

Response of cocoa trees (*Theobroma cacao*) to a 13-month desiccation period in Sulawesi, Indonesia

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Abstract In South-east Asia, ENSO-related droughts represent irregularly occurring hazards for agroforestry systems containing cocoa which are predicted to increase in severity with expected climate warming. To characterize the drought response of mature cocoa trees, we conducted the Sulawesi Throughfall Displacement Experiment in a shaded (*Gliricidia sepium*) cocoa agroforestry system in Central Sulawesi, Indonesia. Three large sub-canopy roofs were installed to reduce throughfall by about 80% over a 13-month period to test the hypotheses that (i) cocoa trees are sensitive to drought due to their shallow fine root system, and (ii) bean yield is more sensitive to drought

than leaf or stem growth. As 83% of fine root (diameter <2 mm) and 86% of coarse root biomass (>2 mm) was located in the upper 40 cm of the soil, the cocoa trees examined had a very shallow root system. Cocoa and *Gliricidia* differed in their vertical rooting patterns, thereby reducing competition for water. Despite being exposed for several months to soil water contents close to the conventional wilting point, cocoa trees showed no significant decreases in leaf biomass, stem and branch wood production or fine root biomass. Possible causes are active osmotic adjustment in roots, mitigation of drought stress by shading from *Gliricidia* or other factors. By contrast, production of cocoa beans

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was significantly reduced in the roof plots, supporting reports of substantial reductions in bean yields during ENSO-related drought events in the region. We conclude that cocoa possesses traits related to drought tolerance which enable it to maintain biomass production during extended dry periods, whereas bean yield appears to be particularly drought sensitive.

Keywords Climate change · Cocoa yield · ENSO · Fine roots · *Gliricidia sepium* · Leaf biomass · Litter fall · LAI · Root water potential · *Theobroma cacao*

Introduction

Cocoa (*Theobroma cacao* L.), one of the world's most important perennial crops, is primarily used for chocolate production, with an estimated global output of 3.5 m t of beans being produced in 2006 (ICCO 2007). The area of cocoa plantations has increased greatly during the last decade in Indonesia, now the largest cocoa producer in South-east Asia, following the decline in production in Malaysia 20 years ago. Cocoa is cultivated in Indonesia and elsewhere using three different cropping systems, i.e. (i) traditionally under the shade of selectively thinned forest, (ii) under planted shade trees such as *Gliricidia sepium* or *Cocos nucifera*, and (iii), increasingly, under unshaded conditions. In some of the Outer Islands of Indonesia, cocoa is currently the most important cash crop, having replaced cultivation of paddy rice for subsistence purposes and fostering the conversion of forest to arable land.

Droughts related to El Niño Southern Oscillation (ENSO) events represent irregularly occurring hazards to intensive cocoa cultivation in Borneo, Sulawesi and other regions of South-east Asia, and are predicted to increase in severity with expected climate warming in the equatorial region (Timmermann et al. 1999; Sheffield and Woods 2008). A recent socioeconomic assessment of the consequences of ENSO-related droughts on cocoa production in Central Sulawesi revealed that bean yield may be reduced in ENSO years to 62% of its normal level (Keil et al. 2008).

As cocoa is cultivated in South-east Asia not only in humid to perhumid regions, but increasingly in semi-humid climates with an annual rainfall <1200 mm and a marked dry season (Cadima

Zevallos 1970; Leite et al. 1980; Beer 1987), the drought response of cocoa and its tolerance of extended rainless periods is of major interest for farmers and the chocolate industry. Moreover, the shift from shaded to unshaded cropping of cocoa in many parts of South-east Asia is likely to increase its exposure to drought as radiation load and atmospheric saturation deficit are typically higher in unshaded systems.

Despite intensive reviews of their ecophysiology (de Almeida and Valle 2007; Schroth et al. 2008), little is known concerning the drought tolerance and adaptation strategies of mature *Theobroma cacao* trees because most studies have focussed on seedlings. Several investigations have produced evidence of a vapour pressure deficit (vpd)-sensitive stomatal regulation in cocoa leaves (Sena Gomes et al. 1987; Willson 1999), but reduced water use efficiency at high vpd (Sena Gomes et al. 1987), which is likely to induce tissue water deficits under conditions of limited soil water supply. Other authors found evidence for active osmotic adjustment in *Theobroma* which could increase its drought resistance (de Almeida and Valle 2007). However, it is unclear whether the results can be extrapolated to adult trees in the field.

To characterise the drought sensitivity of adult cocoa trees and identify soil moisture thresholds under field conditions, a replicated drought experiment was conducted in a shaded cocoa agroforestry system in Central Sulawesi, Indonesia, a region where cocoa is extensively cultivated. Three large sub-canopy roofs reduced throughfall by up to 80% during the 13-month experimental period and allowed effects on productivity, biomass partitioning, and cocoa bean yield to be monitored as a function of soil moisture relative to adjacent control plots. This investigation focussed on the drought response of the belowground compartment (fine, coarse, large roots) and included both cocoa and the most common shade tree (the legume *Gliricidia sepium* H.B. & K.). We tested the hypotheses that: (i) cocoa trees are sensitive to drought due to their shallow fine root system; and (ii) bean yield is more sensitive to drought than leaf or stem growth. Previous studies suggested that an extended experimental drought period would cause the death of parts of the fine root system and lead to pre-senescent leaf shedding.

Materials and methods

Study site

The cocoa agroforest examined was located close to the village of Marena in the Kulawi Valley, Bolabapu District, Central Sulawesi, Indonesia, 3 km from the western border of Lore Lindu National Park, a large area of pre-montane to montane rainforest (UTM coordinates: 51 M, 0168354, 9828202). Cocoa saplings were planted in December 2000 on former rice and maize fields, together with young plants of the woody legume *Gliricidia sepium* and a limited number of coconut palms (*Cocos nucifera* L.) as shade trees. When the study began in September 2006, the cocoa and shade trees were ca. 6-years-old and 5.4 to 8–11 m in height. With ca. 1,000 cocoa trees and 300 shade trees ha⁻¹, the plantation was representative of a common agroforestry system in the region.

The plantation was located 585 m a.s.l. on a mid-slope Cambisol (8–11° inclination) over 30 m above the nearest main river. The soil consisted mainly of sand (ca. 60%) and silt (20–30%) with intermediate layers of gravel; clay content decreased with soil depth, while the sand content increased. Gravel content (grain size >2 mm) was 13% at depths of 0–50 cm and 30–33% at 50–200 cm. pH (KCl) ranged between 3.8 and 4.7.

The study area has a hot perhumid climate with no distinct dry season. Between 2002 and 2006, annual mean temperature at Gimpu meteorological station (5 km south of Marena at 417 m a.s.l.) was 25.5°C and annual mean precipitation was 2,092 mm (Fig. 1). Mean monthly rainfall exceeded 100 mm for all months except July, when an average of ca. 80 mm was recorded (Kreilein, Oltchev and Gravenhorst, pers. comm.). Climatic measurements above the tree canopies at the Marena plantation between

