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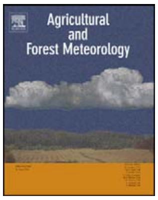

Species-specific tree water use characteristics in reforestation stands in the Philippines

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ABSTRACT

Reforestation in the tropics offers opportunities for restoration of ecosystem services, biodiversity conservation, wood production and carbon sequestration. The potentially high water use rates associated with reforestations will however require that a balance is found between wood production or carbon fixation and the use of water resources. Species selection has been put forward as a measure to control tree water use of reforested stands but species-specific information is at present very limited. We studied ten broad-leaved tree species in 12-year-old reforestations on Leyte island, the Philippines. Objectives were (1) to identify environmental and tree structural controls on water use and (2) to test for differences in water use characteristics across species. The studied species included eight native species, four of which were dipterocarps, and two species not native to the region but widely planted in the tropics. Per species five well-exposed individuals were equipped with thermal dissipation probes to measure sap flux density. A Jarvis-type model, with global radiation and vapour pressure deficit as explanatory variables, was applied at the tree level and successfully predicted measured sap flux densities. The model parameters suggested significant species differences in maximum sap flux density, differing twofold across species, as well as in sap flux response to environmental variables. Maximum transpiration rates per unit crown area varied up to a factor of four across species. Maximum water use rates were strongly related to tree diameter ($R^2_{\mathrm{adj}} = 0.65$) and weaker, though significant, to estimated aboveground biomass ($R^2_{\mathrm{adj}} = 0.34$). Despite its size dependence, tree water use rates differed about twofold for a given diameter or biomass depending on species, which leads us to conclude that species selection indeed offers opportunities to control tree water use in reforested stands.

1. Introduction

Fast paced conversion and destruction of tropical forests has led to an unprecedented decline in biodiversity and disruption of ecosystem services. At the same time, the need to supply local communities and global markets with wood products and other forest commodities remains. These factors have resulted in a strong demand for re- and afforestation in the tropics, which may therefore become a key activity in future tropical forestry. Conventional tree plantations with species from the genera *Pinus*, *Eucalyptus* and *Acacia* in single-species stands address the need for wood products but have been criticised for contributing little to ecosystem functioning and biodiversity (Lamb et al., 2005). In reaction to this, recent reforestation approaches in the tropics highlight the use of native species in mixed stands (Erskine et al., 2006; Petit and Montagnini, 2006), a strategy which can promote multi-functional use of forests creating stands that help restoring biodiversity, produce diverse wood products and sequester carbon.

A major objection to reforestation is the potentially high evapotranspiration rates of reforested stands which could in turn lead to reductions in streamflow and groundwater recharge (Bruijnzeel, 2004). From a global synthesis Farley et al. (2005) concluded that annual runoff was on average reduced by 44% and by 31% when reforesting grass- and shrubland respectively. Long-term catchment studies in South Africa revealed a clear pattern of increased evapotranspiration rates in plantation forests, resulting in reductions in available water resources and subsequent government regulation of the forestry sector (Dye and Versfeld, 2007). Stream flow reductions of up to 50% were observed in the Ecuadorian Andes (Buytaert et al., 2007) under *Pinus* plantations, while a water budget study in eucalypt plantations in the Atlantic rainforest region of Brazil showed that 95% of the precipitation (1147 mm yr^{-1}) was used for evapotranspiration (Almeida et al., 2007). Management options are being intensely discussed and an appropriate tree species selection is one of the first named options,

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as differences in tree physiology among species play a decisive role in plantation forest hydrology (Van Dijk and Keenan, 2007; Gyenge et al., 2008). However, this approach is largely theoretical because information on growth and water use rates exists only for a limited number of species. Also the effectiveness of species selection is under discussion as studies in old-growth forests (Meinzer et al., 2004; McJannet et al., 2007) and single species plantations (Cienciala et al., 2000) repeatedly showed that tree size and stand structure are the main factors influencing tree and stand level water use.

A landmark study on the relationship between tree size and water use characteristics included 24 co-occurring species in old-growth forest in Panama. Tree diameter was highly correlated with sapwood area ($R^2 = 0.98$) and with integrated daily sap flux in the outermost sapwood ($R^2 = 0.91$) regardless of species (Meinzer et al., 2001). This suggests that tree size rather than tree species determines tree water use characteristics. Subsequent analyses, including tropical and temperate angiosperms as well as temperate conifers, supported the hypothesis of size dependence of sap wood area and tree water use (Meinzer et al., 2005). The authors suggested that, as a result of functional convergence, plants operating within given biophysical limitations develop common patterns of sap flux and water use in relation to size characteristics across taxa (see also Meinzer, 2003). This would leave little room for species selection to serve as a tool to influence stand water use when wood production and carbon fixation are the main management objectives. However, other studies in old-growth forest did provide an indication that species differences in sap flux densities exist (Granier et al., 1996). Using a sap flux model, O'Brien et al. (2004) looked into responses of normalised sap flux density to environmental factors for ten co-occurring species with diverse traits in rainforest in Costa Rica. Statistically significant differences in responses of normalised sap flux between species were present, but the overall effect of species was judged to be small. Species differences in absolute sap flux density – which differed more than twofold – and tree water use were not assessed as sufficient data on absolute sap flux densities was lacking.

The above-mentioned studies addressed species differences in sap flux densities and water use characteristics using data gathered in old-growth forest. Such studies conducted in old-growth forest – typically with a diameter range well exceeding diameter ranges encountered in reforestations – may however not provide the most relevant information to plantation forestry. Also, co-occurring species in old-growth forest may occupy different niches in the forest stands and may thus be confined to different size classes and/or subjected to different environmental conditions. In young, even-aged and vertically little structured stands, traits other than diameter may affect tree water use more effectively than in old-growth stands.

Here we present a study on sap flux responses and tree water use in two 12-year-old multi-species stands in the Philippines. The objectives were (1) to identify environmental and tree structural controls on water use and (2) to test for differences in water use characteristics across species. To achieve this, we measured sap flux density using thermal dissipation probes (Granier, 1985) in ten broad-leaved tree species, eight of which were native to the region. Each species was represented by five well-exposed individuals. The measured sap flux patterns were linked to environmental variables using a Jarvis-type sap flux model (Jarvis, 1976) and model parameters were then examined to detect species-specific differences in sap flux density and sap flux responses to environmental factors. The relationship between tree water use characteristics and tree functional traits such as diameter was assessed taking into consideration tree species identity.

Table 1
Characteristics of the two study sites.

