Biogeosciences Discuss., 7, 8553–8589, 2010
www.biogeosciences-discuss.net/7/8553/2010/
doi:10.5194/bgd-7-8553-2010

Biogeosciences Discussions

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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Received: 13 October 2010 – Accepted: 2 November 2010 – Published: 24 November 2010

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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 drought sensitivity of tall trees, and (ii) the exposed upper canopy was not more drought susceptible than the shade canopy.

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

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Lingenfelder, 2008; Sheffield et al., 2008) and South America (Cox et al., 2008; Phillips et al., 2009, 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).

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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

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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.

2 Material and methods

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 (01°29.6′ S 120°03.4′ E 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^{-1} and an average stem density of 456 ha^{-1} (>10 cm DBH, Culmsee and Pitopang, 2009; Culmsee et al., 2010).

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2.2 Experimental design

The STDE consisted of six floristically and structurally similar plots of 0.16 ha (40 m × 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.

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, UK). Rainfall was measured to the nearest 0.1 mm with a tipping bucket rain gauge (ARG100, Campbell Scientific, UK). 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

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(Campbell Scientific, UK). 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 27 March 2007 in the roof plots and on 31 May 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.

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):

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

where θ_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

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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.

2.5 Tree selection and plant material

In June 2009, after 24 months of experimental drought, 14 tree individuals (7 in the roof, 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.

2.6 Wood density and saturated water content determination

Wood density (ρ) was determined for trunk wood cores with a diameter of 5 mm and a mean core length of 69.5 ± 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 ± 7.8 mm and a mean segment length of 120.0 ± 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

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at a precision of 10 mg. The dry mass of each sample was then divided by its volume to obtain ρ. 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 weighed 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).

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 roof 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.

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 ± 34.7 mm length and 10.6 ± 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 µg l^{-1} Ag, 8 mg l^{-1} NaCl, Micropur katadyn, Wallisellen, Switzerland) to prevent microbial growth. The samples were kept cool and transported to a nearby field

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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 µm 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^{-1} s^{-1}) 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^{-1}) and $\Delta P/\Delta X$ is the pressure gradient across the segment (MPa m^{-1}). k_h was used to calculate vessel lumen area-specific (k_s) and leaf area-specific conductivity (LSC, kg m^{-1} MPa^{-1} s^{-1}) by dividing the maximum conductivity by the microscopically determined lumen area of the vessels (m^2) or the supported leaf area (m^2) of the twig segments.

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_{Xylem}, m^2). 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 ± 4.8 mm^2. The images were analyzed with the software ImageJ (v1.42q, http://rsb.info.nih.gov/ij) using the particle analysis-function to

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estimate idealized radii (r) from lumen area ($A = \pi r^2$), vessel density (VD, n mm^{-2}) and cumulative vessel lumen area (m^2). 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^{theo}, m^4 MPa^{-1} s^{-1}) was calculated as:

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

We calculated with the viscosity of water (η) at 20 °C (1.002 10^{-3} Pa s; Zwieniecki et al., 2001). k_h^{theo} was used to calculate the theoretical vessel lumen area-specific conductivity (k_s^{theo}, kg m^{-1} MPa^{-1} s^{-1}) by dividing by cumulative vessel lumen area (A_{Xylem}) and multiplying k_s^{theo} with the density of water (ρ) at 20 °C (998.20 kg m^{-3}, James et al., 2003).

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

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 ± 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, 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, cm^2 g^{-1}). The Huber value (HV) was calculated as the ratio of sapwood cross-sectional

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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^{spec}, 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 δ^{13}C and δ^{15}N were determined with a Delta plus isotope mass spectrometer (Finnigan MAT, Bremen, Germany), a Conflo III interface (Thermo Electron Coorperation, Bremen, Germany) and an NA2500 element analyzer (CE-Instruments, Rodano, Milano, Italy) using standard δ notion:

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

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

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 roof and control plots, the label "treatment" is used.

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3 Results

3.1 Microclimatic conditions

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

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, θ) 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 roof 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), θ 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. 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 depth under the more efficient roof in the experiment's second phase. The lowest θ values were reached shortly before the re-opening of the roof in May 2009. When expressed in relation to the control

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plots, θ 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 (Ψ_{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), Ψ_{soil} dropped to −1.5 MPa at the end of the desiccation (Fig. 1). In contrast, no significant differences in Ψ_{soil} were detected in the lower soil layers (0.5–3.0 m) between roof and control plots, even though θ differed by about 15%.

