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Water use characteristics of cacao and *Gliricidia* trees in an agroforest in Central Sulawesi, Indonesia

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Abstract

Water use characteristics of cacao (*Theobroma cacao*) and *Gliricidia sepium* shade trees were studied in an agroforest on Sulawesi, Indonesia. The objectives were: 1) to identify environmental and tree structural factors controlling water use, 2) to analyze the effect of shade tree cover on cacao water use, and 3) to estimate stand level transpiration. Sap flux density was measured in up to 18 trees per species and described with a Jarvis-type model. Model parameters suggested a 49% higher maximum sap flux density in cacao than in *Gliricidia* and species differences in the response to vapour pressure deficit and radiation. Tree water use was positively related to tree diameter in both species, but this relationship tended to differ between species. In cacao trees maximal tree water use increased with decreasing canopy gap fraction above the trees ($R^2_{adj} = 0.39$, $p = 0.04$). This was paralleled by an increase of cacao stem diameter and leaf area with decreasing gap fraction. Maximum water use rate per unit crown area of cacao was 13% higher than that of *Gliricidia*. At the stand level the average transpiration rate was estimated at 1.5 mm d^{-1} per unit ground area, 70% of which was contributed by cacao. We conclude that, in the given stand, species differed substantially in water use characteristics, while estimated stand transpiration is in line with findings from other studies for cacao stands. Shade trees may enhance stand transpiration through own water use and additionally by increasing water use rates of cacao trees.

Key words: Transpiration, Sap flux density, *Theobroma cacao*, *Gliricidia sepium*, Shade trees, Gap fraction

Introduction

Cacao (*Theobroma cacao* L.) is one of the most important perennial cash crops world-wide and is cultivated in many tropical regions. Cacao, being originally an understorey tree of rainforests in tropical America, is traditionally cultivated below the canopy of shade trees. Shade trees may originate from natural forest, secondary forest or may be planted at stand establishment. If shade trees are being planted as e.g. done on already deforested land, often fast growing potentially nitrogen fixing trees such as *Gliricidia* spp. and *Erythrina* spp. are chosen. Currently, there is a tendency to remove shade trees a few years after establishment, which may give higher cacao yields at least on a short term basis (Steffan-Dewenter *et al*., 2007).

However, a physiological production model (Zuidema *et al*., 2005) did not reveal a strong influence of moderate shading on cacao yield. Only when shade trees intercepted more than 60% of available light, a decrease in cacao yield by more than 30% was predicted. Model outcome rather suggested strong influences of radiation and rainfall during dry periods. The simulated drought related yield reduction was up to 50% (compared to potential yield) under low rainfall and adverse soil conditions. Shade trees can probably mitigate negative effects of droughts and low rainfall as shade reduces evaporative demand of cacao trees and may thereby reduce stress of cacao plants. On the other hand, shade trees may reduce the water available for cacao trees as shade trees in cacao cultivation enhance rainfall interception loss and thus increase stand evaporation (Dietz *et al*., 2006; Poppenborg and Hölscher, in press). Also, shade trees can increase stand transpiration through their own water use, as well as by enhancing transpiration rates of associated cacao trees. For coffee in Costa Rica, the estimated stand level transpiration of coffee grown with shade trees was on average twice as high as that of coffee grown without shade trees (van Kanten and Vaast, 2006). Coffee plants even showed higher transpiration rates underneath a shade tree canopy than grown in full sun, which was explained by an enhanced vegetative growth of coffee under shade (van Kanten and Vaast, 2006). Also for cacao trees in Ghana it was observed that biomass was higher under shade trees and in a given stand biomass increased with proximity to shade trees (Isaac *et al*., 2007).

Stand level evapotranspiration by a cacao plantation (>98% cacao trees) in Central Sulawesi, Indonesia, was 2.6 mm d^{-1} as derived from eddy covariance measurements (Falk, 2004). Comparing the cacao plantation with natural forest suggested that a much smaller fraction of the available energy was used for evapotranspiration. In a model based study for cacao with different shade tree species in Costa Rica (Imbach *et al*., 1989), evapotranspiration was of similar magnitude as for cacao on Sulawesi. To our knowledge only one study determined transpiration rates for cacao stands based on sap flux measurements (Colas *et al*., 1999). This study found comparatively low transpiration rates of cacao stands and little to no effect of the presence of a coconut palm overstorey.

The present study was conducted in an upland region of Central Sulawesi, Indonesia, which is the third largest country with respect to cacao bean production (FAO, 2009). We studied a 6-year-old cacao stand with *Gliricidium sepium* (Jacq.) Kunth ex Steud. agroforest. The stand can be considered young compared to the productive life span of cacao which may last 50 years, with highest yield being achieved at 25 to 30 years of age

(Montgomery, 1981 as cited in Olaiya *et al.*, 2006).). In this stand we applied xylem sap flux techniques to measure water use at the tree level. The objectives were: 1) to identify environmental and tree structural factors controlling water use in the two species, 2) to analyze the effect of shade tree canopy cover on cacao water use, and 3) to estimate stand level transpiration.

Methods

Study site

The study was conducted in the margin zone of the Lore Lindu National Park in Central Sulawesi, Indonesia, in the vicinity of the village of Marena (1.552°S, 120.020°E). Data from a nearby climate station (Gimpu, 5 km south of Marena at 471 m a.s.l.) collected between 2002 and 2006 showed an average annual temperature of 25.5 °C and an annual precipitation of 2092 mm y^{-1} (H. Kreilein, unpublished data). The soil type at the study site was described as a sandy-loam Cambisol. The studied agroforest is located at 560 m a.s.l. on a mild slope (8-12° inclination) about 30 m above the water level of a nearby river. Cacao grows under a cover of *Gliricidia sepium* trees, which originate from cuttings. The stand had a mean stem density of 1030 cacao and 325 *Gliricidia* stems ha^{-1} and covered a total area of 8400 m^2. Some coconut trees occurred scattered on the site (23 stems ha^{-1}). The leaf area index of the stand was 5.3 m^2 m^{-2}. Leaf area index for the cacao tree layer was estimated at 3.8 m^2 m^{-2} and for the shade trees in the stand at 1.3 m^2 m^{-2} (P. Propastin and S. Erasmi, unpublished data). During the study period, pruning of cacao trees was carried out in July and December 2007. *Gliricidia* trees have not been pruned during the study period. No other agricultural operations but harvesting the cacao pods every two weeks and manual weeding were conducted.