	Marcos	Patag
Exposition	WNW	W
Elevation (m asl)	30	40
Slope (%)	25	35
Plot size (ha)	0.26	0.33
Establishment (Year)	1994	1995
Tree height (m)	18.8	17.2
Stem density (n ha^{-1})	796	1367
Basal area (m^2 ha^{-1})	23.0	26.4
LAI (m^2 m^{-2})	5.2	6.0
Tree species (n)	40	33

Trees with DBH > 7 cm were included for the stand description.

2. Methods

2.1. Study site and species selection

This study was conducted on Leyte island in the Eastern Visayas, the Philippines. The two study sites were located in the lowlands adjacent to the Leyte Cordillera near the villages Marcos (10°45′55″N, 124°47′25″E) and Patag (10°44′10″N, 124°48′16″E) and sites will be referred to as such in the text. The sites were within four kilometres distance of each other and exhibited comparable site conditions and stand characteristics (Table 1). A climate station located at the Visayas State University, Visca at 2–3 km from the study sites shows that average rainfall in the region amounts to 2753 mm yr^{-1} (PAGASA, 2007). Rainfall is more or less evenly distributed throughout the year although less rain is received in the period from March to May during which average monthly rainfall remains above 100 mm (Fig. 1). Longer dry spells may occur during ENSO events. Average annual air temperature is 27.5 °C and varies little between months. A pronounced feature of the local weather patterns are typhoons which hit the region on average 19 times per year. The soils developed on volcanic parent material and were classified as Luvisol (Marcos) and Cambisol (Patag) by Marohn (2007). Soils were slightly acidic with a pH (KCl) at 0–10 cm depth of 4.2 in Marcos and 4.1 in Patag (C. Fisher, personal communication, 2008).

The natural vegetation in the region is species-rich lowland dipterocarp forest, but near natural forest only remains on the less accessible slopes of the Leyte Cordillera (Langenberger, 2006). After deforestation and intermittent cultivation of annual crops, coconut plantations were established. In a degraded state the study sites were reforested, following the so-called 'rainforestation' approach while maintaining the coconut present at the site. Rainforestation envisages increasing local livelihood while at the same time restoring biodiversity and essential ecosystem services

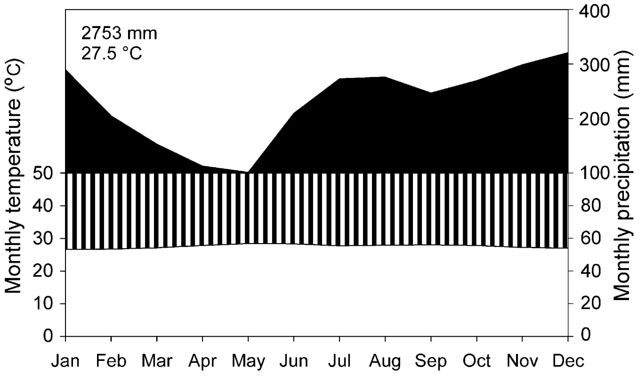

Fig. 1. Climate diagram for the study region based on data obtained at a nearby weather station between 1976 and 2006 (PAGASA, 2007).

Table 2
Characteristics of the study trees (means and standard deviations, $n = 5$).

Species	Family	Study site	Native or exotic	DBH (cm)		Tree height (m)		Crown area (m^2)	
				Mean	SD	Mean	SD	Mean	SD
Shorea contorta	Dipterocarpaceae	Patag	N	18.2	6.9	16.1	3.5	13.7	11.6
Parashorea malaanonan	Dipterocarpaceae	Patag	N	12.0	0.4	13.1	1.6	12.2	2.8
Hopea malibato	Dipterocarpaceae	Patag	N	11.6	2.4	13.3	1.8	10.1	6.1
Hopea plagata	Dipterocarpaceae	Patag	N	6.6	1.0	9.4	1.2	6.6	1.0
Swietenia macrophylla	Meliaceae	Patag	E	14.6	1.3	14.2	1.5	13.8	6.0
Vitex parviflora	Verbenaceae	Marcos	N	20.4	5.5	12.7	1.6	30.3	16.0
Myrica javanica	Myricaceae	Marcos	N	22.1	3.7	11.2	0.6	23.9	10.9
Sandoricum koetjape	Meliaceae	Marcos	N	16.3	2.7	13.2	1.0	17.4	5.4
Durio zibethinus	Bombacaceae	Marcos	N	19.8	7.3	13.8	3.0	32.7	20.6
Gmelina arborea	Verbenaceae	Marcos	E	21.9	4.0	18.1	2.4	16.7	9.0

such as the hydrological cycle (Margraf and Milan, 1996) and in particular targets smallholders. This is attempted by reforesting with a mixture of native species, promoting the incorporation of fruit trees and combining fast growing trees with shade tolerant species. In the Philippines this approach is considered promising and future extensions are planned.

At the time of the study the two stands were 12 years old. On the plot in Marcos, which is 0.26 ha in size, we found in total 40 tree species. A range of native non-dipterocarp species were planted here together with fruit trees such as durian (*Durio zibethinus*) and santol (*Sandoricum koetjape*) in a 3 m × 3 m spacing. Dipterocarps were present in limited numbers. In Patag we found 33 species on the 0.30 ha site with dipterocarps playing a prominent role. The planting distance was 2 m × 2 m. Other than intercropping with pineapple and other shade tolerant crops (mainly in Marcos), coconut harvesting and occasional wood collection, no management activities were conducted on the sites.

For our study we selected ten tree species (Table 2), eight of which were native to the region. Native species belonged to the family *Dipterocarpaceae* (*Shorea contorta*, *Parashorea malaanonan*, *Hopea malibato* and *Hopea plagata*) as well as to other families (*Vitex parviflora*, *Myrica javanica*, *S. koetjape* and *D. zibethinus*). Two more species, *Gmelina arborea* and *Swietenia macrophylla*, are not native to the region but are planted extensively throughout the tropics. Each species was represented by five individuals selected to have well-exposed crowns with the exception of *H. plagata*, which was found in the stand as smaller individuals with only partially exposed crowns. *G. arborea* was present in a site adjacent to the Marcos rainforestation stand. Abiotic site characteristics and stand age of the stand were similar to the rainforestation stand. All data presented for *G. arborea* was obtained from individuals in this stand.

