ 0.5	1.48 $\pm$ 0.07	21.96 $\pm$ 1.41	11.20 $\pm$ 0.76	4.89 $\pm$ 0.30	0.05 $\pm$ 0.00	0.024 $\pm$ 0.003
C24	531.7 $\pm$ 4.6	17.7 $\pm$ 0.3	1.81 $\pm$ 0.13	17.87 $\pm$ 2.28	16.77 $\pm$ 1.78	5.31 $\pm$ 0.76	0.30 $\pm$ 0.24	0.108 $\pm$ 0.015
C25	517.1 $\pm$ 1.8	15.3 $\pm$ 0.3	1.71 $\pm$ 0.10	15.54 $\pm$ 1.71	21.13 $\pm$ 1.95	7.24 $\pm$ 0.59	0.10 $\pm$ 0.01	0.036 $\pm$ 0.010



**Tab. A8.5:** 37 parameters of the remaining 25 investigated tree individuals (see Tab. A8.1). Here, individual tree data on biometric characteristics and wood density are presented. These were crown position (A) or understory (B) is given (Type), tree height class (THC), tree height class (THC), tree height at breast height (DBH), diameter at the insertion point for the sap flux sensors (DBH<sub>sensor</sub>), basal area (A<sub>B</sub>), conducting sap wood area for the sensor length (A<sub>Sensor</sub>), Pilodyn wood hardness, stem wood density at breast height, saturated water content and branch wood density. Number of samples = n. Values are means ± SE.

TAG	Family	Species	Biometric characteristics						Wood density					
			Type	THC	H (m)	DBH (cm)	DBH <sub>Sensor</sub> (cm)	A <sub>B</sub> (cm <sup>2</sup> )	A <sub>S</sub> Sensor (cm <sup>2</sup> )	Pilodyn	WD <sub>stem</sub> (kg m <sup>-3</sup> )	SWC (%)	WD <sub>Branch</sub> (n)	WD <sub>Branch</sub> (kg m <sup>-3</sup> )
C26	Icacinaceae	<i>Platea excelsa</i> Bl. var. borneensis (Heine) Sleum.	A	C	33.2	45.7	45.6	1630	338.1	22.0	375.1	127.5	4	322.9 ± 6.3
C27	Icacinaceae	<i>Platea excelsa</i> Bl. var. borneensis (Heine) Sleum.	B	B	23.2	18.2	17.9	251	120.8	21.5	356.3	133.6	4	357.1 ± 3.9
C28	Icacinaceae	<i>Platea excelsa</i> Bl. var. borneensis (Heine) Sleum.	B	A	15.4	11.7	12.6	125	79.6	19.5	366.5	139.4	4	372.7 ± 7.8
C29	Icacinaceae	<i>Platea excelsa</i> Bl. var. borneensis (Heine) Sleum.	B	B	26.3	30.9	30.9	748	222.7	27.0	373.0	138.0	4	328.3 ± 43.3
C30	Icacinaceae	<i>Platea excelsa</i> Bl. var. borneensis (Heine) Sleum.	B	A	15.6	12.3	11.6	106	71.5	27.0	315.8	152.5	4	334.6 ± 21.6
C31	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	A	C	36.1	66.5	66.5	3473	502.7	14.0	533.5	80.8	4	545.9 ± 4.7
C32	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	B	A	18.2	14.7	14.4	162	93.2	17.0	461.3	96.1	4	390.8 ± 24.5
C33	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	A	D	41.9	62.5	58.2	2659	437.3	14.5	549.1	77.1	4	454.6 ± 8.7
C34	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	A	B	29.6	60.3	60.3	2856	454.0	17.0	437.5	105.0	4	485.3 ± 16.3
C35	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	B	A	19.2	17.6	17.2	233	115.6	19.0	436.7	96.4	4	440.9 ± 26.2
C36	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	B	C	31.5	27.9	25.5	509	180.2	17.0	471.6	94.4	8	459.5 ± 24.6
C37	Sapotaceae	<i>Pouteria firma</i> (Miq.) Baelni	A	B	20.0	20.2	28.7	648	205.9	17.0	451.2	101.1	4	414.4 ± 26.7
C38	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	B	B	24.9	29.7	26.1	535	185.4	15.0	562.7	83.1	4	374.8 ± 27.3
C39	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	A	B	25.8	37.3	36.8	1065	269.5	16.0	529.9	109.3	5	555.8 ± 14.6
C40	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	A	B	29.4	41.1	37.5	1102	274.5	17.0	520.7	101.1	6	522.7 ± 6.5
C41	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	B	A	17.4	14.6	15.1	180	99.3	16.5	441.4	99.8	4	386.0 ± 30.4
C42	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	B	B	24.2	20.7	24.4	467	171.8	16.5	492.7	92.6	4	417.6 ± 51.8
C43	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	B	B	27.6	36.0	34.1	915	248.5	14.0	471.3	107.3	4	421.3 ± 7.8
C44	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	B	B	23.2	58.2	45.6	1630	338.1	14.5	479.0	104.4	4	457.0 ± 19.8
C45	Burseraceae	<i>Santiria apiculata</i> A.W. Benn.	A	B	22.5	29.7	26.9	567	191.5	17.0	495.0	106.1		
C46	Compositae	<i>Vernonia arborea</i> Buch.-Ham.	B	B	21.6	20.1	30.7	741	221.6	30.0	302.3	147.1	4	285.1 ± 14.1
C47	Compositae	<i>Vernonia arborea</i> Buch.-Ham.	B	B	28.7	43.0	35.6	998	260.3	20.0	331.6	127.6	4	362.4 ± 18.2
C48	Compositae	<i>Vernonia arborea</i> Buch.-Ham.	A	B	25.2	24.1	24.1	456	169.6	23.5	311.0	137.9	4	384.7 ± 4.7
C49	Compositae	<i>Vernonia arborea</i> Buch.-Ham.	A	B	26.9	26.8	26.8	564	190.9	25.0	326.4	137.8	4	431.2 ± 6.7
C50	Compositae	<i>Vernonia arborea</i> Buch.-Ham.	A	A	19.5	30.5	30.5	731	219.9	23.0	342.9	124.8		