Micrometeorological and soil moisture measurements

Data on air humidity and air temperature (CS215), global radiation (CS300, Apogee Instruments Inc., Logan, UT, USA) and rainfall (ARG100, Environmental Measurements Ltd., Sunderland, UK) were gathered at a distance of 30 m from the study stand in an area where shade trees were absent at a height of 2 m above the canopy of cacao trees. Data were measured every 5 seconds, averaged and logged in 30 min intervals using a CR800 data logger. Measured global radiation values indicated that the global radiation sensor underestimated real values from October 2007 onwards because of sensor malfunctioning. Based on reference measurements made with two other sensors in June 2008 a correction factor was determined and applied to the data from October 2007 onwards. Therefore, data obtained after October 2007 on global radiation should be taken with caution. At the study site, volumetric soil water content was continuously measured with time domain reflectometry probes (CS616). We installed 8 and 6 probes at 10 and 75 cm depth respectively in 8 soil pits in proximity to the trees studied. Two soil pits could not be equipped with probes at 75 cm due to high stone content. Data were logged hourly with a CR1000 logger. The probes were calibrated for the local soil following the procedure described in Veldkamp and O'Brien (2000). The calibration equation derived was:

$$\theta = 0.0003\tau^2 + 0.0173\tau - 0.3494$$

Where θ (m^3 m^{-3}) is the fractional volumetric soil water content and τ (µs) is the output period of the TDR probe.

Unless otherwise stated, equipment originated from Campbell Scientific Inc., Logan, UT, USA.

Sap flux measurements

Sap flux density was measured with thermal dissipation sensors constructed after Granier (1987). A sensor consisted of a pair of probes with a diameter of 1.5 mm and a length of 24 mm. The probes were inserted in tightly fitting aluminium tubes after heat conductive paste was applied to the probe. These were then inserted into predrilled holes in the outermost xylem spaced on average 14 cm apart in a vertical direction. In cacao the vertical spacing varied at times slightly because of the rough architecture of the cacao bark which was covered with wounds, flowers and old pod peduncles. Two thermal dissipation sensors were installed per tree at the north and south side of the trunk at 130 cm height above the ground in *Gliricidia*. In cacao the sensors needed to be installed below the branching point (jorquette) which was located around 60 to 100 cm above the ground. Sensors were shielded by a box made from insulating Styrofoam and a section of the stem, extending well above and below the installation point, was covered in reflective foil and plastic foil. This protected sensors against damage, prevented rainwater entering the setup and limited temperature gradients caused by incident solar radiation heating the trunk.

The upper probe of each sensor was heated with a constant power of 250 mW. Temperature difference between the two probes of each sensor was measured every 30 seconds, averaged and stored every 30 min (CR1000 data logger and AM 16/32 multiplexer, Campbell Scientific Inc., Logan, UT, USA.). The temperature difference was converted to sap flux density (J_s in g cm^{-2} h^{-1}) according to an empirically derived equation of Granier (1987).

Sap flux density was measured continuously for a 13 month period from February 1st 2007 to February 29th 2008. If sap flux data for single trees was incomplete during a day due to power outage or maintenance the specific tree did not enter the calculations on the respective day. If more than 3 trees per species were not available we did not include the whole day in our species comparison and the calculation of monthly averages (see Tab. 4 for the number of days entering the calculations per month).

During the first month of the study 18 individuals were available per species. Structural characteristics of the trees studied are shown in Tab. 1. Presented relationships between tree water use and tree structural characteristics as well as application of the sap flux model were based on data collected in February 2007. This way we could make use of the 18 replicates. From March 2007 onwards half of the individuals were subjected to drought treatments (Schwendenmann *et al.*, in review). The data presented on water use characteristics over the entire study period were based on the 9 individuals per species growing under ambient conditions.

Sap flux model

The species-specific response towards driving forces of sap flux was described using a sap flux model in analogy to the work of O'Brien *et al.* (2004). In this way the extensive dataset was condensed to a set of few parameters which allowed a straightforward comparison between species. The model was not used to make any predictions of sap flux densities. Preliminary correlation analyses revealed that J_s was highly correlated to R_g and VPD, but not to soil moisture which was therefore omitted from the model. The specific model form used is a modification of the Jarvis model (Jarvis, 1976) and has also been used by Dierick and Hölscher (in press). This model explains sap flux density J_s (g $\mathrm{cm^{-2}\,h^{-1}}$) by global radiation R_g (J $\mathrm{m^{-2}\,s^{-1}}$) and vapour pressure deficit VPD (kPa):

$$J_{s\,model} = a \cdot \frac{R_g}{b + R_g} \cdot \frac{1}{1 + \exp^{\frac{c - \mathrm{VPD}}{d}}}$$

Modelled sap flux density $J_{s\ model}$ reaches a maximum value a (g $\mathrm{cm^{-2}\,h^{-1}}$) when all environmental conditions are optimal. Parameter b (J $\mathrm{m^{-2}\,s^{-1}}$) can be interpreted as a measure of the light saturation level. Assuming VPD is non-limiting, sap flux density reaches just over 90% of the maximum sap flux density a if radiation levels equal ten times parameter b. Parameter c (kPa) equals the vapour pressure deficit for which $J_{s\ model}$ rises to half of the maximum value (R_g non-limiting), whereas d (kPa) is related to the slope i.e. the increase in $J_{s\ model}$ for a given increase in VPD. Model parameters a, b, c and d in the response functions were estimated by minimizing the residual sum of squares using a Gauss-Newton algorithm.

Sapwood area and tree water use

The estimation of water use (Q) for individual trees was based upon the sapwood area of the tree and the radial changes in J_s present in the sapwood. We used two approaches to estimate both the extent and the activity of conducting sapwood in the trunk cross-section.