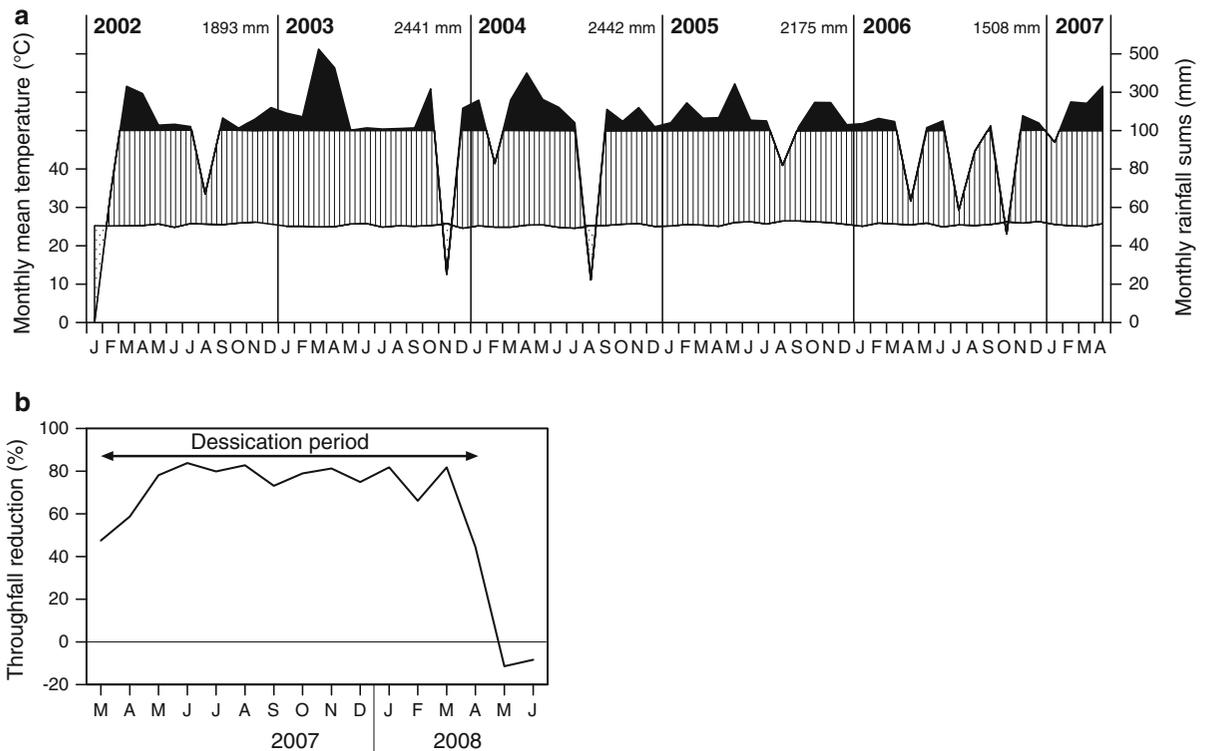


Fig. 1 **a** Climatogram showing monthly mean air temperature (lower line), monthly rainfall (upper line) and annual rainfall between January 2002 and April 2007 at Gimpu village, Kulawi Valley, Central Sulawesi, ca. 5 km south of the Marena study site. Stippled areas, vertical lines and solid black areas

represent dry, moist and very moist periods. **b** Reduction in throughfall in the ‘roof’ treatment relative to control plots between March 2007 and June 2008; the roofs were closed between March 1, 2007 and April 10, 2008

February 2007 and January 2008 gave an annual mean temperature of 24.4°C and an annual rainfall of 2,844 mm. Daily mean relative air humidity was 82% and the lowest daily mean was 69%.

Management of the plantation during the first 6 years included application of insecticides at 3–4 month intervals and N, P, K fertilizer annually. The herbaceous layer was mowed at 3–4 month intervals and the cocoa trees were regularly pruned during the first 6 years; this included the cutting of small twigs and branches by local farmers. The number of shade trees was higher during the first 4 years after planting but subsequently was reduced to ca. 300 ha⁻¹. Fertilizer and insecticide applications ceased after measurements began in September 2006 but mowing continued at 3–4 monthly intervals. The trees were pruned again in July and November 2007.

Throughfall displacement

In an area of the plantation with a homogeneous inclination and a typical cocoa and shade tree density, a rectangular area (80 m × 105 m) was demarcated and subdivided to give six 40 m × 35 m plots. All measurements were conducted in the central area (30 m × 25 m) of each plot, surrounded by a 5 m wide buffer zone to exclude edge effects (Fig. 2). Plots 2, 3 and 6 were randomly selected as roof plots, while the remaining plots served as controls (1, 4, 5). Between September 2006 and February 2007, below-canopy roofs were erected in plots 2, 3 and 6 (each 40 m × 35 m; Fig. 1a, b) to simulate an extended drought period such as occurs irregularly during moderate or severe ENSO events in parts of Indonesia; these remained in place for 13 months between March

1, 2007 and April 10, 2008. Frames (5 m × 0.5 m) constructed from bamboo poles and covered by a transparent UV-insensitive polyethylene sheet were placed ca. 1.2 m above the ground to channel throughfall downhill using the natural inclination of the terrain (Fig. 2). Throughfall captured by the roof was allowed to infiltrate into the soil more than 3 m beyond the

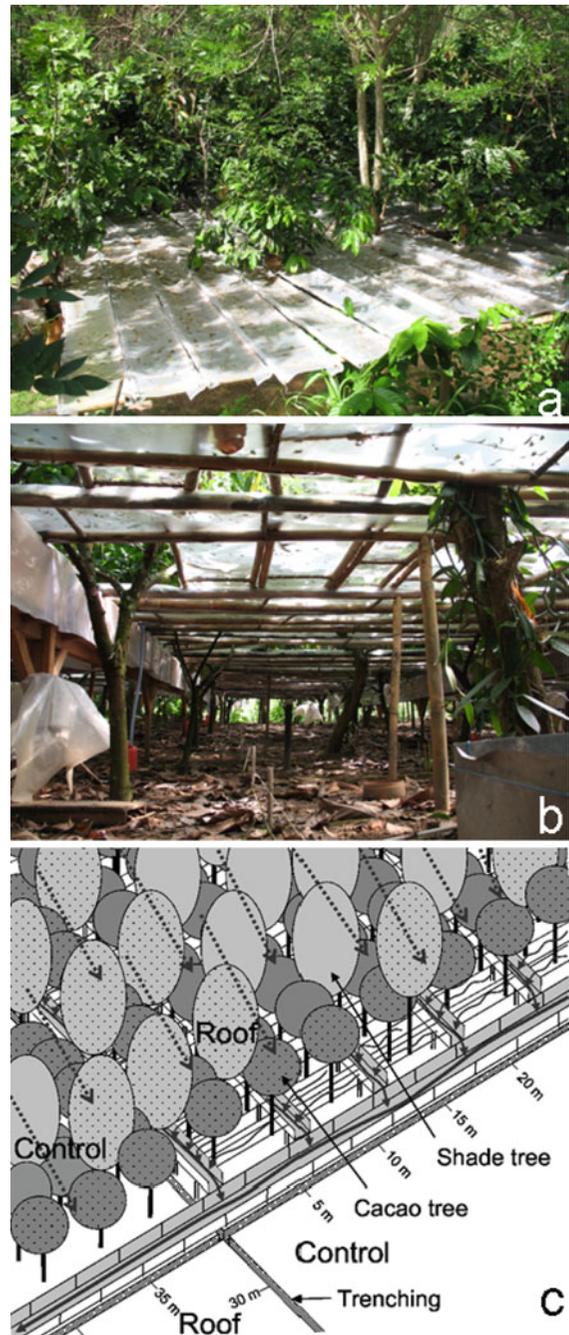


Fig. 2 Photographs taken from **a** above and **b** below the 'roof', and **(c)** schematic representation of the agroforestry system, roof and trenches. **a, b** 1.2 m tall bamboo frames covered with light polyethylene sheets were constructed in all 'roof' plots; water was channelled from the roofs to wooden gutters outside the plots. Gaps in the roof resulting from the use of large standard frames (5 m × 0.5 m) were closed by inserting smaller frames around the trunks of trees. **c** Trenches lined with plastic sheet (40 cm deep × 20 cm wide) were dug around all plots to exclude lateral water flow and sever the dense mat of fine roots in the surface soil. Trees in the 5 m boundary zone around all plots were excluded from measurements to avoid edge effects induced by root damage or interactions with adjacent plots. Trees are shown in one roof plot but are omitted from the others

boundary of the study site, in one case more than 20 m distant. Gaps in the roofs surrounding the stems of cocoa and shade trees were closed using smaller frames that fitted into the openings. Stemflow was not captured. The throughfall reduction was calculated using throughfall data from nine gutters (4 m × 0.2 m) in the control plots, and nine gutters above and nine below the roofs in the desiccation plots.

The roofs reduced throughfall to the ground by 52% in March and 41% in April 2007, and by 73–84% between May 2007 and May 2008 (Fig. 1). Trenches (40 cm deep × 20 cm wide) were dug around all plots and lined with plastic sheet to sever tree roots in the topsoil, where the density of fine and coarse roots was highest, and divert surface flow from upslope areas during heavy rainfall.

Microclimatological and soil physical and chemical measurements

An automatic weather station installed 2 m above the canopy of a cocoa stand 15 m from plot 1 was used to record air temperature and relative humidity (CS 215, Campbell Scientific Inc., Logan, UT, USA), incident global radiation (CS 300, Campbell Scientific Inc.) and rainfall (ARG 100, Campbell Scientific Inc.) at 5 s intervals; data were stored as 30-min averages using a CR800 datalogger (Campbell Scientific Inc.).