**Tab. A8.6: (continuation)** For the same tree individuals as given in Tab. A8.5 (see TAG), here are summarized individual tree data for sap flux measurements and twig hydraulic properties. These are number of days for sap flux measurements (n days), mean xylem flux density (XFD), mean daily maximal sap flux density, calculated daily water use for the conducting sap wood area for the sensor length ( $DWU_{\text{Sensor}}$ ), number of investigated twig segments, mean segment length, mean segment diameter, bark strength, vessel lumen area-specific conductivity ( $K_S$ ), leaf-specific conductivity (LSC) and Huber value (HV). Values are means  $\pm$  SE.

TAG	Sap flux density				Twig hydraulic properties							
	XFD (n days)	XFD (g cm <sup>-2</sup> d <sup>-1</sup> )	XFD <sub>daily Max</sub> (g cm <sup>-2</sup> d <sup>-1</sup> )	DWU <sub>Sensor</sub> (kg d <sup>-1</sup> )	Twigs (n)	Segment length (mm)	Segment Ø (mm)	Bark (mm)	k <sub>s</sub> (kg m <sup>-1</sup> MPa <sup>-1</sup> s <sup>-1</sup> )	LSC (n)	LSC (10 <sup>-5</sup> kg m <sup>-1</sup> MPa <sup>-1</sup> s <sup>-1</sup> )	HV (10 <sup>-4</sup> )
C26	348	24.8 ± 0.6	112.6 ± 2.1	8.4	4	126.4 ± 2.0	11.0 ± 0.6	1.20 ± 0.06	2.70 ± 0.21	4	53.6 ± 12.3	2.0 ± 0.5
C27	348	42.8 ± 0.9	215.9 ± 3.8	5.2	4	117.4 ± 3.3	11.5 ± 0.4	0.60 ± 0.06	0.75 ± 0.25	4	28.0 ± 11.8	2.8 ± 1.2
C28	335	77.3 ± 1.7	357.2 ± 5.5	6.2	4	123.5 ± 0.6	11.2 ± 0.4	0.63 ± 0.11	0.84 ± 0.31	4	38.0 ± 16.4	3.8 ± 1.6
C29	364	71.1 ± 1.4	303.6 ± 4.0	15.8	4	123.0 ± 1.5	10.8 ± 0.5	0.90 ± 0.12	1.60 ± 0.36	4	53.8 ± 4.6	5.4 ± 0.5
C30	364	57.5 ± 0.9	231.4 ± 2.5	4.1	4	120.3 ± 0.8	10.7 ± 0.5	1.07 ± 0.07	1.45 ± 0.02	4	26.8 ± 3.7	2.7 ± 0.4
C31					8	125.7 ± 8.2	8.9 ± 0.4	1.00 ± 0.08	3.44 ± 0.51	8	84.3 ± 10.6	2.5 ± 0.2
C32	348	38.1 ± 0.8	185.2 ± 2.7	3.6	4	124.0 ± 1.3	10.2 ± 0.4	1.10 ± 0.11	1.63 ± 0.34	4	110.0 ± 26.0	11.0 ± 2.6
C33	348	119.4 ± 1.8	415.8 ± 3.2	52.2	11	117.5 ± 4.7	8.6 ± 0.3	0.96 ± 0.08	1.33 ± 0.10	11	35.1 ± 2.3	2.7 ± 0.2
C34					8	130.4 ± 3.8	8.2 ± 0.2	0.81 ± 0.03	2.15 ± 0.21	8	36.9 ± 3.9	1.7 ± 0.1
C35					4	119.5 ± 2.3	10.2 ± 0.3	0.99 ± 0.03	1.58 ± 0.34	4	60.7 ± 12.3	6.1 ± 1.2