2.2. Micrometeorological and soil moisture measurements

Micrometeorological data was gathered in open terrain less than 50 m away from the study site. Air temperature and relative humidity were measured 5 m above the ground with a thermo-hygrometer (MP100A, Rotronic AG, Bassersdorf, Switzerland) equipped with a passive radiation shield. A pyranometer (SP1110, Campbell Scientific Inc., Logan, UT, USA) set up at the same height recorded global radiation R_g ($J\,m^{-2}\,s^{-1}$). Leaf wetness was registered in the forest stand by two arrays of leaf wetness sensors (SKLW 1900, Skye Instruments Ltd., Powys, UK) installed at 2.5, 7.5 and 12.5 m above the ground. The sensor surface was exposed north and mounted at a 45° angle. Volumetric soil water content VWC (%) was measured using a total of twelve time domain reflectometers or TDR probes (CS616, Campbell Scientific Inc., Logan, UT, USA). At six locations, regularly spaced throughout the stand, two probes were inserted horizontally in the soil profile at depths of 10 and 40 cm. In Marcos, two of the six locations were chosen in the adjacent *G. arborea* stand. Soil moisture was calculated based on a site-specific calibration curve established according to the procedure described in Veldkamp and O'Brien (2000).

Data was collected using three dataloggers with multiplexer (CR1000 and AM16/32, Campbell Scientific Inc., Logan, UT, USA) which were also used for recording sap flux densities. Meteorological data was measured every 30 s and the 5 min average was stored. Soil moisture conditions were recorded at 15 min intervals and stored.

2.3. Sap flux measurements

Sap flux density J_s ($g\,cm^{-2}\,h^{-1}$) was measured continuously for three complete months from June to August 2006 in Marcos and from July to September 2007 in Patag. Trees were equipped with 25 mm long thermal dissipation probes (Granier, 1985) installed on north and south sides of the stem at breast height (1.30 m). For *H. plagata* we decided to use 12 mm long sensors as tree diameters were small (DBH < 9 cm). After installation, sensors were shielded with a styrofoam box to provide thermal insulation and mechanical protection. A reflective foil extending one meter below and half a meter above the point of installation shielded the setup from incident radiation thus minimising natural temperature gradients. Plastic foil sealed to the stem above the installation point covered the whole and prevented rain and stemflow from entering the setup. The thermocouple output from the thermal dissipation probes was measured every 30 s and 5 min averages were stored using the dataloggers and attached multiplexers described above. Sap flux density was calculated from raw temperature data using the calibration equation determined by Granier (1987). Each night the maximal nighttime temperature was determined and used as reference temperature for that day. This assumption of zero sap fluxes seems reasonable as nighttime vapour pressure deficits were mostly low and temperature courses of sensors reached equilibrium most nights suggesting that refilling of internal reserves was completed.

2.4. Sapwood area and radial sap flux profiles

Initial trials to determine sapwood depth by injection of indigocarmin in the transpiration stream revealed irregular and at times almost absent dying patterns (see also Giambelluca et al., 2003). This would, in our opinion, lead to a negative bias in estimated sapwood depth. In addition, radial profiles of J_s systematically indicated wider sapwood than suggested by the staining method. For this reason we choose an approach based on radial profiles of J_s to determine tree water use.

For all species J_s was measured at two additional depths below the cambium (20–45 and 40–65 mm) in four individuals. For *H. plagata* smaller increments were used (10–22 and 20–32 mm).

Sensors for measuring the radial profile were installed randomly on the east or west side of the trunk, midway between the two reference sensors to minimize interference between sensors. Measured J_s was expressed relatively to concurrent measurements at reference depth (0–25 mm below cambium) and expressed in percentages. At least three days of good quality data were collected before sensors were moved to the next depth interval. Per species an average normalised J_s profile (%) was constructed from the four replicates. Sap flow in up to three ring shaped stem cross-sections was then calculated, taking into account the cross-sectional area of the ring corresponding with the respective installation depth, J_s as measured at reference depth and the normalised profile of J_s for the species considered (Hatton et al., 1990; Meinzer et al., 2005). Contributions of the different cross sections were added to determine total sap flow (g h^{-1}) and summed over a day to give daily water use rates WU (kg d^{-1}). Water use rates were also expressed as transpiration rates (T, mm d^{-1}) by dividing WU by the crown projection area of the respective tree (m^2). Crown dimensions were measured in four cardinal directions and crown projection area was determined by summing the area of four quarter ellipses connecting these points. We did not attempt to estimate stand level transpiration as data was only available for a subset of the species composing the stand.

2.5. Aboveground biomass and leaf area index

We chose to estimate aboveground biomass AGB (kg) from a relationship with DBH, wood density and tree height established by Chave et al. (2005) based on data from 20 sites in tropical forests on three continents. The recommended equation for tropical moist forest was used.

$$\mathrm{AGB} = \exp(-2.977 + \ln(\rho \mathrm{DBH}^2 H))$$

where AGB is the aboveground biomass (kg); ρ is wood density (g cm^{-3}); DBH is diameter breast height (cm); H is the tree height (m).

Tree diameter at breast height was measured with a tape-measure to the nearest millimetre, while tree height was measured with a Vertex hypsometer (Haglöf, Langsele, Sweden). Wood cores of 5 mm diameter were extracted from 0 and 60 mm below the cambium at breast height with five replications. These samples were oven-dried for 48 h at 70 °C and weighed on an analytical balance to determine wood density for the species studied. For two species (*D. zibethinus* and *H. malibato*) where no wood cores were collected, the average density found for the other species was used.

Within each stand, leaf area index (LAI, m^2 m^{-2}) was estimated from six hemispherical photos taken at regularly spaced locations in the plot taking care to avoid the edges of the stands. Photos were taken at low sun elevation or homogeneous cloud cover with a digital camera (Coolpix 4500 and FC-E8 fisheye lens, Nikon Coop., Tokyo, Japan). The camera was leveled horizontally on a tripod at about 1 m above the ground. Analysis was done using the program CanEye version 4.1 (INRA, 2007) with standard settings and manual classification of pixels. Measurements covering the study period showed that temporal variability of LAI was small.

2.6. Sap flux density model

We used a modelling approach to capture species characteristics of sap flux density and its responses to environmental conditions in analogy with work of O'Brien et al. (2004). By this method, extensive dataset on sap flux density can be efficiently reduced to a small number of interpretable model parameters which are used for making further statistical inferences.