Three soil pits were excavated to a depth of 3 m in all plots to conduct soil physical and chemical inventories and provide access to deeper soil horizons for ongoing measurements. The pits were covered between measurements using plastic sheets and wooden plates to prevent evaporation from the pit walls. Laboratory desorption curves indicated that a matric potential of -1.5 MPa ('permanent wilting point') corresponded to a volumetric soil water content of 22–25% at depths of 5 and 40 cm, and to 28% at 75 cm (van Straaten and Veldkamp, pers. comm.). Volumetric soil water content was monitored by time domain reflectometry probes (TDR, C61 6 probes, Campbell Scientific Inc.) installed horizontally in the pit walls at depths of 10 cm ($n = 3$ per plot), 75 cm ($n = 3$) and 150 cm ($n = 1$); these were logged at 1 h intervals (CR1000 datalogger Campbell Scientific Inc.). The high stone content limited the number of probes installed at 75 cm depth in plots 1, 4 and 5 ($n = 2$). The probes were calibrated for the local soil as described by Veldkamp and O'Brien (2000).

Analysis of stand structure and above- and belowground biomass

The cocoa trees in all six plots were individually labeled, and their stem diameter 80 cm above the ground and tree height were measured using dendrometer tapes (resolution 0.1 mm) and a Vertex height meter (Haglöf, Langsele, Sweden). Aboveground biomass (wood of stems, branches and twigs) was estimated from stem diameter using an allometric relationship established in the nearby Palolo and Napu valleys (40 km north-east of Marena; Smiley and Kroschel 2008). This approach also provided biomass estimates for large, coarse and fine roots. Aboveground biomass of the overstorey *Gliricidia* trees was estimated using the allometric regression described by Foroughbakhch et al. (2006) based on measurements of stem diameter in all stands. Smiley and Kroschel (2008) obtained a root/shoot ratio for *Gliricidia* of 2.05 in the nearby Palolo/Napu stands, and this was applied to the Marena stand on the assumption that the growth habit was similar in both stands. To estimate the leaf area index (LAI) of the cocoa and *Gliricidia* trees separately, hemispherical photographs were taken using a fisheye lens at heights of 0.8 m below and 5 m above the cocoa canopy, but under the *Gliricidia* canopy. These measurements were made in August 2006 at 12 locations per plot in a rectangular grid (10 m × 12.5 m) at the locations of the litter traps (see below). The photographs were analyzed using WinScanopy software. The effective $LAI_{(LAI_{eff})}$ was calculated after Bonhomme and Chartier (1972) for a zenith angle of 57.5° and the true $LAI_{(LAI_{true})}$ was derived by dividing LAI_{eff} by the clumping index (CI) calculated for each image as described by Lang and Xiang (1986). To obtain the leaf biomass of the cocoa and *Gliricidia* trees in August 2006, the LAI values were divided by the corresponding mean specific leaf area (SLA) determined using the litter trap samples.

To determine the depth distribution of fine root (diameter <2 mm), coarse root (20–50 mm) and large root biomass (>50 mm), two soil pits per plot were dug before (December 2006) and after the drought period (May–June 2008) to a depth of 3 m. In each pit, 50 cm × 50 cm wide soil monoliths were excavated and sliced into 20 cm-thick segments, enclosed in polyethylene bags and transported to the University of Palu for analysis. All roots within each

monolith were washed out using a 0.25 mm sieve, separated into living and dead fine and coarse root fractions and sorted by species (cocoa, *Gliricidia* and coconut). Criteria for separating live and dead root mass were the degree of root elasticity and/or an inspection of the root cross-sections to reveal the disintegration of root stele, pericycle and periderm which occurs in dead roots. The roots of cocoa, *Gliricidia* and coconut were distinguished by their colour, branching pattern, diameter and the presence or absence of root nodules. Fine and coarse roots of cocoa have a dark brown periderm and even small diameter roots are already strongly lignified. The fine and coarse roots of *Gliricidia* are light brown to ochre in colour, and the former are very soft and many have nodules. Coconut roots were always thicker than 7 mm, even at their root tips, and were classified as fine roots when their diameter was <20 mm as significant lignification was observed only in roots >20 mm in diameter. The root mass of the herbaceous layer was negligible and the data were omitted. When the desiccation period ended in June 2008, the root systems of six cocoa and three *Gliricidia* trees in the centre of each of the roof and control plots were completely excavated to determine the three-dimensional extension of fine and coarse roots. Most of these trees were located >8 m from the plot boundaries. Twenty cm thick soil layers were excavated within a radius of 100 cm around the stem until the tip of the tap root was reached at a maximum depth of 160 cm. Root biomass distribution data were compiled for three distance classes from the tree stem (0–50, 50–100 and >100 cm). Mean root biomass in each plot was calculated from the excavations, tree densities within the stand, and the soil pit data. Total root biomass (fine, coarse and large) of *Gliricidia* was estimated based on the root/shoot ratios determined by Smiley and Kroschel (2008) in the nearby Palolo/Napu stands and our stem diameter measurements.

Measurement of seasonal biomass dynamics and productivity

To measure increments in stem diameter, 10 cocoa and four *Gliricidia* trees were randomly selected in each stand and fitted with dendrometer tapes (UMS, Munich, Germany) at a height of 50 cm above the ground; these were read at fortnightly intervals between March 2007 and March 2008. The

increments in stem basal area were used to estimate aboveground production of stem, branch and twig wood based on the allometric equations relating stem diameter to wood biomass given by Smiley and Kroschel (2008) for cocoa and by Foroughbakhch et al. (2006) for *Gliricidia*. The increments in basal stem area also allowed approximate estimates to be obtained for the production of large diameter roots for both tree species based on the root/shoot ratios determined by these authors.

Litter fall of leaves and reproductive organs was monitored between March 2007 and March 2008 using 12-l buckets (aperture 75 cm × 75 cm) per plot, arranged at a spacing of 10 m × 12.5 m in a rectangular grid. The litter was sorted by species and analyzed to determine leaf biomass. The 10 cocoa trees per plot monitored for stem growth were also examined fortnightly for the abundance of buds, flowers and fruits to establish the phenology of reproductive growth. On each of the 27 observation dates, the numbers of buds, flowers, and cocoa pods were counted for all trees. The yield of cocoa pods and beans was recorded separately for all trees in the core zone of the plots, including pod and bean fresh weight, the sun-dry weight of beans and the oven-dry weight (70°C, 3 days) of pod and bean subsamples.

Water status and hydraulic properties of roots

Root water potential was measured for cocoa and *Gliricidia* in both the roof and control plots in February 2007, before the onset of the desiccation treatment, and on four occasions during the drought period. On all occasions, 18 root branches (diameter 3–5 mm with all appending fine roots) of cocoa and nine roots of *Gliricidia* per treatment were carefully excavated from the topsoil at randomly selected locations, cut and immediately used to determine their xylem water potential using a Scholander pressure chamber (M600, Mosler Tech Support, Berlin, Germany).

To estimate the proportion of embolized vessels in the xylem of coarse roots, the axial hydraulic conductivity of root segments (diameter 3–5 mm) of cocoa in the roof and control plots was measured in December 2006, and February, July and September 2007. Six cocoa trees per plot were randomly selected and three superficial branch root segments per tree were excised and analysed for actual and maximum

hydraulic conductivity as described by Sperry et al. (1988). Coarse root segments ≥ 12 cm in length were immediately transferred to polyethylene bags filled with cold water and transported to the laboratory in Palu, where they were stored at 4°C prior to measurement. To measure their axial hydraulic conductivity, gravity-induced flow with a potential difference of ca. 6–7 kPa per 5 cm length was applied. In the first round of hydraulic conductivity measurements, a flow period of 5 min was allowed to determine actual conductivity. Water passing through the segment was collected at its distal end in pre-weighed plastic cups for subsequent quantification. The root segments were then flushed for 5 min at a potential difference of 0.12 MPa to remove air bubbles from the vessels before making a second measurement to determine the maximum axial conductivity of the unblocked xylem. Flushing and subsequent flow measurements were repeated at least twice to approach maximum conductivity values. The percentage reduction in hydraulic conductivity was taken as a measure of the proportion of embolized vessels in the root xylem.