C36	364	57.1 ± 1.1	228.3 ± 3.0	10.3	8	123.2 ± 1.0	11.1 ± 0.4	0.88 ± 0.11	1.66 ± 0.22	8	88.6 ± 21.7	8.9 ± 2.2
C37	364	61.3 ± 1.1	237.5 ± 3.1	12.6	4	122.5 ± 1.7	10.8 ± 0.5	0.99 ± 0.06	2.49 ± 0.25	4	64.9 ± 4.1	2.7 ± 0.4
C38	348	55.0 ± 1.1	204.7 ± 2.6	10.2	4	128.7 ± 8.5	20.2 ± 6.5	0.89 ± 0.07	5.19 ± 4.17	4	260.9 ± 192.3	26.1 ± 19.2
C39					7	129.4 ± 2.6	10.0 ± 0.3	0.99 ± 0.05	1.80 ± 0.45	5	69.5 ± 13.6	3.0 ± 0.3
C40					9	134.1 ± 6.7	8.3 ± 0.3	0.80 ± 0.03	3.64 ± 0.50	9	64.9 ± 3.9	2.1 ± 0.3
C41	335	39.4 ± 1.0	151.6 ± 2.5	3.9	4	122.6 ± 1.3	10.0 ± 0.4	0.69 ± 0.06	1.29 ± 0.28	4	97.1 ± 51.7	9.7 ± 5.2
C42	335	28.7 ± 0.8	107.8 ± 2.3	4.9	4	121.0 ± 2.8	11.8 ± 0.2	0.95 ± 0.08	7.75 ± 6.23	4	411.9 ± 304.6	41.2 ± 30.5
C43	335	29.6 ± 0.6	107.3 ± 1.4	7.3	4	121.6 ± 1.1	10.4 ± 0.2	0.90 ± 0.05	1.90 ± 0.23	4	80.3 ± 6.4	8.0 ± 0.6
C44	335	18.1 ± 0.4	69.0 ± 1.3	6.1	4	122.1 ± 3.3	12.3 ± 0.6	0.46 ± 0.02	0.37 ± 0.02	4	33.2 ± 13.6	3.3 ± 1.4
C45					9	142.1 ± 2.6	9.6 ± 0.3	0.99 ± 0.03	2.71 ± 0.51	9	68.5 ± 13.2	3.2 ± 0.9
C46	348	37.5 ± 0.7	139.6 ± 2.0	8.3	4	124.2 ± 1.4	8.0 ± 0.1	0.54 ± 0.11	1.03 ± 0.20	4	30.5 ± 2.9	3.0 ± 0.3
C47	348	52.1 ± 1.0	234.7 ± 3.7	13.6	4	122.7 ± 1.0	10.5 ± 0.4	2.00 ± 1.46	2.77 ± 1.50	4	44.8 ± 8.6	4.5 ± 0.9
C48					8	141.4 ± 2.4	9.7 ± 0.2	0.79 ± 0.04	1.33 ± 0.28	8	30.0 ± 4.6	2.4 ± 0.3
C49					8	140.5 ± 3.1	9.2 ± 0.2	0.73 ± 0.05	1.22 ± 0.17	8	31.0 ± 5.1	2.7 ± 0.4
C50					2	138.8 ± 4.7	8.5 ± 0.1	0.63 ± 0.02	0.49 ± 0.20	2	8.2 ± 2.9	1.7 ± 0.1

**Tab. A8.7: (continuation)** For the same tree individuals as given in Tab. A8.5 (see TAG), here are summarized individual tree data for leaf morphology and isotope signatures. These were specific leaf area (SLA), total number of leaves distal to the twig segment used for hydraulic measurements, total supported leaf area distal to the twig segment ( $A_L^{\text{Total}}$ ), mean leaf size ( $A_L$ ), maximal leaf size ( $A_L^{\text{Max}}$ ), carbon isotope signature ( $\delta^{13}\text{C}$ ) and nitrogen isotope signature ( $\delta^{15}\text{N}$ ). Values are means  $\pm$  SE.