Sapwood depth was determined for trees in the same stand by means of a dye staining experiment. Seven cacao and 14 *Gliricidia* trees, different from the trees used for sap flux measurement, were selected and sapwood depth was estimated at the respective installation height of the Granier sap flux sensors. It was decided to use a larger sample for *Gliricidia* because trees were more variable in shape and size than cacao. At noon on a bright day a 2.3 mm hole was drilled towards the centre of the stem of each tree and an Indigocarmin solution was injected into the drill hole. Three hours later a wood core was taken 50 mm above the injection point using an increment borer. The length of the coloured section of the wood core was measured to the nearest millimetre and taken as an estimate of sapwood depth (Andrade *et al.*, 1998; Meinzer *et al.*, 2001).

To assess sapwood activity with increasing depth under the cambium, profiles of radial sap flux density were measured in 8 trees per species for 10 days. These trees were mostly individuals that were also being used in the long term sap flux measurements. We employed again two sensors per tree, one of which remained at a depth of 0-24 mm below the cambium (reference depth) and the other was installed at the opposite side of the stem at 24-48 mm (2nd depth) below cambium. When measuring radial profiles it was necessary to select trees with a sufficiently large diameter to avoid that the two sensors would influence each other by heat conduction. Other studies (e.g. Delzon *et al.*, 2004) overcame this problem by placing the two sensors at a sufficient axial distance to each other. Since the cacao trees had a very low branching point and many of the *Gliricidia* trees showed disturbances in the lower parts of the trunk due to former management practices we could not opt for this method. A deeper installation at 48-72 mm (3rd depth) was not applicable since the installation depth would exceed the radius of most of the cacao trees. In large *Gliricidia* trees sensors installed at this depth would be in close proximity and potentially influence each other. In addition the staining experiment revealed heartwood formation at limited depth in large *Gliricidia* trees (see result section). To our knowledge there is no information available in literature on radial profiles of sap flux density for the species studied.

Upscaling from a point measurement (sensor) to the tree level water use was done by summing water flow in a number of ring-shaped stem cross sections (Edwards *et al.*, 1996):

$$Q = \sum_{i=1}^{i=n} Q_i \quad with \quad Q_i = \frac{J_{sc\,i}\, A_i}{1000}$$

Where Q (kg d^{-1}) is the water use per tree, Q_i the water flow through ring i, $J_{sc\,i}$ (g cm^{-2} d^{-1}) is the cumulative sap flux density and A_i (cm^2) is the ring-shaped area of sapwood that extents between the tip and the end of each probe for a given depth interval i. Thus we have an outer (reference depth) and an inner ring-shaped area (2nd depth). Except for large *Gliricidia* trees (diameter > 12 cm), the stem cross section consisted mainly out of sapwood. Radial profiles of sap flux density usually show a declining of Gaussian shape with depth regardless of wood anatomy (Phillips *et al.*, 1996). Therefore, if sapwood extended beyond the probe tip of the deepest sensor we approximated the remaining part of the profile assuming that the sap flux density declined linearly from the tip of the deepest probe to zero at the depth where heartwood formation was expected. In large *Gliricidia* trees where sapwood was about 25 mm deep and extended just beyond the sensor, tree water use was determined assuming a uniform sap flux density in the sapwood. With no additional data on the sap flux density profile available, this assumption seems reasonable. Moreover, sap flux sensors are expected to integrate flux differences over their length (Granier *et al.*, 1994; but see Clearwater *et al.*, 1999).

Water use rates of individual trees (kg d^{-1}) were also expressed per unit crown projection area of that tree to yield tree level transpiration rates (T_{tree}, mm d^{-1}). The stand transpiration rate (T_{stand}, mm d^{-1}) expressed per unit ground area was calculated following Garcia Santos (2007). We derived daily relationships between measured tree water use rates and tree diameters for both species, inserted the known diameters of all other individuals of the plot into the respective equations, summed the calculated water use rates of all trees and divided the result by the area of the plot.

Tree dimension, leaf area and gap size above cacao trees

For trees where sap flux was determined, tree diameter was measured between upper and lower probes of the sap flux sensor (60-130 cm above ground) with a tape measure. Tree diameter for other trees on the study site was measured at 80 cm height for cacao (low jorquette) and at 130 cm height for *Gliricidia*. Tree height was measured for the studied trees by means of a measuring stake.

Additional data was collected for trees in which sap flux density was studied in the period from October 2007 to mid December 2007. Crown projection area of trees was estimated by measuring the distance from the stem to the edge of the crown in eight cardinal directions. The crown projection area of a tree was calculated as the sum of eight triangles centred around the stem. Tree leaf area (m^2) was estimated for cacao trees in which sap flux density was measured. To do so the number of leaves of each tree was counted and multiplied with the average area per leaf determined from 50 randomly sampled leaves. Also the gap fraction above studied cacao trees was determined. Hemispherical photographs were taken vertically upward above each of the 9 study trees with a high resolution digital camera (Coolpix S3 and EC-F8 fisheye lens, Nikon Coop. Tokyo, Japan). The camera was placed in a levelling device (Regent Instruments Inc., Saint-Foy, QC, Canada) which in turn was mounted on top of a telescopic tripod. Images were analysed for gap fraction within an angle of 10° from azimuth with CanEye 5.0 (INRA, 2007).

Statistical analyses

The relationships between sap flux density and environmental variables (R_g and VPD) and between water use and tree structural parameters were tested with linear regressions. The response of sap flux density to changes in environmental parameters was evaluated with the above mentioned non-linear model. In analogy to linear models we calculated an adjusted R^2 for this non-linear model. Additionally root mean square error (RMSE) is given to judge model performance. Species differences in estimated model parameters, sap flux and water use were evaluated using a two sided Welch's t test with a level of significance of $p \leq 0.05$. The statistical analyses were conducted with R version 2.8.0 (R Development Core Team, 2008)

Results

Micrometeorological and soil moisture measurements

Rainfall during the first 12 months of the study equalled 2937 mm. All months received over 100 mm of rain except for January 2008 where rainfall was only 44 mm (Tab. 2). The average volumetric soil water content ranged from 0.38 to 0.45 $m^3 m^{-3}$ depending on depth and time of observation. Average daily air temperature was between 23.5 and 25.1°C and the average daily vapour pressure deficit (VPD) ranged from 0.6 to 0.8 kPa (day- and nighttimes were not considered separately). Integrated daily global radiation (R_g) varied from 15.8 to 20.4 MJ $m^{-2} d^{-1}$.