Statistical analyses

To test for significant differences between the roof and control treatments in the biomass and production fractions (leaves, stem and branch wood, roots, cocoa beans, pods without beans), root water potential and the percentage reduction in hydraulic conductivity of the root xylem, non-parametric analyses of variance (Kruskal–Wallis test) and subsequent Mann–Whitney two-sample tests (Wilcoxon *U*-test) were conducted using SAS software (version 9.1; SAS Institute, Cary, NC, USA).

Results

Soil moisture

Volumetric water content (θ) was consistently high in the control plots (0.38–0.48 $\text{m}^3 \text{m}^{-3}$ at depths of 10 and 75 cm, and 0.30–0.37 $\text{m}^3 \text{m}^{-3}$ at 150 cm; Fig. 3). Rainless periods exceeding 2 weeks occurred only in January 2008. The roof plots showed a progressive decrease in θ from March 2007 to reach a minimum in January and February 2008, when θ was

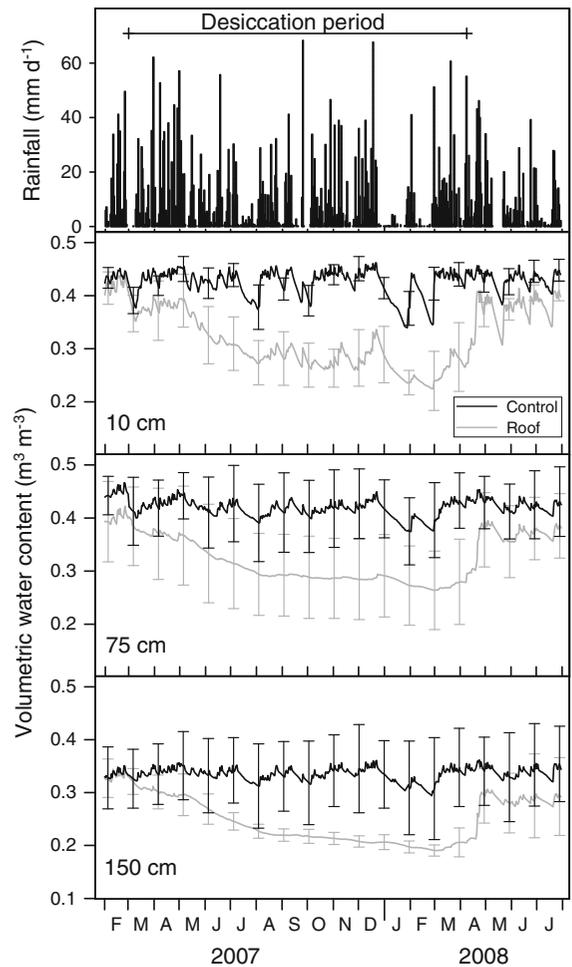


Fig. 3 Daily rainfall and volumetric water content (θ) at soil depths of 10, 75 and 150 cm in the roof and control treatments in the cocoa agroforest in Marena. θ was measured hourly at soil depths of 10 and 75 cm ($n = 9$) and 150 cm ($n = 3$). Daily mean values \pm SD are shown for θ

0.12–0.15 $\text{m}^3 \text{m}^{-3}$ lower than in the control plots. The timecourses of θ were similar for all sampling depths, although the deepest horizon, with its higher bulk density, invariably exhibited lower values. The minimum values recorded during winter 2007/2008 were close to the permanent wilting point (–1.5 MPa; van Straaten and Veldkamp, pers. comm.).

Aboveground/belowground biomass partitioning

Stand structure was very uniform in all plots and showed no significant variation between treatments (Table 1). The 6-year-old cocoa stands and their shade trees had an estimated total above- plus

Table 1 Stand structure of six agroforestry plots containing cocoa in Marena, Kulawi Valley, Central Sulawesi, Indonesia, prior to the desiccation treatment

Plot	Cocoa			<i>Gliricidia</i>			Coconut			LAI		
	Trees ha ⁻¹	Tree height	Stem diameter	Trees ha ⁻¹	Tree height	Stem diameter	Trees ha ⁻¹	Tree height	Stem diameter	Total	Cocoa	Shade trees
1 C	1,014	4.6 ± 0.04	9.7 ± 0.1	264	11.0 ± 0.2	12.7 ± 0.2	21	9.7 ± 0.3	27.8 ± 0.2	5.3 ± 0.4	3.97 ± 0.39	1.29 ± 0.29
2 R	979	4.5 ± 0.05	8.9 ± 0.1	364	11.9 ± 0.2	12.9 ± 0.2	0	N/A	N/A	5.3 ± 0.4	3.86 ± 0.45	1.38 ± 0.19
3 R	986	4.7 ± 0.03	10.1 ± 0.1	329	10.0 ± 0.2	13.5 ± 0.1	0	N/A	N/A	5.7 ± 0.3	4.50 ± 0.42	1.21 ± 0.21
4 C	986	4.6 ± 0.04	9.3 ± 0.1	279	10.2 ± 0.2	11.5 ± 0.3	43	12.1 ± 0.2	37.9 ± 1.0	5.5 ± 0.4	3.43 ± 0.59	1.25 ± 0.19
5 C	1,114	4.4 ± 0.02	9.6 ± 0.1	293	8.0 ± 0.3	13.4 ± 0.1	64	11.7 ± 0.2	37.5 ± 0.6	4.5 ± 0.3	3.13 ± 0.40	1.37 ± 0.16
6 R	1,100	4.7 ± 0.03	9.4 ± 0.1	421	9.9 ± 0.2	12.6 ± 0.2	14	8.3 ± 2.1	21.8 ± 2.6	5.8 ± 0.4	3.87 ± 0.47	1.41 ± 0.25
Overall												
Mean	1030 ± 0.8	4.5 ± 0.01	9.5 ± 0.03	325 ± 1.3	10.1 ± 0.1	12.6 ± 0.1	23 ± 2.1	11.2 ± 0.2	36.6 ± 0.6	5.3 ± 0.1	3.78 ± 0.19	1.32 ± 0.08

Means ± SEM are shown for tree height (m), stem diameter (cm) 80 cm above ground level and leaf area index (LAI) derived by P. Propastin and S. Erasmi (unpubl.) from hemispherical photographs. N/A represents 'not applicable'.

belowground biomass of 40–42 Mg ha⁻¹ prior to the imposed drought period, with ca. 20% of this being contributed by *Gliricidia* and the remainder by cocoa (Table 2); the biomass of the small number of coconut trees was not determined. The roof and control treatments did not differ significantly for either total stand biomass or for leaf, wood or root biomass. Estimated leaf biomass was 4.8 and 5.4 Mg ha⁻¹ in the control and roof treatments, while the cocoa trees contributed remarkably high stem and branch wood biomasses of ca. 22 Mg ha⁻¹. The estimated total root biomass (large, coarse and fine roots) of cocoa ranged between 5.7 and 7.2 Mg ha⁻¹, corresponding to root/shoot ratios of 0.22–0.28 in the control and roof plots. For the more irregularly spaced *Gliricidia* trees, estimated root biomasses of 2.5 and 3.1 Mg ha⁻¹ were obtained for the control and roof plots using the allometric equations given by Smiley and Kroschel (2008; root:shoot ratio = 0.49).

Effects of drought on root distribution and root water status

The excavations immediately before the drought treatment revealed a superficial distribution of roots in the soil profile, with >83% of fine roots and >86% of the coarse roots of cocoa being located in the upper 40 cm (Fig. 4). However, significant quantities of fine root biomass in cocoa were present to a depth of 100 cm, while the deepest fine roots reached 200 cm; coarse roots extended to 150 cm. In the uppermost 20 cm, root density for cocoa was 270–280 g m⁻³ for fine roots and 55–71 g m⁻³ for coarse roots. No significant differences in root biomass were detected between the roof and control treatments either at the beginning or end of the drought treatment (Fig. 4). Comparison of the fine root biomass of cocoa at distances of 0–50, 50–100 and >100 cm from the stem revealed no clear differences in total biomass or vertical root distribution (Fig. 5), although coarse and large roots (2–150 mm in diameter) were concentrated within 50 cm of the cocoa stems and few extended to distances >100 cm.