TAG	<i>Leaf morphology</i>						<i>Isotope signatures</i>		
	SLA (n)	SLA ( $\text{cm}^2 \text{g}^{-1}$ )	Leaves (n)	$A_L^{\text{Total}}$ ( $\text{cm}^2$ )	$A_L$ ( $\text{cm}^2$ )	$A_L^{\text{Max}}$ ( $\text{cm}^2$ )	$\delta^{13}\text{C}$ (n)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
C26	4	99.29 $\pm$ 3.2	163	22872	140.3 $\pm$ 5.7	309.0	4	-30.3 $\pm$ 0.3	5.94 $\pm$ 1.84
C27	4	106.79 $\pm$ 2.5	41	9457	230.7 $\pm$ 9.6	373.5	4	-31.8 $\pm$ 0.1	-0.45 $\pm$ 0.32
C28	4	75.59 $\pm$ 3.5	40	7625	190.6 $\pm$ 10.3	294.1	4	-31.4 $\pm$ 0.2	-1.71 $\pm$ 0.09
C29	4	65.99 $\pm$ 3.3	65	6930	106.6 $\pm$ 6.1	239.0	4	-30.1 $\pm$ 0.4	-0.68 $\pm$ 0.19
C30	4	78.59 $\pm$ 5.7	97	12847	132.4 $\pm$ 5.5	245.8	4	-30.5 $\pm$ 0.3	-0.87 $\pm$ 0.10
C31	8	43.59 $\pm$ 0.8	464	9603	20.7 $\pm$ 0.3	46.9			
C32	4	101.79 $\pm$ 3.6	109	2959	27.1 $\pm$ 1.6	64.9	4	-30.6 $\pm$ 0.2	-0.04 $\pm$ 0.14
C33	11	53.69 $\pm$ 1.1	1282	25980	20.3 $\pm$ 0.3	61.5	4	-27.2 $\pm$ 0.1	0.01 $\pm$ 0.07
C34	8	70.99 $\pm$ 1.5	462	14280	30.9 $\pm$ 0.7	77.8			
C35	4	86.99 $\pm$ 5.2	154	5766	37.4 $\pm$ 1.3	80.3	4	-30.9 $\pm$ 0.2	-0.28 $\pm$ 0.09
C36	8	83.39 $\pm$ 3.6	372	13200	35.5 $\pm$ 1.1	111.6	8	-30.7 $\pm$ 0.1	1.60 $\pm$ 0.18
C37	4	68.59 $\pm$ 2.4	507	17196	33.9 $\pm$ 0.6	77.1	4	-30.3 $\pm$ 0.1	-0.84 $\pm$ 0.02
C38	4	124.39 $\pm$ 4.4	191	6976	36.5 $\pm$ 1.1	96.8	4	-31.4 $\pm$ 0.2	-0.22 $\pm$ 0.02
C39	5	88.29 $\pm$ 2.9	471	8345	17.7 $\pm$ 0.4	49.1			
C40	9	89.3 $\pm$ 2.3	499	13612	27.3 $\pm$ 0.5	85.0			
C41	4	113.3 $\pm$ 6.8	140	5208	37.2 $\pm$ 1.4	81.6	4	-30.9 $\pm$ 0.3	-0.75 $\pm$ 0.06
C42	4	111.3 $\pm$ 3.8	190	5271	27.7 $\pm$ 0.7	65.9	4	-30.9 $\pm$ 0.2	0.70 $\pm$ 0.49
C43	4	105.9 $\pm$ 6.4	173	5459	31.6 $\pm$ 0.8	63.4	4	-32.4 $\pm$ 0.1	-0.61 $\pm$ 0.04
C44	4	149.8 $\pm$ 8.3	313	7080	22.6 $\pm$ 0.6	75.9	4	-31.0 $\pm$ 0.3	-0.19 $\pm$ 0.15
C45	9	106.8 $\pm$ 3.8	451	15921	35.3 $\pm$ 0.7	83.6			
C46	4	179.4 $\pm$ 11.2	113	5387	47.7 $\pm$ 3.0	133.9	4	-29.5 $\pm$ 0.1	7.87 $\pm$ 0.52
C47	4	174.6 $\pm$ 0.9	67	7012	104.7 $\pm$ 5.8	221.5	4	-32.7 $\pm$ 0.1	2.22 $\pm$ 0.07
C48	8	131.6 $\pm$ 4.9	418	18311	43.8 $\pm$ 1.4	160.5			
C49	8	139.5 $\pm$ 4.3	280	16228	58.0 $\pm$ 2.1	161.1	4		
C50	2	171.0 $\pm$ 11.6	102	4748	56.5 $\pm$ 2.4	103.2			