The sap flux model used is a modification of the Jarvis-type model (Jarvis, 1976) which was originally developed to describe stomatal responses to environmental drivers. The model takes the form of a multiplication of non-linear response functions, each depending on a single environmental factor. Each individual response function takes a value between zero and one, thus limiting the overall response if one or more environmental factors become suboptimal. The fact that environmental variables appear isolated in the model enhances the interpretation of model parameters. This type of model has been widely used in a number of variations to describe canopy conductance (Herbst et al., 1999; Granier et al., 2000; Harris et al., 2004) and stand transpiration (Oren and Pataki, 2001; Whitley et al., 2008) and to describe sap flow patterns in individual trees (Cienciala et al., 2000).

We opted for a sap flux density model with radiation R_g and vapour pressure deficit VPD (kPa) as explanatory variables, as these have often been found to be most closely related to sap flux density (Hogg and Hurdle, 1997; Oren et al., 1999) and performed best with our data. Although several studies showed an effect of additional factors such as wind speed, soil moisture conditions and leaf wetness (O'Brien et al., 2004; Kume et al., 2007; Whitley et al., 2008) on water use, we decided not to include these, as a preliminary exploration of the data indicated that this would not improve model fit much. The model form used was

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

where $J_{s\ \mathrm{model}}$ is the modelled sap flux density (g cm^{-2} h^{-1}); a is maximum modelled sap flux density (g cm^{-2} h^{-1}); b is parameter describing R_g response; c,d are the parameters describing VPD response.

Modelled sap flux density $J_{s\ \mathrm{model}}$ reaches a maximum value a when all environmental conditions are optimal. To account for the influence of radiation we introduced a commonly used hyperbolic response function (Herbst et al., 1999; Cienciala et al., 2000; Granier et al., 2000) which asymptotically approaches a value 1 at high R_g. Parameter b can be interpreted as a measure of the light saturation level. Assuming VPD is non-limiting, the sap flux reaches just over 90% of a if radiation levels equal ten times parameter b. The response function used to describe the influence of VPD was taken from O'Brien et al. (2004). The latter found a strong s-shaped relationship between sap flux density and a synthetic environmental variable which was closely linked to VPD, R_g and wind speed, and which was well described by a sigmoid. In this response function parameter c equals the vapour pressure deficit for which $J_{s\ \mathrm{model}}$ rises to half of the maximum value (R_g non-limiting), whereas d is related to the slope, i.e. the increase in $J_{s\ \mathrm{model}}$ for a given increase in VPD. Note that the specific function does not allow describing a decline in sap flux density with high VPD. From the datasets it did not however become evident that sap flux was reduced at times of high VPD. Model parameters a, b, c and d in the response functions were estimated by minimising the residual sum of squares using a Gauss–Newton algorithm.

2.7. Statistical analyses

Sap flux densities and most environmental variables were available at 5 min resolution. In order to reduce the dimensions of the datasets these were converted into half hourly averages. Mean and standard deviation are reported as measures of central tendency and dispersion. Although the model is nonlinear we calculated an adjusted R^2 in analogy with linear models. Root mean square error is used to characterise model prediction error. Model parameter estimates were analysed simultaneously using a multivariate analysis of variance MANOVA on the significance of a species effect. As this was an observational study we included tree size characteristics such as tree height, crown projection area and DBH as covariates, as they were expected to influence sap flow

Table 3
Summary of average daily environmental conditions during the study periods. Both study periods cover 92 days.

	Marcos (01 June–31 August 2006)				Patag (01 July–30 September 2007)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Global radiation (MJ m^{-2} d^{-1})	15.8	6.1	3.1	26.8	16.6	6.4	3.6	27.7
Air temperature (°C)	26.6	0.9	24.1	29.1	26.9	1.0	24.2	28.8
Air humidity (%)	82.3	3.7	74.3	91.7	76.6	5.2	63.6	88.2
VPD (kPa)	0.66	0.17	0.26	1.03	0.87	0.23	0.36	1.47
Leaf wetness (% of day)	23.7	23.3	0.0	95.1	33.8	26.0	0.0	86.1
Soil moisture 10 cm (vol.%)	50.1	4.3	40.2	55.3	47.0	3.5	38.8	52.2
Soil moisture 40 cm (vol.%)	63.0	2.2	56.9	65.9	53.3	2.4	48.4	57.7
Precipitation (mm d^{-1})	6.4	13.1	0.0	90.4	6.9	11.0	0.0	49.4

response within a species. Significant differences for individual model parameters among species were determined with a post hoc Tukey HSD test on corrected means. Univariate analyses of variance were used to establish if species and one or more of the covariates had an influence on individual model parameters. The relationships between tree water use rate and tree size or biomass measures were established by simple linear regression. Although curvilinear relationships may be more appropriate (Meinzer et al., 2005) the small tree size range, in our opinion, justifies this. All statistical analyses were performed with R version 2.6.2 (R Development Core Team, 2008).

3. Results

3.1. Micrometeorological and soil moisture measurements

Environmental conditions were comparable between the two sites at the time of the study (Table 3). Recorded air temperature and relative humidity were in line with long-term weather records (1976–2006) available from the local weather station. Precipitation during the study periods was 6.4 and 6.9 mm d^{-1} for respectively Marcos and Patag, about 1.8 mm d^{-1} lower than the long-term observations for corresponding months. Soil moisture was consistently higher in Marcos than in Patag with the difference most pronounced at a depth of 40 cm. We assume this was caused by different soil characteristics and site topography rather than different precipitation regimes preceding and during the two study periods.

3.2. Measured sap flux densities and sapwood characteristics

A wide range of sap flux densities was encountered in the studied species as can be seen from diurnal courses of sap flux on a bright day for representative individuals (Fig. 2). Maximum J_s observed in the field differed twofold among species (Table 4). Low values were found for *V. parviflora* with maxima of 16.9 g cm^{-2} h^{-1}. At the other end of the spectrum was *M. javanica* with 34.2 g cm^{-2} h^{-1}. The maximum J_s measured correlate strongly ($R^2 = 0.90$) with maximum daily integrated sap flux densities during the study period which ranged from 146 to 280 g cm^{-2} d^{-1} for *G. arborea* and *M. javanica*, respectively (data not shown).

Radial profiles of J_s indicated noticeable sap flux densities beyond the standard installation depth in most trees and revealed contrasting patterns of J_s with depth for the studied species. The species *S. koetjape* was characterised by deep sapwood and normalised J_s amounted to 80% and 75% at 20–45 and 40–65 mm below cambium, respectively (average of 4 replicates). *G. arborea* was found to have a steeper profile with normalised J_s declining to 42% and 10% at the same depths under the cambium. Other species showed intermediate profiles.