The roots of *Gliricidia*, in particular the fine roots, penetrated much deeper than those of cocoa, being present in considerable numbers to a depth of 250 cm (Fig. 6). The fine roots of *Gliricidia* were more

Table 2 Comparison of biomass fractions ($\text{Mg ha}^{-1} \pm \text{SEM}$, $n = 3$) for cocoa and *Gliricidia* trees in the control and roof plots prior to the drought treatment

Biomass fraction	Control			Roof		
	Cocoa	<i>Gliricidia</i>	Total	Cocoa	<i>Gliricidia</i>	Total
Leaves	3.76 ± 0.26^a	1.00 ± 0.05^A	4.76 ± 0.43^x	4.37 ± 0.32^a	1.03 ± 0.07^A	5.40 ± 0.53^x
Stem + branches	22.32 ± 0.99^a	4.17 ± 0.78^A	26.49 ± 2.09^x	21.35 ± 1.48^a	5.36 ± 1.06^A	26.72 ± 2.63^x
Roots	5.74 ± 1.42^a	2.52 ± 0.39^A	8.26 ± 1.69^x	7.21 ± 1.76^a	3.12 ± 0.54^A	10.33 ± 2.08^x
Total	31.80 ± 2.15^a	7.69 ± 1.18^A	39.51 ± 3.26^x	32.89 ± 2.32^a	9.51 ± 1.64^A	42.45 ± 3.68^x

Since fine and coarse root biomass remained constant over time and no significant drought treatment effect was detected, the table presents the detailed root biomass data for cocoa determined after the drought period at different distance classes from the stem base (0–50 cm, 50–100 cm, <100 cm; $n = 6$). Different letters indicate significant differences between roof and control plots ($P < 0.05$; lower case letters: cocoa, upper case letters: *Gliricidia*, Greek letters: total biomass)

evenly distributed in the soil profile than those of cocoa and did not exhibit such a pronounced density peak in the 0–20 cm horizon. The biomass of coarse and large roots of *Gliricidia* reached a maximum of 40 g m^{-3} at 30 cm depth, greatly exceeding the corresponding value for cocoa ($<5 \text{ g m}^{-3}$). In contrast to cocoa, the fine root biomass of *Gliricidia* was smaller at the end than at the beginning of the drought period at most soil depths in both the roof and the control plots (Fig. 6b). Complete excavation of the root systems of six *Gliricidia* trees revealed no significant difference between the desiccation and control treatments (data not shown), with the deepest roots extending to 250 cm in both treatments.

The decrease in water potential (Ψ_r) in the coarse roots of cocoa (diameter 3–5 mm) was much more pronounced in the roof treatment than in the control during the desiccation period (Fig. 7a). Thus, Ψ_r in the roof treatment decreased from ca. -0.12 MPa in February 2007 to -0.95 MPa in September 2007 after 6 months of throughfall displacement before increasing again. The roots of the control trees maintained median Ψ_r values of -0.15 to -0.20 MPa for most of the desiccation period, and reached a minimum of -0.40 MPa in September 2007. Ψ_r values for droughted cocoa trees were 0.3–0.5 MPa lower than in control trees. *Gliricidia* roots reached a seasonal minimum of Ψ_r between September 2007 and March 2008, although the values did not differ between the roof and control treatments (Fig. 7b). The lowest median Ψ_r values for *Gliricidia* (-0.5 MPa) were much higher than in cocoa. The coarse roots of cocoa showed no significant difference between the roof and control treatments with respect to the extent of the

reduction in axial hydraulic conductivity caused by xylem embolism (Fig. 7c), although the apparent degree of embolism increased in both treatments between February and September 2007 with ongoing desiccation.

Effects of drought on aboveground biomass production and cocoa bean yield

Cocoa and *Gliricidia* both showed remarkably high above- and belowground net primary productivity (NPP) between March 2007 and February 2008, and there was no significant difference between the control ($13.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$) and roof treatments ($14.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$; Table 3). A remarkably large proportion of NPP (total of leaf, wood and root production) was contributed by leaf turnover (ca. 45%), while stem and branch wood production (3.0 – $3.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$) comprised only 22–23% of NPP. Cocoa bean and pod production comprised 31–37% of NPP (bean production alone was 7–9%; Table 3). Relative to their contribution to the total number of trees present (ca. 30%), individual *Gliricidia* trees were more productive than cocoa, providing 37–41% of system NPP. Leaf production was particularly high in *Gliricidia*.

Contrary to expectation, the 13-month desiccation period had no significant effect on the primary production of either cocoa or *Gliricidia*; thus, leaf biomass production was unaffected in both species, although the wood increment was slightly, but significantly, higher for cocoa in the roof plots than in the control plots. Cocoa bean yield was 10% lower in the roof treatment during the 13-month

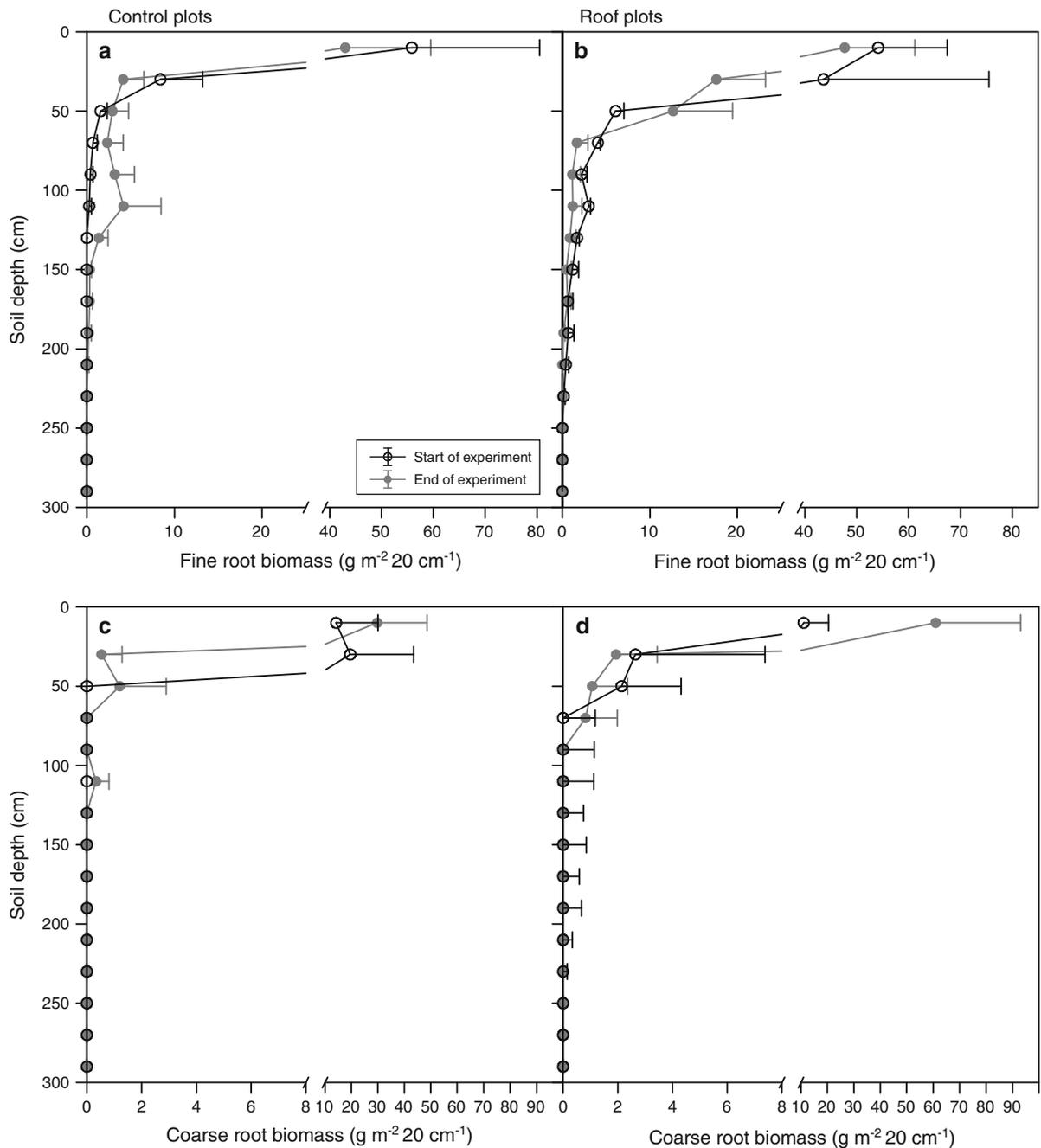


Fig. 4 Vertical distribution of fine (a + b) and coarse roots (c + d) of cocoa at a minimum distance to the nearest tree of 1 m in the control and the roof plots at the start and the end of

the 13-month desiccation period. Mean values \pm SEM are shown ($n = 3$). Coarse roots refer to diameters of 2–150 mm

treatment, although this difference was not significant, but exhibited a significant reduction of ca. 53% in the roof treatment relative to control trees

during the first fructification event shortly after the desiccation treatment ended (April–July 2008; Fig. 8).