Sapwood area and radial profiles of sap flux

For cacao, the staining experiment revealed that the stem cross section consisted almost entirely of conducting sapwood. Only the very central portion (< 1 cm radius) of the stem was left uncoloured in all studied individuals. Also in sampled *Gliricidia* trees up to 12 cm diameter (4 individuals) staining showed that the stem was mainly composed of sapwood. In *Gliricidia* trees with a larger diameter (10 individuals) only the outer 25 mm of the xylem were active in water transport, indicating that heartwood formation occurred in these larger trees. The heart and sapwood could also be distinguished based on wood colour.

In cacao trees the sap flux density at a depth of 24 to 48 mm below cambium was on average 82% of the sap flux density in the outer reference depth. In *Gliricidia* average normalized sap flux density at that depth was 62%.

Sap flux and sap flux model parameters

Diurnal patterns of sap flux density observed in cacao and *Gliricidia* differed (Fig. 1). In *Gliricidia* sap flux density increased rapidly after sunrise and reached a maximum early in the day. Near-maximal sap flux densities were then maintained for several hours and sap flux only declined in the late afternoon. In contrast, sap flux density in cacao showed a later rise after sunrise, reached a maximum later in the day and started to decline around midday so that a pronounced plateau was absent. Average daily maximum sap flux density in *Gliricidia* (22.5 ± 5.2 g $cm^{-2} h^{-1}$) was significantly lower than in cacao (31.1 ± 8.6 g $cm^{-2} h^{-1}$). Nevertheless, there were no significant differences in daily integrated flux which was 151.9 ± 36.5 and 149.9 ± 37.7 g $cm^{-2} d^{-1}$ for cacao and *Gliricidia* respectively. We assume that nighttime sap flux densities were negligible as temperature outputs of the thermal dissipation sensors returned to stable values most night suggesting that refilling of internal reserves was completed. Moreover, VPD was close to zero because of rainfall which occurred during most nights.

The sap flux model predicted half hourly flux densities satisfactorily (Tab. 3). For individual trees R^2_{adj} ranged from 0.88 to 0.96 for cacao and from 0.93 to 0.96 for *Gliricidia*. The estimated model parameters for individual cacao trees were in general more variable as for *Gliricidia* trees (Tab. 3). For a single *Gliricidia* tree estimated model parameters showed outlying values, although the model fit for that specific tree was appropriate. The differences in measured maximum flux density between the two species were reflected in model parameter *a,* which was on average 29.8 and 20.0 g $cm^{-2} h^{-1}$ for cacao and *Gliricidia* respectively. Also the other model parameters, which determine the shape of light and VPD responses, differed significantly between cacao and *Gliricidia*. Higher values of *b* indicated higher light requirements for cacao, while higher values of *c* and *d* for cacao suggested that sap flux in *Gliricidia* responded earlier to increasing VPD than did sap flux in cacao.

Daily integrated sap flux density (average over 18 individuals) showed a strong linear relationship with both daily average VPD and the daysum of R_g (Fig. 2). The relationship with VPD gave values for R^2_{adj} of 0.83 and 0.76 for cacao and *Gliricidia* respectively ($p < 0.001$). The relationship with R_g was weaker in both species with an R^2_{adj} of 0.70 for cacao and 0.56 for *Gliricidia*. Similar graphs covering the whole study period revealed that daily integrated sap flux density saturates at days with higher VPD. The analysis of data obtained in January 2008, a month characterised by low precipitation and relatively low soil moisture content, showed no clear effect of soil moisture on the relationship between daily integrated sap flux and VPD. This indicates that soil moisture was not limiting during the study period.

Water use and transpiration in relation to tree characteristics

Over the 13-month study period, daily water use rates (Q_{mean}) of cacao trees averaged 10.0 kg d^{-1}, while values for *Gliricidia* trees were in general higher and averaged 14.0 kg d^{-1} (Tab. 4). Averaged over the individuals, the maximum daily water use rate (Q_{max}) was 17.3 kg d^{-1} in cacao and 23.0 kg d^{-1} in *Gliricidia*. In both species maximum water use rates were positively correlated with tree diameter (Fig. 3). In cacao there was also a significant relation between tree height and maximum water use ($R^2_{adj} = 0.31$, $p = 0.010$, not shown). For *Gliricidia* this relationship was not significant ($R^2_{adj} = 0.14$, $p = 0.070$).

In cacao maximum tree water use was positively correlated to leaf area measured in October-December 2007 ($R^2_{adj} = 0.72$, $p = 0.002$, $n = 9$). Increasing openness of the overstorey canopy (gap fraction) also influenced maximal tree water use rates in cacao. Maximum water use in cacao trees increased significantly with decreasing gap fraction ($R^2_{adj} = 0.39$, $p = 0.04$). This trend was particularly clear at gap fractions above 0.5. Tree diameter and leaf area also increased with decreasing gap fractions and had values for R^2_{adj} of 0.33 ($p = 0.062$) and 0.34 ($p = 0.057$), respectively. In *Gliricidia* maximum water use tended to increase with increasing crown projection area ($R^2_{adj} = 0.33$, $p = 0.061$).

Average tree level transpiration over the study period varied strongly between individuals. It was between 0.3 and 1.1 mm d^{-1} (average 0.51 mm d^{-1}) for cacao trees and 0.1 to 1.3 mm d^{-1} (average 0.46 mm d^{-1}) for *Gliricidia* trees (Tab. 4). Stand level transpiration averaged 1.5 mm d^{-1} over the 13 month study period to which cacao trees contributed 70%.