3.3. Sap flux model parameters

Our model accurately described half hourly observations of J_s in relation to environmental variables. For individual trees R^2_{adj} was between 0.83 and 0.97 while the average over all studied trees was

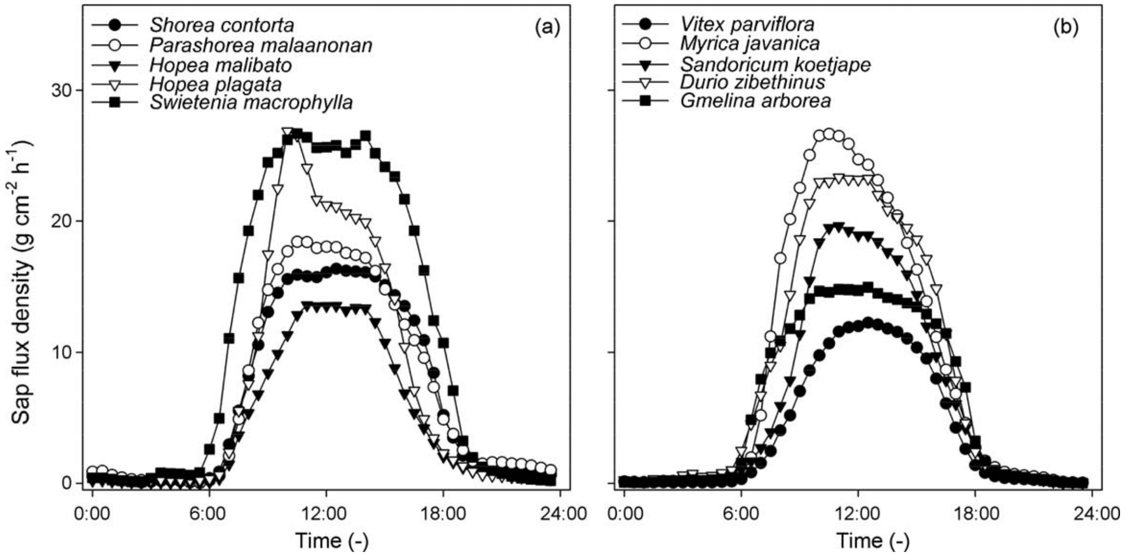

Fig. 2. Diurnal courses of sap flux density on a bright day for species studied in Patag (a) and Marcos (b). Representative individuals are shown. Data presented was gathered on 6 June 2006 in Marcos (daysum $R_g = 26.6$ MJ m^{-2} d^{-1}, daily average VPD = 0.82 kPa) and 21 July 2007 in Patag (daysum $R_g = 27.6$ MJ m^{-2} d^{-1}, daily average VPD = 1.19 kPa).

Table 4
Summary of maximum ($J_{s\ max}$) and average ($J_{s\ mean}$) half hourly sap flux density (means and standard deviations, $n = 5$) and average normalized radial profile of J_s (means and standard deviation, $n = 4$).

Species	$J_{s\ max}$ (g cm^{-2} h^{-1})		$J_{s\ mean}$ (g cm^{-2} h^{-1})		Normalised J_s (%)			
					Depth 1		Depth 2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
S. contorta	17.7	6.1	4.7	1.9	36.3	28.1	7.0	4.4
P. malaanonan	21.8	1.6	5.5	0.7	28.8	15.5	14.0	2.4
H. malibato	18.2	6.0	4.4	1.9	35.5	4.1	28.3	10.1
H. plagata	28.1	4.6	5.9	1.0	60.8	7.9	46.5	13.8
S. macrophylla	28.9	3.0	8.6	1.0	57.5	22.5	26.0	13.2
V. parviflora	16.9	2.7	3.9	0.6	81.8	83.6	38.5	39.3
M. javanica	34.2	6.5	8.1	1.5	62.3	24.5	21.8	25.0
S. koetjape	22.5	4.3	5.3	1.6	80.3	29.1	74.5	27.5
D. zibethinus	27.9	7.1	6.7	1.8	65.5	23.0	54.0	23.9
G. arborea	17.1	1.8	4.4	0.6	42.0	25.0	9.5	3.1

The normalised radial profile of J_s was measured at 20–45 mm (depth 1) and 40–65 mm (depth 2), except for *H. plagata* where the radial profile was measured at 10–22 and 20–32 mm below cambium.

0.92 (data not shown). Averaged per species R^2_{adj} ranged from 0.88 for *P. malaanonan* to 0.96 for *G. arborea* (Table 5). The species average of root mean square error on predicted J_s was between 1.1 and 2.8 g cm^{-2} h^{-1} with an obvious link to the absolute level of J_s observed for the species considered (Table 5). That model performance was adequate could also be inferred from the agreement of model prediction and actual measurements when these were integrated to daily sap fluxes (data not shown). Daily cumulated flux was predicted less accurate than half hourly data with R^2_{adj} between 0.63 for *V. parviflora* and 0.92 for *S. macrophylla*, but R^2_{adj} was still as high as 0.80 averaged over all species.

A multivariate analysis of variance on the set of four model parameters indicated a significant effect of species and the covariates tree diameter, tree height and crown projection area on one or more of the model parameters (all p-values < 0.01). Subsequent univariate analyses (Table 6) showed that species acted on all four model parameters whereas covariates only influenced specific model parameters. Average model parameters and associated standard deviations for the ten species studied are presented together with the results of a post hoc Tukey test showing species with significantly different means (Table 5).

Estimates for model parameter *a* accurately reflect differences in observed maximal sap flux at the species level ($R^2 = 0.96$, compare also Tables 4 and 5) as well as for individual trees ($R^2 = 0.91$) illustrating the ability of the model to capture tree and therefore species characteristics. Model parameter *a* suggest significant differences in maximal sap flux density among species, while parameters *b*, *c* and *d* indicate species-specific responses to radiation and vapour pressure deficit. In relation to species differences in the light response (parameter *b*) it should be noted that the high value for *H. plagata* was likely caused by the small dimensions of the sampled individuals resulting in partial shading of the crowns. Tree species in Patag generally pointed out higher values for model parameter *c* than species in Marcos, whereas the reverse was true for parameter *d*. Rather than species differences, we assume this is caused by micrometeorological data not being fully representative for conditions in the nearby stand or stand structural differences.