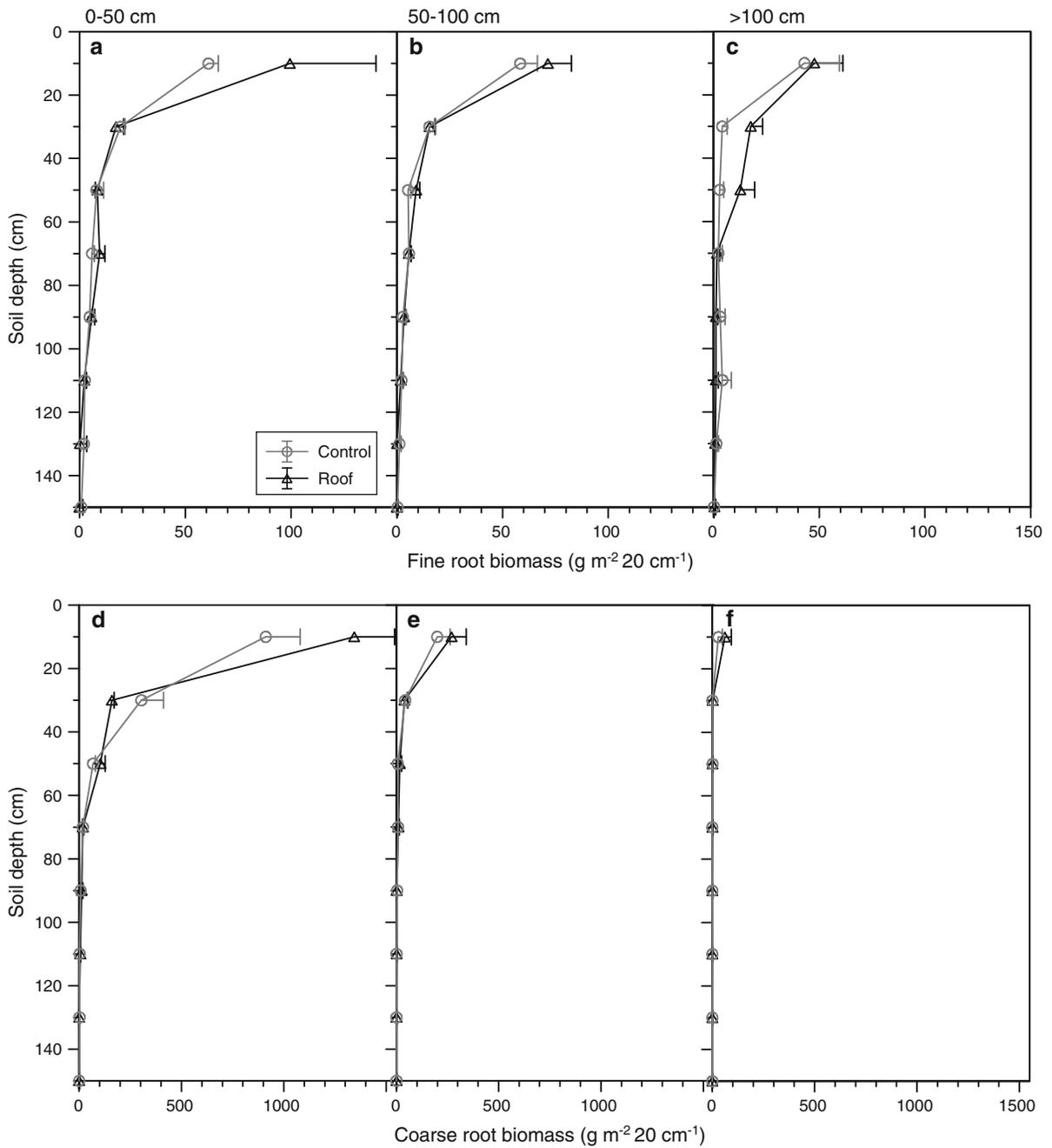


Fig. 5 Vertical distribution of fine (a–c) and coarse roots (2–150 mm diameter, (d–f) of cocoa in the roof and control plots at distances of 0–50, 50–100 and >100 cm from the stem base at the end of the experiment (June 2008). Mean values \pm SEM are shown ($n = 6$)

Discussion

Drought responses at leaf and stem levels

During the 13-month desiccation period, almost 80% of the throughfall which would normally have

occurred in the roof plots was intercepted and channeled outside the experimental plots, inducing a persistent depletion of soil moisture content and causing soil matric potential (Ψ_s) to approach permanent wilting point throughout much of the rooting profile. The duration of the drought period

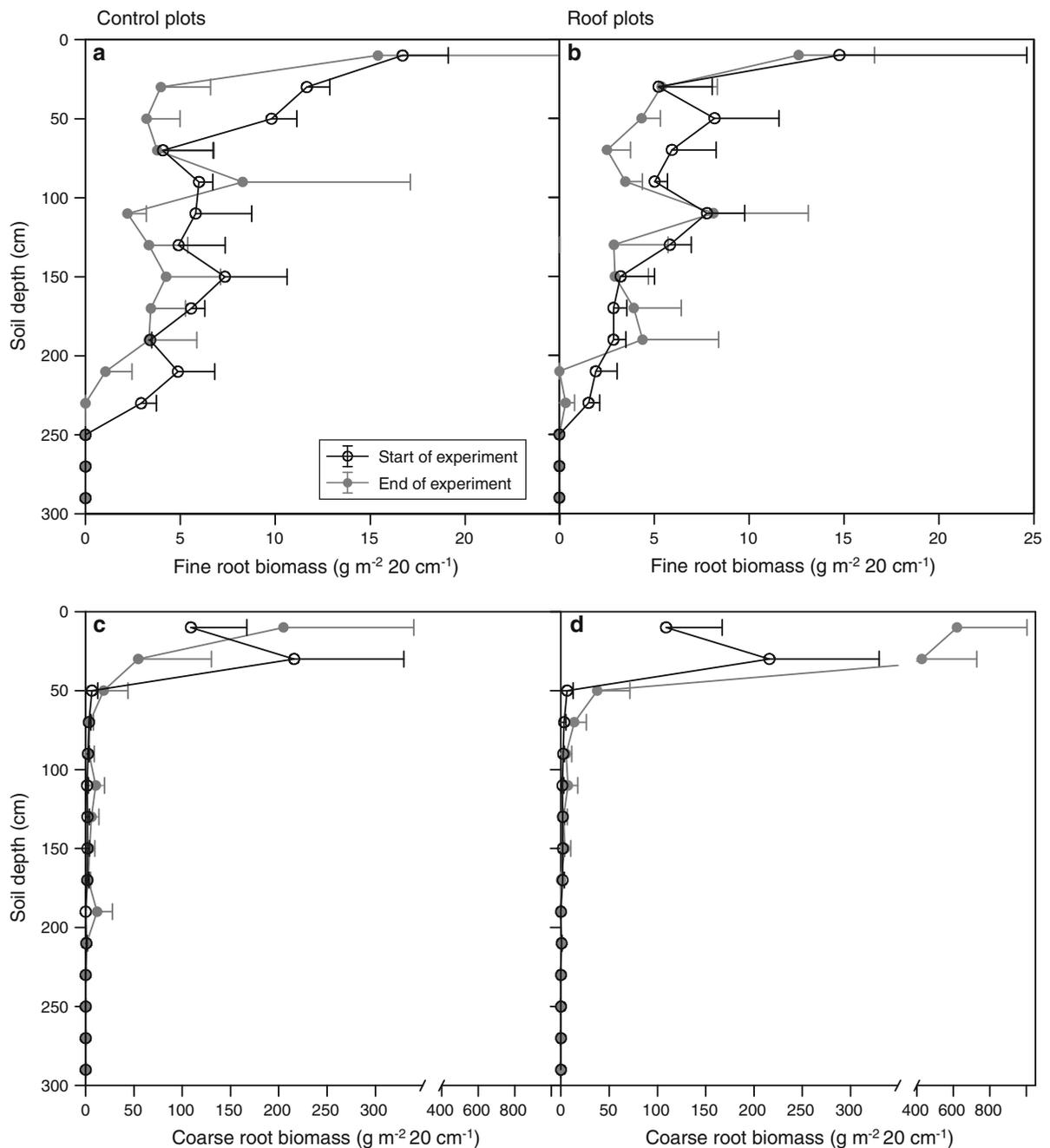


Fig. 6 Vertical distribution of fine (a + b) and coarse roots (c + d) of *Gliricidia sepium* at a minimum distance to the nearest tree of 1 m before (December 2006) and after (June 2008) the desiccation period in the control and roof plots. Mean values \pm SEM

approached or exceeded severe ENSO-drought events such as occurred in Kalimantan in 1997/1998 (Wooster and Strub 2002; Boyd et al. 2006). With respect to the physiological meaning of low soil matric potentials, the precise value of the ‘permanent

wilting point’ for cocoa remains unclear. However, independently of our drought intensity assessment based on Ψ_s , Schwendenmann et al. (2010) reached similar conclusions when calculating the fluctuation of ‘relative extractable water’ in the soil profile of the