**Tab. A8.8: (continuation)** For the same tree individuals as given in Tab. A8.5 (see TAG), here are summarized individual tree data for leaf nutrient concentrations. These were foliar contents of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn) and iron (Fe). Values are means  $\pm$  SE. For number of samples see isotope signatures (Tab. A8.7).

TAG	<i>Leaf nutrient concentrations</i>							
	C (g kg <sup>-1</sup> )	N (g kg <sup>-1</sup> )	P (g kg <sup>-1</sup> )	K (g kg <sup>-1</sup> )	Ca (g kg <sup>-1</sup> )	Mg (g kg <sup>-1</sup> )	Mn (g kg <sup>-1</sup> )	Fe (g kg <sup>-1</sup> )
C26	504.2 $\pm$ 2.9	18.9 $\pm$ 0.4	1.68 $\pm$ 0.15	12.15 $\pm$ 0.54	14.55 $\pm$ 0.70	6.10 $\pm$ 0.39	0.21 $\pm$ 0.01	0.135 $\pm$ 0.020
C27	481.6 $\pm$ 0.8	16.7 $\pm$ 0.9	1.49 $\pm$ 0.04	11.83 $\pm$ 0.81	13.33 $\pm$ 0.51	7.97 $\pm$ 0.30	0.51 $\pm$ 0.04	0.030 $\pm$ 0.004
C28	483.0 $\pm$ 2.0	15.9 $\pm$ 0.3	1.53 $\pm$ 0.04	9.12 $\pm$ 0.57	19.33 $\pm$ 0.32	8.67 $\pm$ 0.19	0.34 $\pm$ 0.01	0.031 $\pm$ 0.003
C29	501.0 $\pm$ 5.5	18.4 $\pm$ 0.4	1.76 $\pm$ 0.08	9.13 $\pm$ 0.18	17.62 $\pm$ 2.73	6.01 $\pm$ 0.61	0.17 $\pm$ 0.02	0.044 $\pm$ 0.006
C30	484.9 $\pm$ 1.3	17.2 $\pm$ 0.4	1.80 $\pm$ 0.08	9.29 $\pm$ 0.22	16.86 $\pm$ 1.61	6.48 $\pm$ 0.36	0.17 $\pm$ 0.01	0.025 $\pm$ 0.006
C31								
C32	489.2 $\pm$ 1.8	14.1 $\pm$ 0.2	1.36 $\pm$ 0.05	15.46 $\pm$ 0.33	9.17 $\pm$ 0.24	2.68 $\pm$ 0.11	0.46 $\pm$ 0.03	0.046 $\pm$ 0.003
C33	527.9 $\pm$ 1.2	13.5 $\pm$ 0.1	1.40 $\pm$ 0.11	9.87 $\pm$ 0.28	9.40 $\pm$ 0.45	3.09 $\pm$ 0.06	0.78 $\pm$ 0.04	0.025 $\pm$ 0.003
C34								
C35	493.0 $\pm$ 1.6	14.5 $\pm$ 0.4	1.57 $\pm$ 0.05	12.49 $\pm$ 1.91	11.30 $\pm$ 1.03	2.10 $\pm$ 0.06	0.46 $\pm$ 0.05	0.022 $\pm$ 0.004
C36	489.6 $\pm$ 2.2	16.8 $\pm$ 0.4	1.54 $\pm$ 0.06	14.63 $\pm$ 0.87	10.07 $\pm$ 1.38	2.53 $\pm$ 0.07	0.65 $\pm$ 0.03	0.039 $\pm$ 0.011
C37	518.4 $\pm$ 0.2	14.3 $\pm$ 0.6	1.29 $\pm$ 0.07	13.66 $\pm$ 0.66	9.08 $\pm$ 0.67	2.61 $\pm$ 0.10	0.49 $\pm$ 0.03	0.035 $\pm$ 0.011
C38	454.9 $\pm$ 1.5	17.3 $\pm$ 0.3	1.66 $\pm$ 0.05	13.20 $\pm$ 0.23	12.96 $\pm$ 1.03	3.67 $\pm$ 0.17	1.85 $\pm$ 0.21	0.046 $\pm$ 0.003
C39								
C40								
C41	463.5 $\pm$ 0.7	19.1 $\pm$ 0.4	2.16 $\pm$ 0.12	16.16 $\pm$ 1.09	9.97 $\pm$ 0.32	2.68 $\pm$ 0.28	1.51 $\pm$ 0.11	0.048 $\pm$ 0.003
C42	466.0 $\pm$ 1.9	18.3 $\pm$ 0.1	1.94 $\pm$ 0.04	18.25 $\pm$ 0.72	6.17 $\pm$ 0.71	2.77 $\pm$ 0.09	0.68 $\pm$ 0.07	0.044 $\pm$ 0.007
C43	469.9 $\pm$ 1.8	17.4 $\pm$ 0.5	2.06 $\pm$ 0.09	13.93 $\pm$ 0.49	7.27 $\pm$ 0.46	2.74 $\pm$ 0.07	0.66 $\pm$ 0.02	0.043 $\pm$ 0.004
C44	488.2 $\pm$ 0.8	19.8 $\pm$ 0.2	3.00 $\pm$ 0.08	19.86 $\pm$ 1.02	6.00 $\pm$ 0.53	3.93 $\pm$ 0.07	0.85 $\pm$ 0.14	0.081 $\pm$ 0.011
C45								
C46	457.9 $\pm$ 1.0	29.6 $\pm$ 0.9	2.81 $\pm$ 0.14	33.87 $\pm$ 2.53	15.30 $\pm$ 0.86	8.29 $\pm$ 0.29	0.86 $\pm$ 0.06	0.111 $\pm$ 0.009
C47	447.6 $\pm$ 1.5	25.7 $\pm$ 0.7	2.49 $\pm$ 0.13	23.34 $\pm$ 0.68	16.96 $\pm$ 0.86	11.62 $\pm$ 0.34	1.03 $\pm$ 0.05	0.104 $\pm$ 0.006
C48								
C49								
C50								