3.4. Tree water use rates in relation to tree characteristics

Maximum water use rates WU_{max} (kg d^{-1}) for individual trees were highly variable encompassing values from 3.7 kg d^{-1} for a 6.1 cm diameter *H. plagata* to 78.2 kg d^{-1} for a *M. javanica* with

Table 5
Estimated model parameters and measures of model performance for the species studied (means and standard deviations, $n = 5$).

Species	R^2_{adj}	RMSE (g cm^{-2} h^{-1})		*a* (g cm^{-2} h^{-1})		*b* (J m^{-2} s^{-1})		*c* (kPa)		*d* (kPa)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
S. contorta	0.91	1.49	0.33	16.4^{d}	5.8	80.2^{de}	39.5	0.77^{a}	0.17	0.22^{a}	0.05
P. malaanonan	0.88	2.10	0.14	18.7^{cd}	2.6	81.2^{de}	25.9	0.77^{a}	0.04	0.23^{b}	0.02
H. malibato	0.91	1.63	0.56	17.9^{cd}	5.6	162.5^{cd}	73.6	0.80^{a}	0.09	0.21^{b}	0.04
H. plagata	0.91	2.34	0.38	27.7^{ab}	5.4	292.6^{a}	34.5	0.72^{bc}	0.03	0.15^{c}	0.02
S. macrophylla	0.95	2.23	0.40	26.4^{abc}	2.5	55.3^{e}	29.3	0.69^{ab}	0.04	0.20^{b}	0.02
V. parviflora	0.92	1.33	0.21	14.4^{d}	2.1	86.4^{cde}	38.4	0.63^{bc}	0.10	0.24^{b}	0.03
M. javanica	0.93	2.44	0.43	33.5^{a}	5.7	175.7^{ab}	69.5	0.57^{c}	0.06	0.24^{b}	0.04
S. koetjape	0.89	1.99	0.37	19.3^{cd}	3.1	68.4^{de}	35.4	0.74^{ab}	0.16	0.25^{ab}	0.01
D. zibethinus	0.92	2.18	0.58	25.2^{bc}	6.5	164.0^{bc}	79.8	0.49^{c}	0.01	0.18^{b}	0.02
G arborea	0.96	1.02	0.08	17.3^{d}	2.4	103.4^{de}	28.6	0.59^{a}	0.12	0.28^{a}	0.02

Significant differences ($p < 0.05$) between species for the individual model parameters are indicated by different letters.

Table 6
Influence of species and covariables on individual model parameters.

Source	Dependent model parameter	Direction of change	SSE	df	MSE	*F*	*p*-value
DBH	*b*	–	31627.00	1	31627.00	15.23	<0.001
	c	–	0.25	1	0.25	37.41	<0.001
	d	–	0.01	1	0.01	15.10	<0.001
Height	*a*	+	303.80	1	303.80	15.05	<0.001
	b	+	12159.00	1	12159.00	5.85	0.021
Crown area	*d*	+	0.01	1	0.01	14.77	<0.001
Species	*a*	na	1448.41	9	160.93	7.97	<0.001
	b	na	206086.00	9	22898.00	11.02	<0.001
	c	na	0.36	9	0.04	6.10	<0.001
	d	na	0.05	9	0.01	7.05	<0.001

Only significant dependencies ($p < 0.05$) are given. For covariables the direction of change is indicated.

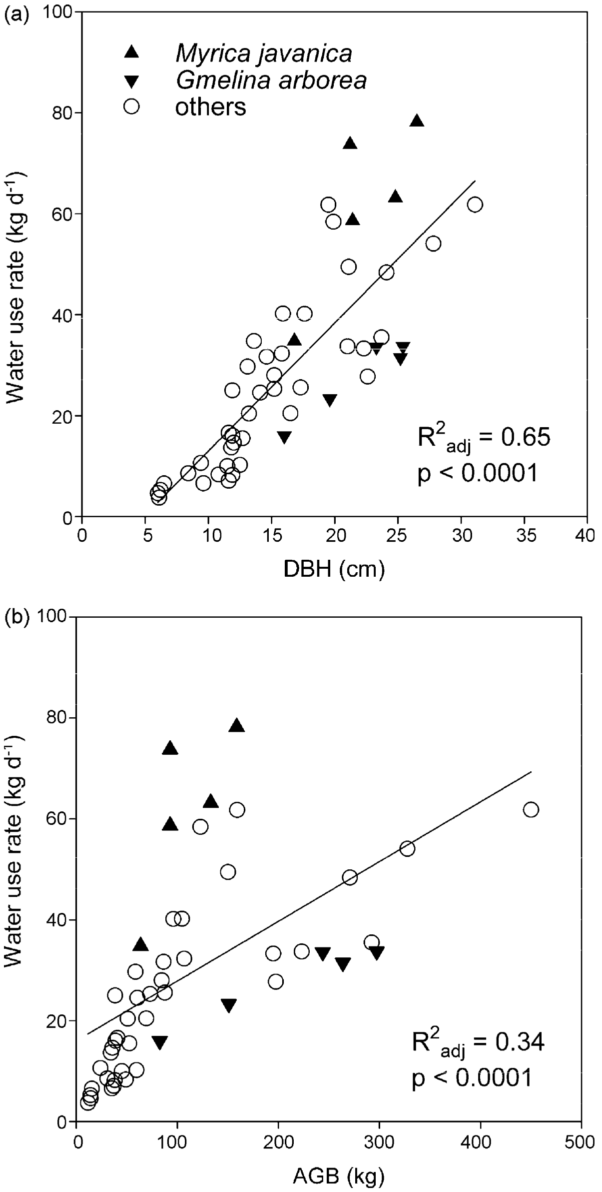

Fig. 3. Maximum daily water use rates WU_{max} during the study period for each individual in relation to tree diameter DBH (a) and aboveground biomass AGB (b). Two contrasting species *M. javanica* and *G. arborea* are shown with different symbols.

Table 7
Maximum (WU_{max}) and mean water use (WU_{mean}) and maximum (T_{max}) and mean (T_{mean}) transpiration rates (means and standard deviations, $n = 5$).