Fig. 7 a and b Volumetric soil water content, and the water potential of coarse roots of cocoa and *Gliricidia* trees, and **c** the reduction in conductivity of cocoa roots prior to (February 2007) and during the early (July–September 2007) and late stages (March 2008) of the 13-month drought treatment. Box-whisker-plots with median, 25 and 75% percentiles and minima and maxima are shown. Asterisks denote significant differences in root water potential ($P < 0.05$) between the roof and control treatments

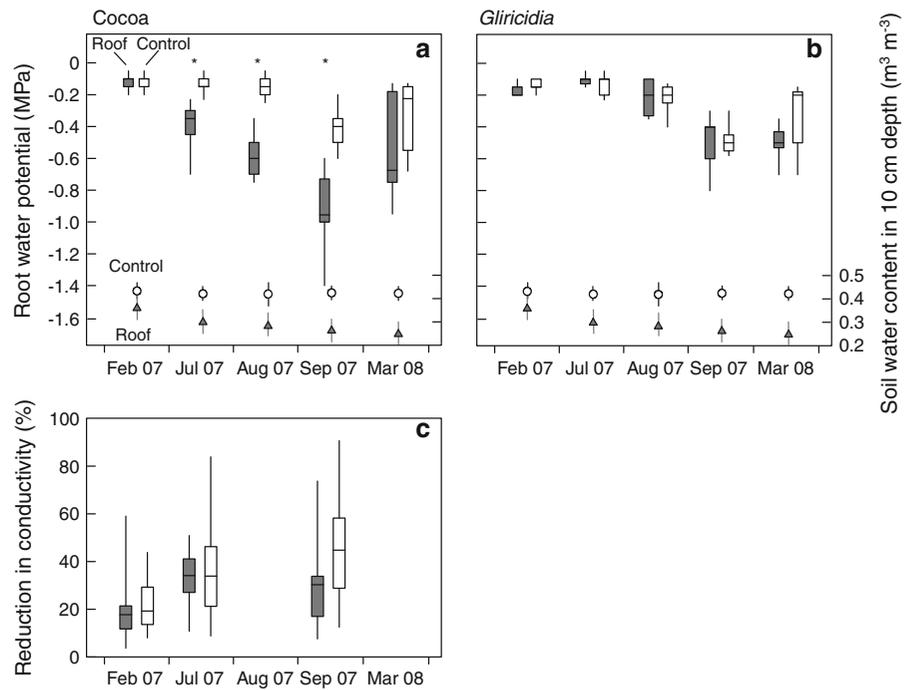


Table 3 Components of net primary production by cocoa and *Gliricidia* trees between March 2007 and February 2008 in the roof and control plots ($\text{Mg ha}^{-1} \text{ year}^{-1} \pm \text{SEM}$, $n = 3$)

Biomass production	Control			Roof		
	Cocoa	<i>Gliricidia</i>	Total	Cocoa	<i>Gliricidia</i>	Total
Leaves	2.77 ± 0.09 ^a	3.91 ± 0.32 ^A	6.26 ± 0.23 ^z	2.98 ± 0.24 ^a	3.87 ± 0.41 ^A	6.85 ± 0.24 ^z
Cocoa beans	0.74 ± 0.18 ^a	N/A	0.74 ± 0.18 ^z	0.67 ± 0.03 ^a	N/A	0.67 ± 0.03 ^z
Pods without beans	2.43 ± 0.90 ^a	N/A	2.43 ± 0.90 ^z	2.20 ± 0.09 ^a	N/A	2.20 ± 0.09 ^z
Stem + branches	1.81 ± 0.21 ^a	1.20 ± 0.22 ^A	3.01 ± 0.32 ^z	2.35 ± 0.21 ^b	0.97 ± 0.31 ^A	3.32 ± 0.47 ^z
Roots	0.71 ± 0.08 ^a	0.59 ± 0.11 ^A	1.30 ± 0.14 ^z	0.93 ± 0.08 ^b	0.47 ± 0.15 ^A	1.40 ± 0.21 ^z
Total	8.46 ± 0.14 ^a	5.70 ± 0.32 ^A	13.74 ± 0.41 ^z	9.13 ± 0.57 ^a	5.31 ± 0.66 ^A	14.44 ± 0.53 ^z

Different letters indicate significant differences between roof and control plots ($P < 0.05$; lower case letters, cocoa; upper case letters, *Gliricidia*; Greek letters: total biomass). N/A represents ‘not applicable’

stand examined here using data for maximum observed water storage and actual soil moisture content. They identified a 9-month drought period during which pronounced water deficits were experienced, substantiating our assessment based on soil matric potential. Some fluctuation in subsoil water content was observed after closing the roofs in the present study which may have resulted from penetration of the remaining throughfall water to the subsoil, although fluctuation in soil moisture resulting from local infiltration would have been expected to be greatest in the surface soil horizon; however, this

would not have been monitored by the shallowest TDR probes installed at a depth of 10 cm. Stemflow is a less likely cause of fluctuations in soil moisture as this has been shown to comprise <2% of rainfall in cocoa plantations (de Miranda 1994; Dietz et al. 2006).

Neither cocoa nor *Gliricidia* showed significant increases in pre-senescent leaf shedding in response to drought, as leaf production was high in the roof treatment ($6.85 \text{ Mg ha}^{-1} \text{ year}^{-1}$) and both species maintained their leaf area throughout the desiccation period. The LAI of cocoa was ca. 3.8 in both

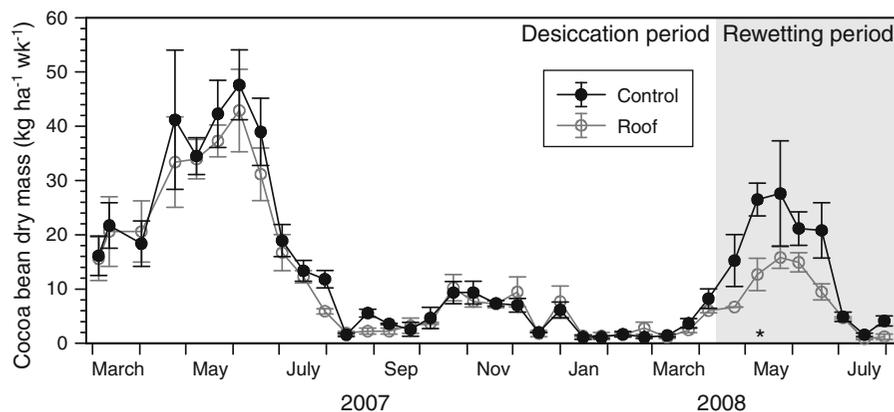


Fig. 8 Seasonal variation in the dry biomass of cocoa beans harvested at biweekly intervals between March 2007 and July 2008 (means \pm SEM; $n = 3$); the drought period extended

from March 1, 2007 to April 10, 2008. The asterisk in May 2008 denotes a significant difference between the roof and control treatments ($P < 0.05$)

treatments, close to that reported for a shaded cocoa plantation in humid Bahia, Brazil (3.9; Miyaji et al. 1997). In many tropical and temperate tree species, pre-senescent leaf shedding and permanent reductions in leaf area represent early responses to drought, as observed during ENSO-droughts in South-east Asian lowland forests (Kogan 2000; Nagai et al. 2007), or in a throughfall reduction experiment in a tropical lowland forest in Amazonia (Nepstad et al. 2002). According to Zuidema et al. (2005), the rates of leaf production and abscission in *Theobroma* depend largely on the water and light regimes. The present observations contrast with previous studies in which reductions in leaf area in cocoa during severe drought (Orchard and Saltos 1988) were accompanied by decreased CO_2 assimilation (Hutcheon 1977), flowering and yield (Sale 1970; Khan et al. 1988).