The calculated relative extractable water for the upper soil layers (REW_{top}) dropped below the threshold value of 0.4 in the roof plots immediately after the beginning of the second phase of the desiccation in early 2008, enhanced by rather low rainfall in this period (Fig. 1). Interrupted by a short recovery due to strong rainfall in March/April 2008, REW_{top} decreased further in the roof plots, leading to a 90% smaller amount of available water in the roof plots compared to the control. On the other hand, the relative extractable water of the lower soil layers (REW_{low}) only dropped below the threshold of 0.4 in the driest phase of the experiment from February 2009 onwards. Nevertheless, REW_{low} was by 50% smaller in the roof than in the control plots from June 2008 until May 2009.

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. 4). 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 on a unit branch sapwood area (leaf number-based Huber value, Fig. 2, Table 4). The droughted trees also showed a higher wood density in

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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 roof plots both in the sun and shade canopy branches.

Analysis of isotope composition in leaf dry mass indicated no drought effects on $\delta^{13}C$ and $\delta^{15}N$ (Fig. 3). The $\delta^{13}C$-N_A relationship was not different between roof and control plots (Fig. 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 (Tables 3 and 4).

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 ($p = 0.03$), an increase in the wood density of the peripheral xylem sections (by 5%, $p = 0.09$) and an associated significant reduction in saturated water content (SWC, $p = 0.05$) of the xylem by 10% when comparing roof and control plots (Table 2).

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 $\delta^{13}C$ and a more positive $\delta^{15}N$ 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

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leaves, Tables 3 and 4). 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. 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 roof plots, while lumen area-specific conductivity was the same (Table 4).

4 Discussion

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 ($\Psi_{soil} < -1.5$ MPa, 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 ($Ø \leq 2$ 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 ($Ø > 2$ 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 ($0.12\,g\,L^{-1}$) 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.

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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-Gonzáles 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 enfold larger leaves. A similar effect has been observed in saplings of silver birch (*Betula pendula*) that produced fewer but larger leaves 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 $\delta^{13}C$ 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

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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 roof 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 $\delta^{13}C$ in the course of 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 $\delta^{15}N$ signature of leaves typically shows no strong drought signal (Peuke et al., 2006; Hartman and Danin, 2010). Thus, the lack of differences in $\delta^{15}N$ between roof and control trees fits to the expectation, while the absence of $\delta^{13}C$ differences comes as a surprise. It appears that leaf conductance was not significantly reduced in response to the 24-month desiccation. Further, the foliar nitrogen-leaf area relationship was similar in roof and control trees (see Fig. 5) which suggests that stomatal and biochemical photosynthesis were not larger in the drought-exposed trees than in the control. The $\delta^{13}C$ 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.

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

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in the outermost xylem of the trunks of the roof plots which also showed up in a higher wood density and 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 roof 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 inside the roof 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 Tapajs 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 characteristic 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

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simulated in our experiment where relative humidity did not drop below 88% in the experimental period (see Table 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.

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

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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.

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 atmosphere saturation deficit; these hydrologic characteristics allows 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 smaller tree species showed signs of critical damage which reflects 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.

Acknowledgements. This study was conducted in the framework of the joint Indonesian-German Collaborative Research Center “Stability of Tropical Rainforest Margins, Indonesia (STORMA)” funded by the German Science Foundation (SFB 552). We thank Heike Culmsee

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for tree species identification, Oliver van Straaten for providing valuable data, Wolfram Lorenz for organizing the logistics in Palu, our Indonesian counterparts, especially Henry Barus, the field assistants, the Indonesian Research Foundation LIPI and the authorities of the Lore Lindu National Park for the research permission.

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This Open Access Publication is funded by the University of Göttingen.

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Table 1. 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. Values are means ±1 SE.

	Full day (24 h)			Daylight hours (12 h)		
	T (°C)	RH (%)	D (kPa)	T (°C)	RH (%)	D (kPa)
1st year	20.76 ± 0.03	88.51 ± 0.27	0.34 ± 0.01	22.41 ± 0.05	82.35 ± 0.36	0.54 ± 0.01
2nd year	20.61 ± 0.04	88.94 ± 0.21	0.32 ± 0.01	22.29 ± 0.06	82.94 ± 0.31	0.53 ± 0.01

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Table 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 (ρ_{stem}, g cm^{-3}), saturated water content (SWC, %), vessel lumen area (A_{Lumen}, %), vessel density (VD, n mm^{-2}), mean vessel diameter (d, µm, mean ± SE, control n = 788, roof n = 1033), hydraulic mean diameter (d_h, µm), theoretical lumen-specific conductivity (k_s^{theo}, kg m^{-1} MPa^{-1} s^{-1}) between the treatments (control: C1–C7, roof: R1–R7).

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

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Table 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 g kg^{-1} or 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 ± 1 SE. The number of replicates for the control are $n = 56$, for the roof $n = 63$.