Species	WU_{max} (kg d^{-1})		WU_{mean} (kg d^{-1})		T_{max} (mm d^{-1})		T_{mean} (mm d^{-1})	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
S. contorta	25.6	14.4	18.4	19.5	2.15^{ab}	0.98	1.54^{ab}	0.75
P. malaanonan	15.3	1.1	10.6	1.2	1.30^{ab}	0.27	0.89^{ab}	0.17
H. malibato	13.1	6.7	9.1	8.5	1.38^{ab}	0.46	0.93^{ab}	0.31
H. plagata	5.7	1.3	4.0	1.9	0.86^{b}	0.17	0.60^{b}	0.12
S. macrophylla	33.7	3.6	25.5	4.1	3.29^{a}	2.53	2.50^{a}	1.95
V. parviflora	20.7	9.3	30.7	14.6	1.19^{ab}	0.46	0.80^{ab}	0.30
M. javanica	43.2	12.5	61.7	17.0	2.77^{ab}	0.62	1.92^{ab}	0.39
S. koetjape	23.4	12.6	32.8	16.5	2.03^{ab}	1.21	1.46^{ab}	0.94
D. zibethinus	32.9	14.8	44.6	18.5	1.56^{ab}	0.83	1.14^{ab}	0.64
G. arborea	19.8	6.1	27.6	7.8	1.90^{ab}	0.60	1.35^{ab}	0.42

Significant differences ($p < 0.05$) are indicated by different letters.

diameter of 26.5 cm. The large differences in water use rates observed reflect in part a dependence of water use rates on tree diameter and the range of diameters covered. A linear regression of WU_{max} in individual trees against DBH explained 65% of the observed variability (Fig. 3a). Despite this relationship between WU_{max} and DBH it becomes clear from the same graph that differences in water use remain for trees with similar dimensions. In trees with a diameter between 20 and 25 cm diameter for example, we see a twofold difference in water use rates with a pronounced effect of species (compare *M. javanica* and *G. arborea*).

Tree aboveground biomass, which depends strongly on tree diameter but further takes into account tree height and wood density, showed a weak ($R^2_{adj} = 0.34$) but significant relationship with maximum water use rates (Fig. 3b). Note that the data suggests two distinct groups of species. The single linear regression only aims at indicating a general trend and is not appropriate for predictive purposes. From the same graph it can be seen that trees with a comparable biomass are expected to have very different water use rates depending on the species considered.

3.5. Transpiration rates

Expressing daily water transport per unit crown projection area resulted in maximum transpiration rates between 0.82 and 7.8 mm d^{-1} for individual trees (data not shown). Averaged per species, the maximum transpiration rate T_{max} ranges from 0.86 mm d^{-1} for *H. plagata* to 3.3 mm d^{-1} for *S. macrophylla* (Table 7). Mean transpiration rates over the entire study period equal 0.6 and 2.5 mm d^{-1} for the same species. A Tukey HSD test results in two largely overlapping groups but shows that *H. plagata* and *S. macrophylla* have significantly different maximum and mean transpiration rates. The low value found for *H. plagata* most likely reflects the moderate exposure of these individuals. Linear regressions between transpiration rates and tree size related variables (analogous to above) were not significant.

4. Discussion

4.1. Sap flux density and influencing factors

In the course of our study maximum sap flux densities between 16.9 and 34.2 g cm^{-2} h^{-1} were observed in ten different species growing under comparable conditions. This is in line with values published for tropical forest tree species which are mostly situated between 5 and 50 g cm^{-2} h^{-1} (Granier et al., 1996; Meinzer et al., 2001; Dünisch and Morais, 2002), although values of up to 70 g cm^{-2} h^{-1} have been reported (Becker, 1996; O'Brien et al., 2004). High variability of sap flux densities in tropical trees has been attributed to environmental controls (Phillips et al., 1999; Giambelluca et al., 2003; Fisher et al., 2007), tree architecture and crown characteristics (Granier et al., 1996; Meinzer et al., 2001; O'Brien et al., 2004) and species characteristics (Granier et al., 1996; Dünisch and Morais, 2002).

Temporal variability of J_s in individual study trees was well described using a simple model based on global radiation R_g and vapour pressure deficit VPD, demonstrating the tight control environmental factors exert on J_s. The actual sap flux densities and responses to these environmental factors however depended significantly on tree species (Table 5) and the covariables considered in this study, which are essentially tree size related (Table 6). Species reaction to light differed, which was particularly noticeable for *H. plagata*. The high light saturation found for that species should be seen in relation to the partially shaded crown typical for this species. Significant differences found for model parameters *c* and *d* suggest a different response to VPD across species, although interpretation was hampered by the systematic difference between the two study plots.

Species differences in J_s were also found for several species in old-growth forest in French Guiana and a link with species successional status was suggested (Granier et al., 1996). Late successional species were characterised by higher flux densities (30–40 g cm^{-2} h^{-1}) when compared to early successional species (10–15 g cm^{-2} h^{-1}). We did not encounter a similar pattern as both early successional species (e.g. *G. arborea* and *M. javanica*) as well as late successional species (e.g. *S. contorta* and *H. plagata*) were found at opposite ends of the range of sap flux densities observed. Differences in J_s in three *Meliaceae* species were attributed to the ring- or diffuse-porous wood anatomy of the respective species (Dünisch and Morais, 2002). This did not play a role in our study as all species studied were diffuse-porous.

The increasing maximal sap flux density with tree height encountered in our study (Table 6) is likely a consequence of better crown illumination and atmospheric coupling leading to higher transpiration rates and J_s. This interpretation is in agreement with observations made in four rainforest types in Queensland, Australia (McJannet et al., 2007). Although not significant, consistent increases in J_s with tree diameter were found and attributed to a higher position in the canopy and consequently better crown exposure of large diameter trees. Also for trees in old-growth neotropical forest it was observed that J_s increased with better exposure of the crown (Granier et al., 1996). Related to this is our finding that sap flux responses to vapour pressure deficit were linked to tree diameter. Decreasing values of parameter c and d with increasing diameter would imply an onset of sap flux under lower VPD and more pronounced increase of J_s with rising VPD in large trees. This is in line with the finding that trees showed enhanced responses to evaporative demand when crowns extended above the surrounding canopy (O'Brien et al., 2004). In our study, tree height and tree diameter thus probably served as an approximation for tree canopy exposure. Use of a canopy height index, which takes the height of surrounding trees into account and better reflects crown exposure, as used by O'Brien et al. (2004), is likely better able to account for differences in maximum J_s and responses to environmental variables.

O'Brien et al. (2004) found that species responses of normalised J_s to a single synthetic environmental factor characterising evaporative demand were significantly different, but concluded that the overall effect of species was small. The authors suggested that this could be due to functional convergence resulting in similar responses to environmental factors in the different species. An alternative hypothesis was that strong uncoupling from the atmosphere would lead to it that existing physiological differences are not reflected in sap flux responses, thus effectively mitigating species differences. In addition, our study considered absolute levels of sap flux density, which turned out very different between species. This illustrates that excluding absolute levels of J_s from the analysis and focussing on sap flux responses only might have resulted in the apparent similarity across species found by O'Brien et al. (2004).