Discussion

Sap flux density and diurnal sap flux patterns

Measured maximum sap flux densities were 31.1 and 22.5 g cm^{-2} h^{-1} in cacao and *Gliricidia*, respectively and are comparable with observations made for different tropical tree species, belonging to a large number of genera, where maximum sap flux density is roughly between 5 and 40 g cm^{-2} h^{-1} (Granier *et al*., 1996; Meinzer *et al*., 2001). However, values as high as 70 g cm^{-2} h^{-1} have been reported (Becker, 1996; O'Brien *et al*., 2004). In 8-year-old cacao trees in Sumatra, Indonesia maximum sap flux densities were between 15 and 35 g cm^{-2} h^{-1} (Colas *et al*., 1999). For 2-year-old *Gliricidia* trees in an alley cropping system, maximum sap flux densities were around 20 g cm^{-2} h^{-1} (Tournebize and Boistard, 1997).

The diurnal course of sap flux differed between cacao and shade trees (Fig. 1). In cacao sap flux peaked late during the day and declined gradually after that. In contrast, sap flux in *Gliricidia* reached a maximum early in the day, followed by a plateau lasting for several hours. Physiological differences between the two species possibly contributed to this. Colas *et al*. (1999) observed a similar pattern in cacao where sap flux density reached a peak and then decreased gradually throughout the late morning and afternoon. This was explained by stomatal closure in cacao under conditions of high evaporative demand. However, the same study suggested that cacao trees in a monoculture were able to maintain high sap flux rates for a longer time when soil water availability was sufficient. Another possible explanation for the different diurnal courses of sap flux density is the different microclimate (R_g and VPD) to which cacao trees and *Gliricidia* trees are subjected. A recent study in coffee agroforestry systems (van Kanten and Vaast, 2006) provides strong indications of the influence of shading regimes and associated microclimate on diurnal sap flux patterns in coffee plants. During the dry season coffee plants under dense shade started reducing transpiration at higher VPD levels compared to coffee plants under light shade or in full sun. This was attributed to the distinct microclimate these coffee trees growing under a dense shade canopy experienced as a result of strong uncoupling from the bulk atmosphere.

Our data also provide indications for the role of microclimate on observed sap flux density patterns. Model parameters suggested higher light saturation levels in cacao compared to *Gliricidia*, which could result from a different canopy structure of both species. In a sparse canopy of well exposed shade trees, leaf illumination can be expected to become optimal under relatively low R_g. In the shaded and multi-layered canopy of cacao, individual leaves can still make use of increasing light levels even when R_g is already high, hence the higher value of b. The remaining model parameters c and d suggest a rise in sap flux density in *Gliricidia* under conditions of lower evaporative demand (VPD) compared to cacao. As in the study of van Kanten and Vaast (2006), this could reflect a stronger uncoupling of cacao trees from the atmosphere due to the effect of shade trees, although a stronger uncoupling at the leaf level (cacao has a larger leaf size as *Gliricidia*) could contribute to this as well.

Tree water use

Scaling of sap flux density data to tree water use rates gave, for the two species combined, maximum water use rates between 9.1 and 32.4 kg d^{-1} for trees with a diameter between 8.3 and 19.7 cm. This range of maximum water use rates is in agreement with observations for trees of similar diameter in four Australian rainforest types (McJannet *et al.*, 2007) and data presented for trees in mixed young tree plantations in the Philippines (Dierick and Hölscher, in press). The mean daily tree water use over the 13 month study period differed between the two species, being on average 10.0 kg d^{-1} in cacao trees compared to 14.0 kg d^{-1} in *Gliricidia* trees (Tab. 4). This difference can be attributed to the smaller average diameter of sampled cacao trees compared to *Gliricidia* trees (Tab. 1). Even though daily cumulated sap flux densities did not differ among species, higher water use rates are predicted for the larger *Gliricidia* trees due to a larger conductive sapwood area in large trees.

However, Fig. 3 clearly shows that both species exhibit a different relationship between estimated maximum water use and tree diameter. The lower water use rates in *Gliricidia* compared to cacao for trees of a given diameter are a consequence of the limited sapwood depth in larger *Gliricidia* trees. Differences in sap flux density do not play a role here as cumulated daily flux is almost identical for the two species. The different water use to diameter relation in cacao and *Gliricidia* would contrast with the hypothesis that tree water use scales universally with tree size and is essentially species independent (Meinzer, 2003; Meinzer *et al.*, 2005). Note however that the narrow diameter in this study potentially highlights the differences between the two species and that the latter statement should thus be taken with care. Fig. 3 also suggests that the relation between tree diameter and tree water use is weaker for *Gliricidia* than for cacao. This might be explained by a higher variability of the conducting sapwood area and/or incorrect assumptions on how sapwood activity declined with depth.

Maximum tree water use rates in cacao were negatively correlated to gap fraction, suggesting higher water use in trees with increased shading. Although the reverse could be expected, similar observations exist for coffee (van Kanten and Vaast, 2006). Coffee grown in full sun had higher transpiration rates when expressed per unit leaf area than coffee grown under shade trees, but the reverse was generally true when transpiration rates were expressed per unit ground area. The increased transpiration per unit ground surface of coffee under shade trees was attributed to increased vegetative growth. Also for cacao stands in Ghana enhanced vegetative growth under shade trees was observed (Isaac *et al.*, 2007). Under three shade tree species cacao tree biomass was higher (in two treatments this was significant) than in unshaded cacao trees. It was also found that cacao tree biomass decreased with increasing distance to the shade tree. The correlations we found for individual trees between gap fraction on the one hand and tree diameter and tree leaf area on the other hand, would suggest that also in our study enhanced vegetative growth under increased shading occurred. This enhanced vegetative growth in combination with increasing water use rates of shaded cacao trees suggests that shading could lead to increasing transpiration rates per unit ground area at stand level as the study of van Kanten and Vaast (2006) demonstrated. In addition, water use by the shade trees would further increase the total stand transpiration.

Transpiration rates

Tree level transpiration rates, i.e. tree water use expressed per unit crown area, were around 0.5 mm d^{-1} for both species with a high variability between individuals. In a secondary forest patch in Vietnam, estimated tree level transpiration rates were generally higher, between 0.4 and 2.9 mm d^{-1}, and also highly variable between individuals (Giambelluca *et al.*, 2003). The authors suggested a possible role of tree species, tree crown exposure, edge effect, vine infestation and leaf area index in explaining the different tree level transpiration rates.