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

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Table 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). Level 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	
Hydraulic traits								
LSC	0.90	*	0.67	**	0.67	**	0.49	*
k_s	0.74	***	0.75	**	1.10	n.s.	1.12	n.s.
HV	1.19	n.s.	0.87	**	0.56	***	0.41	***
n_L^{spec}	0.72	**	0.88	n.s.	0.94	n.s.	1.14	n.s.
Leaf morphology								
Leaf area	1.29	***	1.39	***	1.60	***	1.72	***
SLA	0.95	n.s.	1.06	n.s.	1.19	***	1.32	***
Wood density								
ρ_{branch}	1.06	**	0.98	n.s.	0.98	n.s.	0.91	***
Isotope composition								
$\delta^{13}C$	0.99	n.s.	0.99	n.s.	1.04	***	1.04	***
$\delta^{15}N$	1.53	n.s.	–	*	0.43	*	–	***
Nutrient concentrations								
Mass-specific								
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.
Area-specific								
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	*

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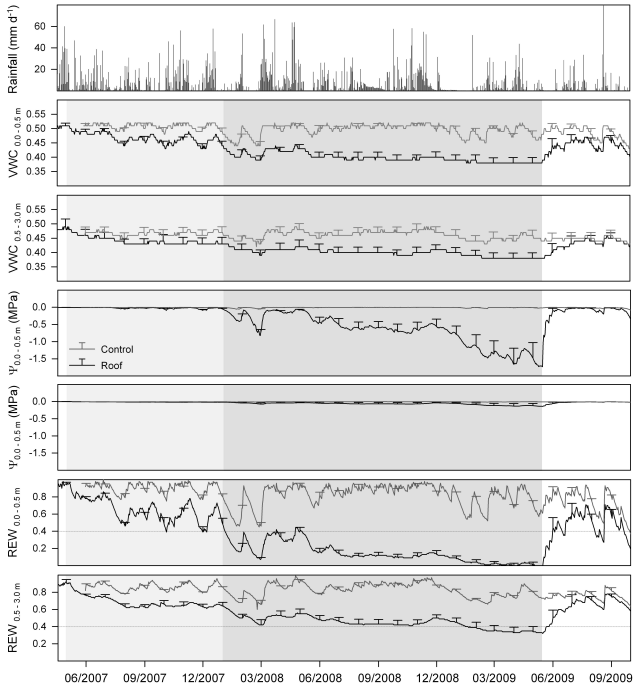

Fig. 1. Volumetric soil water content (θ), soil water potential (Ψ MPa) and relative extractable water (REW) of the control (grey line) and the roof (black line) plots during the 2-year experimental period (in both soil layers depicted each three measuring depths were instrumented and averaged). For 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 ± 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.

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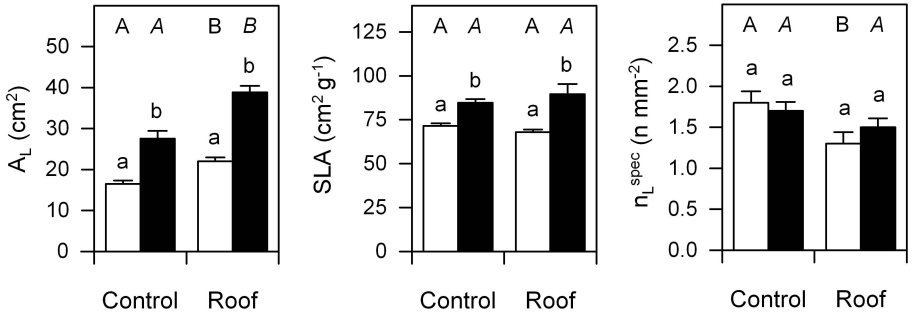

Fig. 2. Mean leaf size (A_L, cm^2), specific leaf area (SLA, cm^2 g^{-1}), specific leaf number (n_L^{spec}, n mm^{-2}) in the upper sun-lit (□) and the lower shade crown (■) of *C. acuminatissima* in the control and the roofs plots. Lower-case letters indicate significant differences between crown positions within a given treatment and upper-case letters stand for significant differences between roof and control. Values are means ± SE. Number of replicates were: control $n = 56$, roof $n = 60$ (number of leaves measured: control $n = 7987$, roof $n = 5015$).

