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Partitioning Light and Water Use Efficiencies (LUE, WUE) between cover tree (*Cocos nucifera* L.) and grass under-storey, using eddy covariance, LAI-2000 and Net Primary Productivity (NPP).

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Abstract

Net Primary Productivity (NPP) is a key driver of ecosystem C balance. Its seasonal and annual variations can be measured directly at the stand level. However, estimating NPP on larger areas would require indirect methods such as: (*i*) process models, e.g. ε-models based on the fraction of intercepted PAR (*f*IPAR) and on the light use efficiency (LUE = NPP/IPAR), or else models based on the water-use-efficiency (WUE = NPP/E, where E = evapo-transpiration); (*ii*) remote sensing, to estimate *f*IPAR (from the Normalized Difference Vegetation Index: NDVI) or else E (from the energy balance closure). However, two main impediments may interfere with such estimations of NPP: first, LUE and/or WUE may vary in time, and second, remote sensing may be unable to distinguish between the layers of the stands, which sounds critical for agroforestry systems.

In a 20-year-old coconut grove from Vanuatu (South Pacific), we monitored NPP, E, LUE and WUE separately for the coconut layer (subscript "c"; LAI = 3; canopy cover around 75%) and for the under-storey composed of grasses (subscript "g"; LAI = 2.7). Light interception by the coconuts ($IPAR_c$) was estimated by optical indirect techniques (LAI-2000). Evapotranspiration of the whole stand (subscript "s"), E_s, was measured directly by eddy-covariance, and the contribution of the coconuts was assessed by sapflow (T_c). Light interception and evapotranspiration from the under-storey ($IPAR_g$ and E_g) was estimated from the difference. We reported elsewhere that NPP_c represented 75% of NPP_s (amounting to 32 t_{DM} ha^{-1} $year^{-1}$), T_c represented 68% of E_s (amounting to 950 mm $year^{-1}$) and $IPAR_c$ amounted to 73% of incident PAR. This partitioning results were very close to the rule-of-thumb evaluation, based on the simple observation of the canopy closeness (0.75%).

We found here that WUE_s (mean annual value = 3.7 g_{DM} kg_{H2O}^{-1}) was mainly driven by the coconuts (4.0), and to a lesser extent by the understorey (2.4). WUE_s had high seasonal variations, between 2 and 6, being dependent mainly on E_s rather than on NPP_s. LUE_s (mean annual value = 0.29 g_{DM} $mol_{PARinc.}^{-1}$) appeared to be similar for coconuts and for the understorey. LUE_s also had high seasonal variations, between 0.18 and 0.52, which was mainly explained by seasonal variations of incident PAR rather than by variations of NPP.

The large seasonality observed for LUE and WUE could be modelled empirically ($0.82 < R^2 < 0.95$), which appears to be useful for running large scale process-models on similar plantations.

Key Words: Two-layers systems / Partitioning of fluxes / Seasonal variations / Spatialization

Introduction

Net primary productivity (NPP), defined as the organic matter produced (build-up of standing biomass + mortality) over a specified interval (Clark et al. 2001) is a key driver for ecosystem C balance. Reviewing NPP across the major biomes, Gower et al. (1999), Pregitzer and Euskirchen (2004) and Luyssaert et al. (2007) stressed the need for more NPP surveys in tropical ecosystems and forests, especially for the southern hemisphere, for young and middle-aged classes, and for the belowground compartment. NPP or C balance assessments, and process models remain scarce for tree-crops (*Cocos nucifera* or coconut palm, *Elais guineensis* or oil palm, *Coffea sp*. or coffee, *Theobroma cacao* or cocoa, *Hevea brasiliensis* or rubber, etc.), although these perennial crops occupy over 47 Mha in the humid tropics (FAO 2003). The coconut tree (*Cocos nucifera* L.) is the largest contributor (23% of that area), being a multi-purpose tree-crop, with important domestic and industrial uses and opportunities for the Clean Development Mechanism (CDM) (Tan et al. 2004, Roupsard et al. 2004).

The direct monitoring of NPP, for both coconut and grass layers of an adult stand, has recently been reported by Navarro et al (2007). Spatialisation at the scale of larger coconut groves, requires indirect methods for estimating NPP such as: (*i*) process models: e.g. ε-models (Monteith, 1972; Gower et al., 1999; Nouvellon et al., 2000) based on the fraction of intercepted PAR, (*f*IPAR), on the light use efficiency (LUE = NPP/IPAR), or on water-use-efficiency (WUE = NPP/E, where E = evapo-transpiration); (*ii*) remote sensing, used to estimate *f*IPAR (from Normalized Difference Vegetation Index, NDVI) or E (from energy balance) on large scales and to drive the process models (e.g. Earth Observing System, EOS).