During our study, the average stand transpiration rate in the cacao-*Gliricidia* agroforestry system was estimated at 1.5 mm d^{-1}. We only know of one study where transpiration in cacao was measured by means of xylem sap flux measurements. Also using the Granier method, Colas *et al.* (1999) estimated the transpiration in a cacao monoculture and cacao growing under coconut in Sumatra, Indonesia. In these stands transpiration was 1.2 and 1.3 mm d^{-1} in a monoculture and in association with coconut respectively.

Rather than transpiration rates, most literature on water relations in cacao stands provides estimates of stand evapotranspiration which includes evaporation from trees and litter layer after interception. Using eddy covariance techniques, evapotranspiration was determined experimentally for a mature cacao plantation near our study area in Central Sulawesi at 2.6 mm d^{-1} (Falk, 2004). For cacao with *Erythrina poeppigiana* and *Cordia alliodora* as shade trees in Costa Rica, Imbach *et al.* (1989) calculated a daily evapotranspiration of 2.7 to 2.8 mm d^{-1} respectively from pan-evaporation, a crop coefficient and measurements of rain interception. In a cacao stand under remaining forest trees in Sulawesi interception losses were estimated at 19% of gross precipitation (Dietz *et al.*, 2006). For the particular cacao agroforest where this study was conducted, interception was estimated to be around 14% (L. Schwendenmann and G. Moser, unpublished data). Taking into account the amount of rainfall during our study, approximately 1.1 mm d^{-1} evaporated back to the atmosphere after interception. When added to our estimate of stand transpiration, this would give an average evapotranspiration rate (2.6 mm d^{-1}) which is in good agreement with results from Falk (2004) and Imbach *et al.* (1989).

Conclusions

In the stand studied, water use characteristics of the two species differed substantially with respect to maximal sap flux density, response to atmospheric factors, and tree size relationships. The resulting transpiration rates at the stand level combined with estimates of rainfall interception are comparable to other observations of evapotranspiration. Remarkable was the influence shade trees may exert on stand level transpiration. Our data suggested that shade trees may increase enhance stand transpiration by their own water use and furthermore by enhancing water use rates of cacao trees.

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Tab 1. Structural characteristics of the trees studied (mean and standard deviation, n = 18).

Species	Diameter (cm)		Height (m)		Projected crown area (m^2)		Leaf area (m^2)		Sapwood area (cm^2)	
	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Theobroma cacao	10.1	1.6	4.5	0.8	20.2	8.5	34.3	14.2	68.1	22.9
Gliricidia sepium	15.0	2.5	10.9	2.1	40.4	27.5	57.3	29.7	95.5	11.4

Tab 2. Monthly rainfall, meteorological conditions and volumetric soil water content (means and standard deviations) as measured during the study period.

Month	Days (n)	Cumulated rainfall (mm)	Daysum R_g ($MJ\ m^{-2}\ d^{-1}$)		Mean daily VPD (kPa)		Mean daily air temperature (°C)		θ 10 cm ($m^3\ m^{-3}$)		θ 75 cm ($m^3\ m^{-3}$)	
			Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Feb-07	28	288	19.0	2.9	0.58	0.12	23.8	0.5	0.44	0.01	0.45	0.01
Mar-07	31	293	18.5	3.8	0.58	0.16	23.5	0.6	0.42	0.02	0.42	0.01
Apr-07	30	473	19.8	2.8	0.60	0.12	24.3	0.5	0.44	0.01	0.43	0.01
May-07	31	271	18.4	2.8	0.63	0.14	24.6	0.6	0.43	0.01	0.43	0.01
Jun-07	30	222	15.8	3.5	0.59	0.13	24.5	0.8	0.43	0.01	0.41	0.01
Jul-07	31	116	16.0	3.5	0.68	0.15	24.3	0.7	0.41	0.02	0.41	0.01
Aug-07	31	238	16.5	3.9	0.67	0.16	24.1	0.6	0.43	0.03	0.41	0.01
Sep-07	30	210	18.1	4.0	0.80	0.25	24.4	0.8	0.42	0.02	0.42	0.01
Oct-07	31	241	20.4	3.1	0.81	0.19	25.1	0.7	0.43	0.02	0.41	0.01
Nov-07	30	204	19.5	3.5	0.66	0.13	24.8	0.6	0.44	0.01	0.42	0.01
Dec-07	31	337	19.7	4.3	0.67	0.15	24.8	0.9	0.44	0.01	0.43	0.01
Jan-08	30	44	18.6	4.1	0.76	0.19	24.7	0.9	0.38	0.02	0.40	0.01
Feb-08	29	142	17.4	4.1	0.76	0.18	24.5	0.7	0.40	0.03	0.39	0.01

Tab 3. Estimated model parameters (28 days in Feb 2007) for cacao and *Gliricidia* trees (means and standard deviations, n = 18). Significant differences ($p < 0.05$) between species for the individual model parameters are indicated by different small letters.

Species	R^2_{adj}	RMSE		*a*		*b*		*c*		*d*	
	(-)	(g cm^{-2} h^{-1})		(g cm^{-1} h^{-1})		(J m^{-2} s^{-1})		(kPa)		(kPa)	
		Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
Theobroma cacao	0.94	1.58	0.39	29.8^{a}	8.17	192.5^{a}	107.59	0.8^{a}	0.15	0.2^{a}	0.06
Gliricidia sepium	0.95	2.13	0.57	20.0^{b}	4.30	79.6^{b}	33.08	0.5^{b}	0.14	0.1^{b}	0.05

Tab 4. Monthly averages of daily tree water use rates (Q) and transpiration at tree level (T_{tree}) for cacao and *Gliricidia* trees (n = 9 per species) over the study period. Also given is the estimated stand transpiration (T_{stand}).