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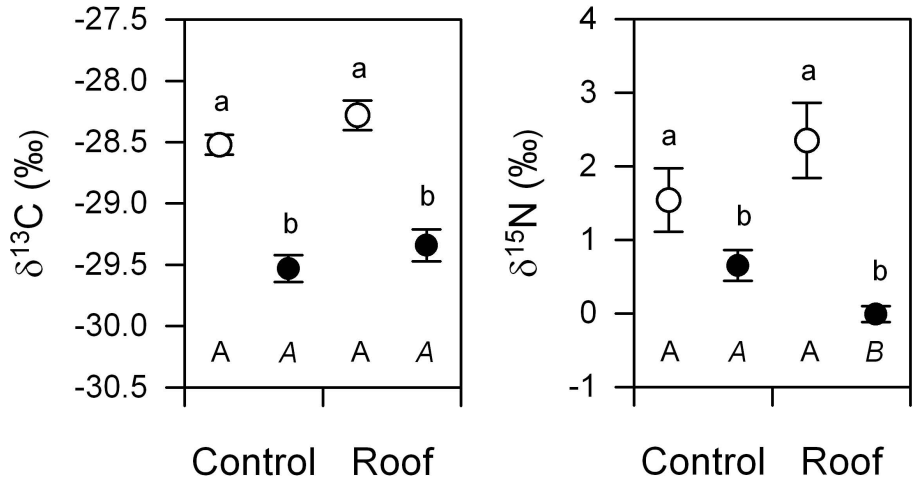

Fig. 3. Isotope signatures of carbon (δ^{13}C, left) and nitrogen (δ^{15}N, right) in leaf biomass harvested distal to the twig segments used for hydraulic investigations from the upper sun-lit crown (○) and lower shade crown (●) of *C. acuminatissima*. Values are means ± SE. For the number of replicates see Table 3.

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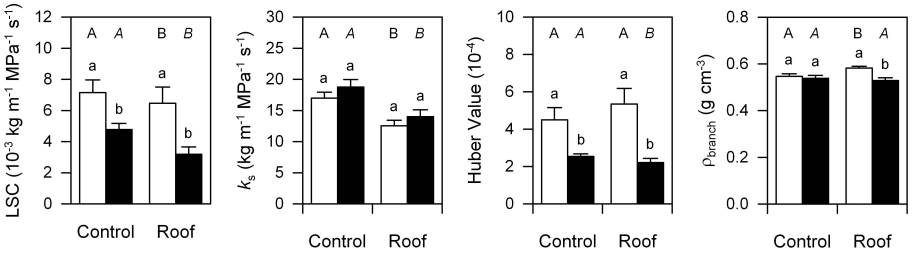

Fig. 4. Leaf-specific conductivity (LSC), vessel-lumen specific conductivity (k_s), Huber value and branch wood density (ρ_{branch}) of the upper sun-lit crown (□) and lower shade crown (■) of *C. acuminatissima* trees in the control and roof plots. Lower-case letters indicate significant differences between the crown positions of a given treatment, and upper-case letters stand for significant differences between the two treatments. Values are means ± SE. Number of replicates for LSC, k_s and HV were: control $n = 56$, roof $n = 60$; for ρ_{branch}: control $n = 52$, roof $n = 57$.

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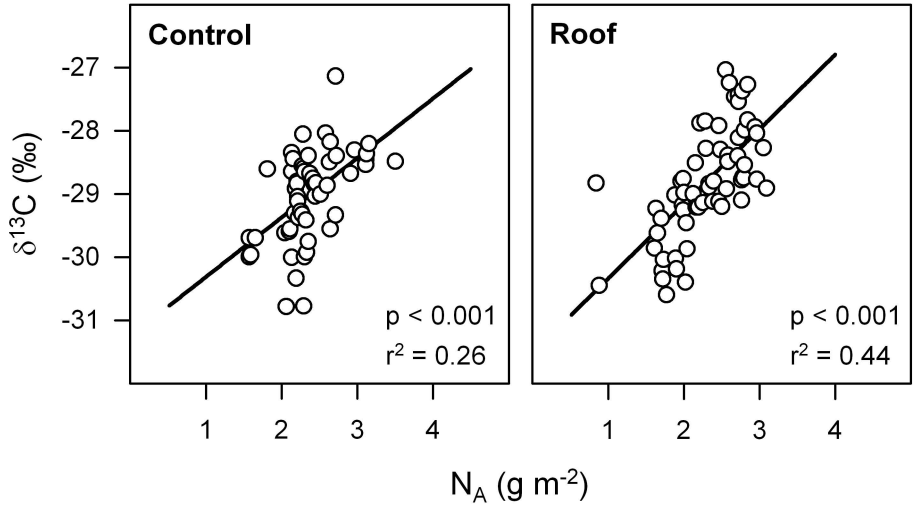

Fig. 5. Relation between area-specific nitrogen content (N_A) and $\delta^{13}C$ in *C. acuminatissima* from the lower and upper crown in the control and roof plots. Slope b = 0.80 (control), 1.18 (roof). For number of replicates see Table 3.

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