At first view, our data contradicts the hypothesis of functional convergence (Meinzer et al., 2001, 2005). Their work in Panama revealed a strong inverse relationship ($R^2 = 0.85$) between maximum sap flux density and tree diameter in 24 co-occurring species in Panamanian old-growth forest. Also in a patch of advanced secondary forest in Vietnam, a weak but significant ($R^2 = 0.23$) decline of J_s with tree diameter existed (Giambelluca et al., 2003). The same study however also acknowledged the presence of large differences in sap flux density across and within species. Our data did not reveal a similar pattern of declining J_s with tree diameter. A possible explanation for this finding is the limited diameter range covered in comparison with the original work (Meinzer et al., 2001). As is evident from the data presented in the latter study, considerable scatter is present, especially in the lower diameter range where the steepest decline in J_s is predicted. A possible implication is that general patterns resulting from functional convergence may remain unnoticed if the range of tree dimensions sampled is not sufficiently wide. We are therefore the opinion that the species differences in J_s and response of J_s to environmental drivers that we observed, do not necessarily contradict the hypothesis of functional convergence (see also Meinzer, 2003). They may merely reflect that considerable variation remains within general patterns observed across species, which is in part due to species specific adaptation to a given set of growth conditions and possibly to stand structural differences (see also Cienciala et al., 2000). The remarkably strong common patterns observed for co-occurring trees in Panamanian forest are possibly related in part to particular stand structural or environmental conditions to which trees are exposed. Where functional convergence can be demonstrated, it would prove an invaluable tool in assessing stand transpiration, in particular in species rich and highly structured natural forest stands (Meinzer et al., 2001; McJannet et al., 2007). However, our results indicate it may be less relevant in relatively young and little structured mixed reforestation stands where traits other than tree diameter may affect tree water use more effectively. This is especially true when we realise that co-occurring species can differ significantly in sap flux density.

4.2. Tree water use and transpiration rates

In our study measured maximal water use rates varied between 3.7 and 78.2 kg d^{-1}. Taking into account tree diameter, this is broadly in line with extensive data reviewed by Wullschleger et al. (1998). For fifty individuals belonging to ten different species we found that maximum tree water use rates were strongly related to DBH (Fig. 3a). In a number of studies allometric relations between tree water use and tree diameter or biomass were introduced that applied across species (Meinzer et al., 2004) or species groups (Meinzer et al., 2005). The latter study found that a sigmoid function described the relation between WU and DBH in 18 mainly tropical angiosperm species better than a power function. That a simple linear regression to DBH explains a considerable part ($R^2_{adj} = 0.65$) of the variance in our dataset should be seen in relation to the small diameter range covered. Some theoretical relationships describing water use versus tree size characteristics may be inappropriate from a biological point of view, even though they provide an adequate fit in a certain dataset (Meinzer et al., 2005). Despite the strong dependence of WU$_{max}$ on DBH for the individuals studied, considerable scatter was present around the fitted curve with species located on distinct trajectories. This resulted from a combination of both species-specific J_s and species differences in hydroactive xylem depth (Table 4). Apart from these factors, the relationship would be determined strongly by cross correlation between estimated water use rates and tree diameter. This can be expected to be most pronounced in the lower diameter ranges (Meinzer et al., 2001), making the deviations from a common relationship even more significant.

The relationship found between WU$_{max}$ and estimated AGB was rather weak ($R^2_{adj} = 0.34$) and tree water use differed considerably for trees with a given biomass (Fig. 3b). The study of Meinzer et al. (2005) mentioned earlier also pointed out a strong sigmoid relationship between water use and tree biomass for the 18 angiosperm tree species. The weak relationship for the ten tropical angiosperms examined in our study could follow from species differences in water use rates. This interpretation should be viewed with caution because of uncertainties related to the biomass estimates which are based on an equation that is neither site nor species specific. However, despite this limitation, it is safe to state that trees accumulated different amounts of biomass during the 12 years of stand development at our study sites and that this was partially species dependent. Furthermore, water use rates at the time of study were highly variable across species providing evidence that water use efficiency and biomass production in forest ecosystems could be influenced by an appropriate choice of species.

Maximum transpiration rates observed in individual trees varied from 0.4 to 4.0 mm d^{-1}, except for a single *S. macrophylla* which had a maximum transpiration rate of 7.8 mm d^{-1}. Excluding this single tree, results are comparable with findings from Giambelluca et al. (2003) who measured daily transpiration rates in individual trees between 0.9 and 4.6 mm d^{-1} in a patch of advanced secondary forest in Vietnam. In our study, transpiration rates over the study periods differed fourfold across species from 0.6 to 2.5 mm d^{-1}. Also for the mentioned study in Vietnam, transpiration rates in individual trees were found to be different among species and were in addition influenced by crown exposure, seasonality and enhanced transpiration at the forest edge (Giambelluca et al., 2003).

Even though stand level transpiration was not estimated in the course of the study, the important differences observed in transpiration rates and water use rates would still suggest an influence of species composition on stand level transpiration. This contrasts with studies showing that water use at tree or stand level is predominantly influenced by tree size and stand structure in old-growth forest (Meinzer et al., 2001, 2005; McJannet et al., 2007). For example, in Australian stands, a small number of large trees (>70 cm) contributed proportionally more (~20%) to total stand transpiration (McJannet et al., 2007). Another study conducted in *Acacia mangium* stands in Indonesia also demonstrated the effect of stand structural differences on stand level transpiration (Cienciala et al., 2000). The latter study acknowledged that differences in understory and associated transpiration were not taken into account and might mitigate different transpiration rates found for the tree layer component of the stands. Where stand structural differences are the main factors determining transpiration in highly structured natural stands or mono-specific stands, this may well be different in young multi-species stands where structure is largely lacking. We hypothesise that in such stands species traits consequently become relatively more important as a factor controlling stand level transpiration.

In summary, it was found that water use and transpiration rates found in ten co-occurring tropical angiosperm tree species showed considerable variation across species. Even though tree diameter exerted strong control over tree water use, twofold differences between trees of similar diameter belonging to different species were suggested. Species selection may indeed be an effective tool to control water use of reforested stands and optimise the balance between wood production or carbon sequestration and the use of water resources. In our opinion, this applies in particular to little structured reforestation stands, which in the future might become more widespread in the tropics.

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