The partitioning of evapo-transpiration of the same stand has been reported by Roupsard et al (2006). Roupsard et al (2007) also described the partitioning of IPAR using field optical methods (LAI-2000) and proposed a simple model to estimate *f*IPAR in various coconut canopies differing by planting density and age, which was designed as a tool to calibrate remote sensing estimations of *f*IPAR. However, remote sensing usually provides an integrated estimation of *f*IPAR, without distinction of the storeys. Further distinction of NPP for both coconut and under-storey layers requires separate assessment of LUE or WUE at two or more levels. In addition, process models are prone to seasonality of WUE and LUE, and it is proposed here to assess their variability and to highlight their key dependence factors.

The aim of this paper is: *(i)* to describe the seasonal and interannual variations of WUE and LUE in both strata of a coconut stand (coconut palm + grass under-storey); *(ii)* to assess the key seasonal dependence factors of WUE and LUE for the purpose of modeling and upscaling.

Materials and Methods

Location, climate and stand

The study was carried out during three years, 2002 to 2004, in a mature coconut plantation, 19-21 years after planting (YAP), which was part of the Vanuatu Agricultural Research and Technical Centre (VARTC), on Espiritu Santo, Vanuatu, South Pacific (15° 26.6´ S, 167° 11.5´ E; altitude 80 masl). The climate was tropical and humid. No hurricane or El-Niño event affected this experiment. The growing conditions (soil texture and fertility, absence of seasonal water shortage, climate) were considered to be close-to-optimum (Roupsard et al. 2006).

The stand had been row-planted in 1983 with the Vanuatu Red Dwarf x Vanuatu Tall (VRD x VTT) high-yielding hybrid coconut variety (Labouisse et al. 2005). The planting design was triangular and equilateral. Coconut tree canopies covered around 75% of the ground. The grass under-storey, including mainly *Paspalum* sp. (21% of soil coverage), *Mimosa pudica* (11%)

Desmodium heterophyllum (9%), *Mikania micrantha* (9%) and *Sida* sp. (8%). In the clear interrow (accounting for 49% of the area), the grass was managed by slashing every 2-3 months but was left untouched in the windrow. The true leaf area index (LAI), obtained by destructive sampling, was similar for both layers; i.e. around three (Navarro et al, 2007).

NPP of coconut tree (NPP_c) and grass (NPP_g)

The NPP experiment has been reported in Navarro et al (2007). Briefly, for every plant organ monitored, net primary productivity (NPP) was linked to dry mass (DM) variations over time (t, on a monthly basis) and to mortality or litter production (L), as follows:

$$NPP = \frac{\Delta DM}{dt} + L \tag{1}$$

Sampling of 10 trees was stratified, based on a preliminary stand survey of tree height and nut load distributions. They were monitored non-destructively (January 2002 to December 2005, 19 to 22 YAP), climbed every month (2002-2003) and then every week (2004-2005), i.e. 1,200 climbs to measure nut growth, new leaf emission and stem height. Above ground NPP was derived, using specific allometric equations developed by Navarro et al (2007), based on destructive samplings (10 other representative trees felled for biomass; sub-samples dried in a ventilated oven at T° = 70°C to constant weight)). Belowground tree NPP was assessed by large rhizotrons and sequential trenching, in order to assess root lifespan and turnover.

Above-ground grass NPP was assessed by successive harvests (n = 8), during 18 months between 2002 and 2004, within in two subplots, covering a total of 101 m^2 and representative of the horizontal heterogeneity. Those results were extrapolated to the entire 2002-2004 period. Below-ground, NPP_g was estimated from root:shoot allocation ratios available in the literature for tropical fertile and wet grasslands (Scholes and Hall 1996; House and Hall 2001).

Although NPP_c has been monitored more accurately than NPP_g, NPP_s agreed very well, on a yearly basis, with the difference between measured GPP (the ecosystem photosynthesis, measured by eddy-covariance and reported in Luysseart et al., 2007) and R_a (the autotrophic respiration), supporting that at least on a yearly basis, NPP_s and its partitioning were realistic (Navarro et al., 2007).

Micro-climate and radiation measurements and models

Micro-climate variables were logged at reference height (22 m on top of the eddy covariance tower) on a CR10X and AM416 Multiplexer (Campbell Scientific, Shepshed, UK). The measurement period was 30 s, integrated half-hourly. Instruments used were: global radiation-silicon cell pyranometer SKS1110 (Skye Inst. Ltd); net radiation-NR-Lite (Kipp & Zonen, Delft, The Netherlands); incident photosynthetic photon flux density (Qp)-home-made probe (Dauzat and Eroy, 1997) calibrated against commercial probes; temperature and humidity-MP103A (Rotronic, Bassersdorf, Germany); rainfall tipping-bucket-ARG100 (R.M. Young, MI, USA); wind-speed and direction-03001 Wind Sentry ARG100 (R.M. Young, MI, USA).