Month	Days (n)	Mean Q (kg d^{-1})				Mean T_{tree} (mm d^{-1})				Mean T_{stand} (mm d^{-1})
		Theobroma cacao		*Gliricidia sepium*		*Theobroma cacao*		*Gliricidia sepium*		
		Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	
Feb-07	28	9.2	4.2	13.4	3.2	0.46	0.20	0.46	0.39	1.4
Mar-07	31	9.5	4.4	13.1	3.5	0.47	0.21	0.44	0.36	1.4
Apr-07	30	9.6	4.5	13.1	3.9	0.47	0.21	0.42	0.29	1.4
May-07	30	10.3	5.1	14.9	4.2	0.50	0.22	0.48	0.35	1.6
Jun-07	30	9.6	4.9	14.7	4.2	0.47	0.20	0.50	0.42	1.5
Jul-07	31	10.2	5.1	14.6	4.6	0.50	0.21	0.45	0.29	1.5
Aug-07	27	9.6	4.3	13.3	4.5	0.47	0.19	0.41	0.25	1.4
Sep-07	0	-	-	-	-	-	-	-	-	-
Oct-07	31	11.1	5.6	14.2	4.2	0.57	0.33	0.50	0.50	1.6
Nov-07	30	10.1	6.3	14.6	3.5	0.51	0.31	0.53	0.53	1.5
Dec-07	30	10.0	4.8	14.3	3.3	0.53	0.36	0.51	0.49	1.5
Jan-08	30	10.8	4.5	14.2	3.9	0.58	0.40	0.44	0.27	1.6
Feb-08	22	10.3	4.8	14.1	4.6	0.55	0.41	0.42	0.23	1.5
Overall		10.0	4.6	14.0	3.3	0.51	0.26	0.46	0.36	1.5

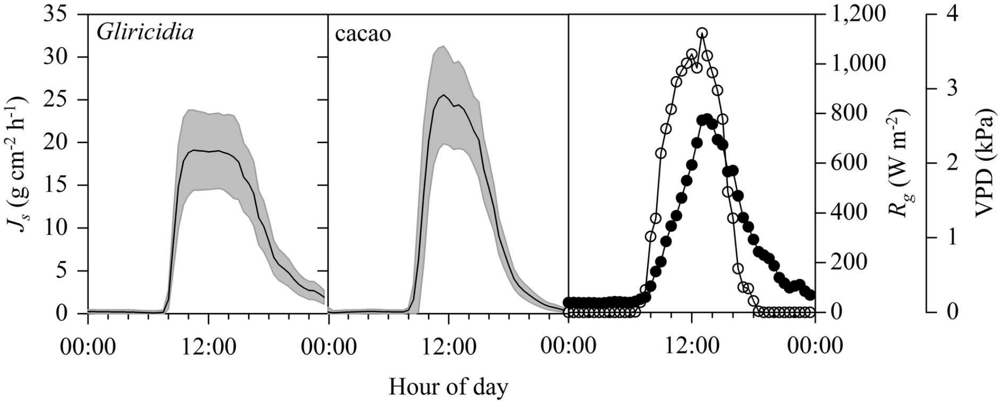

Fig 1. Course of mean sap flux density (J_s) in *Gliricidia* and cacao trees (n = 18 per species, means and standard deviation as shaded area) on a bright day (Feb/22/07) under moist soil conditions. Additionally global radiation (R_g, open symbols) and vapour pressure deficit (VPD, filled symbols) are given.

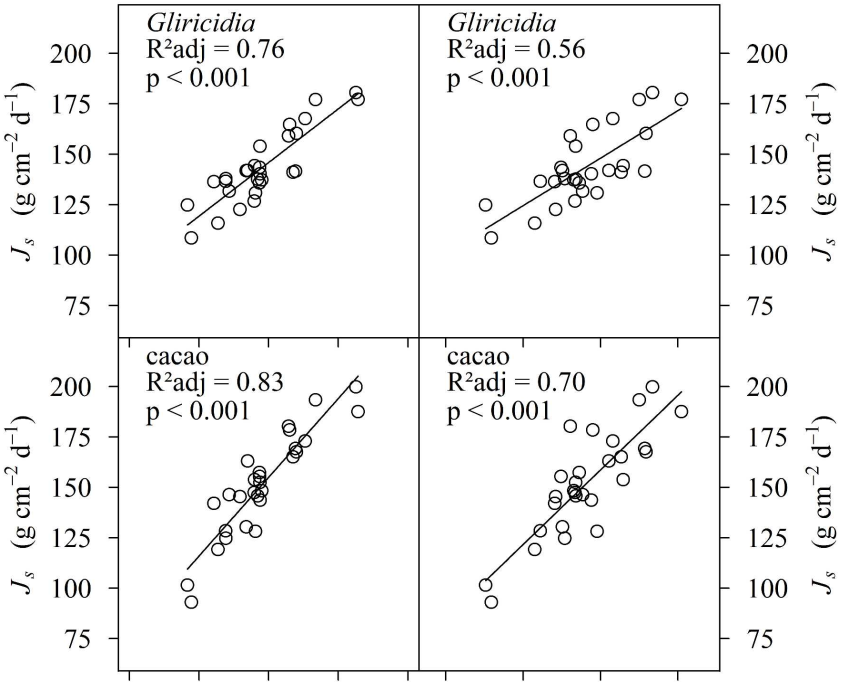

Fig 2. Average integrated daily sap flux of cacao (n = 18) and *Gliricidia* (n = 18) trees in relation to vapour pressure deficit (VPD) and global radiation (R_g) for a period of 28 days in February 2007.