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## 8.5 CURRICULUM VITAE

### PERSONAL DETAILS

*Dipl.-Biol. Bernhard Schuldt*

Date of birth: 02. December 1978  
 Place of birth: Vejle, Denmark  
 Nationality: German

### EDUCATION

2006 – 2010 PhD study at the Department of Plant Ecology, Albrecht von Haller Institute for Plant Sciences, University of Göttingen, Germany.

1999 – 2006 Diploma study of biology at the University of Göttingen, Germany (Major: Botany, Minors: Soil Science and Microbiology)  
 Degree obtained: Diplom-Biologe  
 Thesis title: The influence of elevation on the water balance of tropical montane rainforest tree species in South-Ecuador (*Original title*: “Untersuchungen zum Wasserhaushalt tropischer Baumarten in Abhängigkeit der Meereshöhe in Süd-Ecuador”)

1989 – 1998 Gymnasium Christianem, Hamburg, Germany  
 High school graduation: Allgemeine Hochschulreife

### WORK EXPERIENCE

2006 – 2009 PhD field work in the Lore Lindu National Park (Palu, Central Sulawesi, Indonesia)

2004 Diploma thesis in the Podocarpus National Park (Loja, South Ecuador)

2002 – 2006 Graduate assistant at the Department of Plant Ecology, Albrecht von Haller Institute for Plant Sciences, University of Göttingen, Germany

1998 – 1999 Alternative civilian service at the Grün- und Umweltamt Mölln, Germany

## **8.6 DECLARATION OF ORIGINALITY AND CERTIFICATE OF OWNERSHIP**

I, Bernhard Schuldt, hereby declare that I am the sole author of this dissertation entitled ‘EFFECTS OF EXPERIMENTAL DROUGHT ON HYDRAULIC PROPERTIES AND LEAF TRAITS OF UPPER CANOPY AND UNDERSTORY TREE SPECIES IN A PERHUMID TROPICAL FOREST IN CENTRAL SULAWESI, INDONESIA’. All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Göttingen, September 21, 2010

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(Bernhard Schuldt)