The absence of reductions in stem and branch wood production in cocoa and *Gliricidia* in the present study is surprising. Unlike temperate trees, which often show reductions in stem increments with a lag phase of up to 1 year following drought, woody species in tropical perhumid climates frequently exhibit woody growth responses within two or 3 months after the beginning of a dry period (Schöngart et al. 2005). However, there is little information concerning seasonal woody growth dynamics in cocoa, whose seedlings exhibit alternating phases of shoot and root growth (Taylor and Hadley 1987), suggesting that phases of enhanced wood and/or leaf growth coincide with periods of reduced root growth. Further research involving

synchronous monitoring of root and stem growth during periods of drought are needed to elucidate this possibility.

Drought response of roots

The estimated total fine root biomass (diameter < 2 mm) for cocoa ($62\text{--}84$ g m^{-2}) for the Mareña plantation is comparable to the values of $40\text{--}80$ g m^{-2} reported by Kummerow et al. (1981, 1982), but is lower than those obtained by Muñoz and Beer (2001) and Hartevelde et al. (2007) for shaded cocoa plantations ($100\text{--}185$ and ca. 220 g m^{-2} , respectively). Hartevelde et al. (2007) concluded that cocoa agroforestry systems in Sulawesi maintain a much smaller fine root biomass than the native tropical moist forests they have replaced (ca. 400 g m^{-2}). Possession of a small fine root biomass might increase the drought susceptibility of *Theobroma* by reducing its ability to absorb water but, perhaps more importantly, the fine roots of cocoa were located primarily in the upper soil horizons where they are rapidly exposed to drought. Indeed, Silva and Kummerow (1998) reported a mean functional life of only 3 days for the finest roots (< 1 mm diameter), with growth rate being closely dependent on rainfall frequency; the number of root tips was also significantly reduced during the drier months (Kummerow et al. 1982).

Excavation of the tree roots to a depth of 3 m showed a pronounced vertical root stratification for cocoa and *Gliricidia* as the fine roots of the former

were concentrated in the 0–40 cm horizon, while those of the latter were more evenly distributed and reached to greater depth. The use of deuterium as a natural tracer in this stand showed that these species absorbed water from different horizons (Schwendenmann et al. 2010) as the δD signature, i.e. the deuterium to H ratio in the water molecules, measured for xylem sap in February 2007 suggested that water uptake by cocoa occurred primarily in the 0–30 cm horizon, whereas *Gliricidia* obtained most of its water from depths >30 cm. Despite their contrasting root architecture, no inter-specific variation in drought sensitivity was apparent and neither cocoa nor *Gliricidia* showed significant reductions in fine root biomass in the roof treatment. However, as only standing root biomass was examined, effects of drought on the turnover rate of fine roots cannot be excluded.

The measurements of apparent vessel embolism and water potential (Ψ_r) in the xylem of cocoa roots suggest that they remained hydraulically active throughout the desiccation period, but responded to drying soil by increasing the soil-to-root water potential gradient. The much larger decrease in Ψ_r as desiccation progressed in the roof treatment compared to control trees suggests that the roots of cocoa underwent active osmotic adjustment, which may represent an effective adaptive trait to minimize the impact of drought.

Drought effects on cocoa bean yield

While only 7–9% of the annual net primary production (NPP) of cocoa trees was invested in the production of beans (Table 3), this carbon sink appeared particularly sensitive to drought as bean yield was significantly reduced after a lag period of several months in the roof treatment, whereas leaf, stem wood, branch wood and root growth were unaffected (Fig. 8). There are reports that bean yield in cocoa is strongly affected by low rainfall (Zuidema et al. 2005) and variation in the depth of the water table (Leite and Cadima Zevallos 1991). As cocoa pods require 6–7 months to mature, the observed decline in bean yield in May/June 2008 may have resulted from reduced fruit set and ripening during the period of most intense drought between November 2007 and March 2008. Similarly, Alvim (1988) suggested that production of coffee beans may

depend on rainfall distribution during the preceding six-month period. Simulations by Zuidema et al. (2005) suggested that annual radiation and rainfall during the dry season explained 70% of the variation in annual bean yield in 30 cocoa plantations throughout the tropics.

There is extensive evidence of substantial reductions in cocoa bean yield in ENSO-drought years in Sulawesi and adjacent regions of South-east Asia (Keil et al. 2008). Socio-economic studies of the consequences of ENSO-related droughts for cocoa production in Central Sulawesi revealed that bean harvests in ENSO years may be reduced to 62% relative to the normal level (Keil et al. 2008). ENSO droughts have caused the death of many cocoa trees in the area and significantly increased infestation by pests in others (N. Binternagel and H. Faust, pers. comm.). Spatial analyses of these socio-economic results suggest that the drought sensitivity of *Theobroma* is markedly influenced by local soil physical conditions in Central Sulawesi.

Several factors may contribute to the finding that net primary production in cocoa was generally insensitive to the 13-month drought treatment with the exception of bean production, which showed the expected decline. First, the droughted trees may have exploited water reserves that were not monitored in the study, notably the remaining throughfall water which would have added moisture to the superficial soil horizons. However, this effect would have been limited because throughfall was reduced to ca. 20% of incident rainfall and stemflow is negligible in cocoa plantations (de Miranda 1994; Dietz et al. 2006). Further, local areas of moist soil may have stimulated the trees to produce long horizontal or vertical roots to access these water reserves, as has been reported for trees growing in semi-humid climates (Hauser et al. 1993); however, such effects have rarely been examined in perhumid climates such as Central Sulawesi. Considerable effort was devoted to searching for sinker roots which might provide access to water reserves in the subsoil. Complete excavation of two cocoa and one *Gliricidia* tree in the core zone of each plot, mostly situated over 8 m from the plot border, showed that the deepest tap root of cocoa reached a depth of 1.6 m in a control plot, while the coarse roots of *Gliricidia* penetrated no deeper than 2.5 m (data not shown). The capture of lateral water resources is highly unlikely due to the

large border zones around each plot, while the ‘mining’ of deep water reserves can be excluded for the excavated trees as none showed any reduction in aboveground productivity compared to control trees in response to the drought. Cocoa and *Gliricidia* therefore appear able to avoid severe desiccation despite the lack of deep or laterally extensive roots.

Second, cocoa showed a substantial decrease in root water potential during the desiccation, thereby improving root water uptake. While this decline in Ψ_r may be partly attributable to tissue dehydration, it may also suggest that cocoa can achieve significant osmotic adjustment within its roots, thereby helping to stabilise plant water status and sustain continued leaf, stem and root growth. Third, the overstorey *Gliricidia* trees are likely to have reduced water use by cocoa by shading its canopy (Valle et al. 1987), while competition for water was presumably limited by the spatial segregation of the root systems (Schwendenmann et al. 2010). A further possible explanation for the absence of any reduction in productivity may be that the experiment was not designed to reduce relative humidity in the stands, as happens during natural droughts. As daily mean relative humidity was ca. 80% for most of the desiccation period, an increase in atmospheric forcing of transpiration would not have occurred.

We conclude that the cocoa trees in the 6-year-old plantation shaded by *Gliricidia sepium* examined here showed unexpected tolerance of a 13-month experimental desiccation. Despite soil water content approaching permanent wilting point for several months in the roof treatment and the shallow fine root system of cocoa, no significant decrease in standing biomass or the productivity of leaves, stem and branch wood and roots was found relative to control trees. A possible explanation is that the permanent wilting point of cocoa trees may be lower than -1.5 MPa, the assumed value for non-woody crops (Lösch 2001). Further possible explanations include physiological adaptations such as active osmotic adjustment in roots, mitigation of drought stress by shading from *Gliricidia*, complementary use of water resources, the relatively high air humidity during the soil desiccation period, or access to additional water reserves in the top soil or deep soil horizons, although our root studies do not support the latter suggestion. The economic importance of our results lies in the observation that cocoa bean yield

was significantly reduced by drought, supporting earlier reports of substantial reductions in yields during ENSO-related drought events in South-east Asia.

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