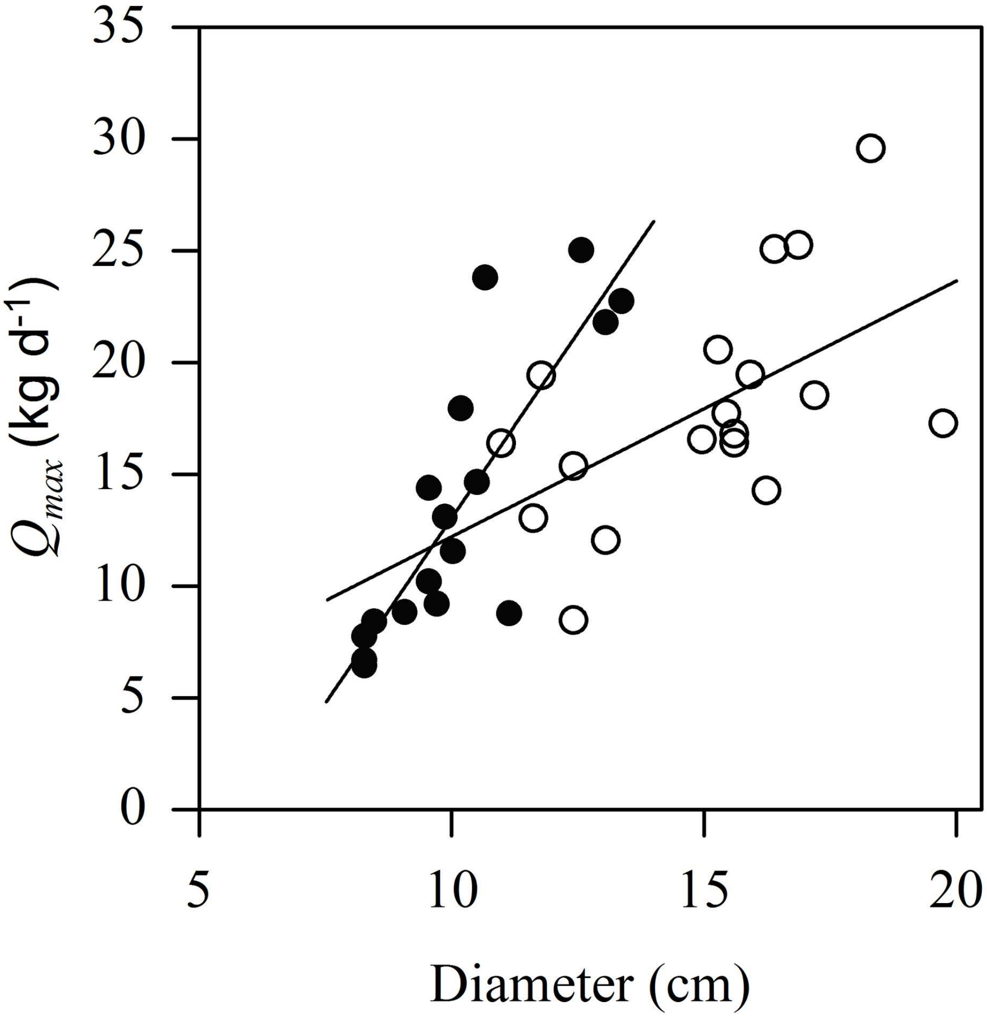

Fig 3. Relationship between tree diameter and average maximum water use (28 days in Feb 2007) for cacao ($R^2_{adj} = 0.68$, $p < 0.001$, closed symbols) and *Gliricidia* ($R^2_{adj} = 0.27$, $p = 0.016$, open symbols). Data from 18 trees is presented for both species.

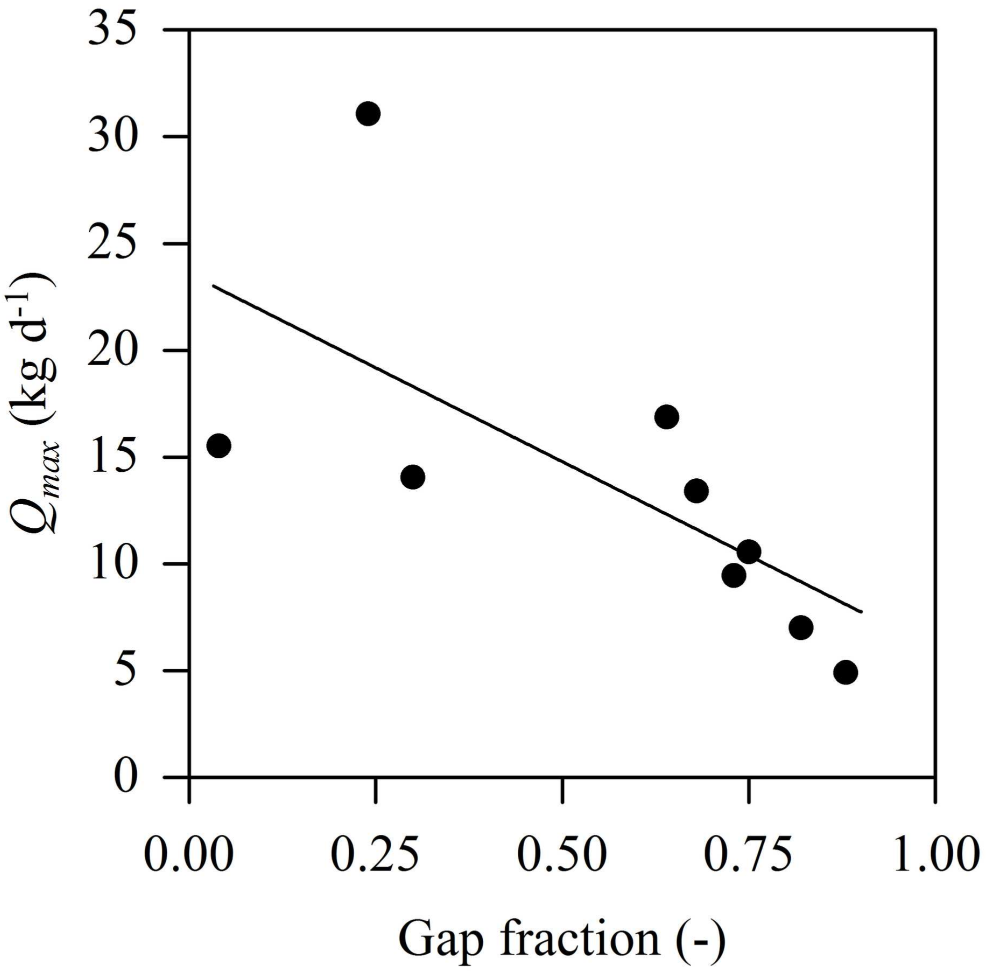

Fig 4. Gap fraction (-) above cacao trees and average maximum water use in cacao from October-December 2007 ($R^2_{adj} = 0.39$, $p = 0.043$, $n = 9$).