Solar position was calculated from the geometry of planetary rotation and revolution. Solar elevation angle (β), solar declination angle, hour angle of the sun, solar noon, equation of time, day angle and extra-terrestrial radiation (R_x) were derived from FAO (1998) models. The fraction of diffuse radiation (R_d/R_g) was computed half-hourly, based on the ratio between global radiation, R_g and extra-terrestrial radiation, R_x, as described by Spitters et al. (1986).

Light interception by coconut ($IPAR_c$) and grass ($IPAR_g$) layers

*f*IPAR (the fraction of intercepted PAR, i.e. the complement of PAR transmittance below the canopy) can be measured at the scale of a canopy using indirect optical gap-fraction methods, such as LAI-2000 Plant Canopy Analyser (Welles and Norman, 1991; Weiss et al., 2004). In the same coconut plantation as studied here, Roupsard et al. (2007) reported successful comparison between LAI-2000 field measurements and 3D architectural model (3DM) simulations of the gap-fractions (related to cos(β), for beam and for diffuse PAR) and also for structural characteristics (leaf angle distribution function). Coconut *f*IPAR (*f*IPAR$_c$) was thus inferred on a semi-hourly time-step between 2002 and 2004, as the inverse of the simulated gap-fractions. The intercepted PAR (IPAR$_c$: μmol_{PAR} m^{-2} s^{-1}) was derived, using the measured instant PAR$_i$, and its partitioning into beam and diffuse radiation.

Grass *f*IPAR (*f*IPAR$_g$) was assumed to represent all the radiation transmitted by the coconut canopy, which sounds reasonable, considering that the cumulated LAI (coconut + grass) was around 6 (little radiation assumed to impinge on the soil).

Evapo-transpiration

Evapo-transpiration results have been reported in detail by Roupsard et al (2006). Briefly, the experiment was set up in accordance with the Carboeuroflux recommendations (Aubinet et al., 2000). Eddy-covariance measurements were performed continuously above the canopy (22 m), yielding the evapo-transpiration of the stand, E$_s$. 3D wind components and temperature were measured with a WindMaster Pro ultrasonic anemometer (Gill Instruments, Lymington, UK) at 10 Hz. H_2O fluctuations were measured with a Li-7500 open path (LiCor, Lincoln, NE, USA). Raw data were collected and pre-processed by “Tourbillon” software (INRA-Bioclimatologie, Bordeaux, France) for a time-integration period of 300 s. Raw-data were post-processed using EdiRe software (University of Edinburgh, UK) into half-hourly values. All data were de-spiked according to variance filters, the axes were rotated three times in order to fit the “natural wind coordinate system” (McMillen, 1998; Lee et al., 2004), all data were linearly de-trended, and vapour fluxes were corrected for buoyancy (Webb et al., 1980).

Tree transpiration (T$_c$) was measured by sapflow (Granier, 1985), on the 10 trees monitored for NPP, and using home-made probes specifically calibrated in the laboratory, and validated in the field (Roupsard et al, 2006).

It is assumed here that E$_s$-T$_c$ yields E$_g$, the evapo-transpiration of the under-storey (grass + soil) during non-rainy days. For rainy days, the unknown contribution of rain interception and re-evaporation by the coconut and under-storey strata make the estimation un-realistic. Rainy days were thus discarded from the E$_g$ dataset, leaving 50% of data.

Results and Discussion

Light interception

Incident PAR (PAR$_i$) showed high seasonal variation by a factor of 2.4 (Fig.1a; between 19 mol m^{-2} d^{-1} (cooler season) and 46 mol m^{-2} d^{-1} (warm season)), due to variations of solar angle (vertical in November and in February) and of cloudiness (the fraction of diffuse radiation ranged from 0.5 during the warm season to 0.75 during the cool season). PAR$_i$ drove the seasonal variations of temperature and of VPD, more rainfall occurred during the warm period. As an average, PAR intercepted by the coconut canopy (IPAR$_c$) amounted to 73 ± 1% (SD) of PAR$_i$, which was close to the rule-of-thumb, considering that the coconut canopy covered around 75% of the soil. For low solar elevations (cooler season, but also mornings and evenings), PAR available for the under-storey (IPAR$_g$) could become very low. However, the magnitude of variations in PAR$_i$, IPAR$_c$ and IPAR$_g$ remained similar (factor between 2.4 and 3).

NPP

Compared with radiation, the temporal variation of stand and coconut NPP (Fig. 1b) was less (factor 1.3). As an average, NPP$_c$ represented 75% of NPP$_s$, peaking around September-October, when light available for the under-storey was moderate, due to a large investment in the growth of the fruit compartment (Navarro et al, 2007). Interestingly, seasonal variations of NPP_s appeared to be more influenced by the under-storey (NPP_g: seasonal variation with a factor 2.5), than by coconuts. The under-storey appeared to be much more prone to seasonal NPP limitations than the coconut layer, due to insufficient incoming radiation or occasionally from superficial soil water depletion, which did not affect the coconut trees (rooted down to 3 meters).

Transpiration

The time-course of stand evapo-transpiration (Fig. 1c) varied seasonally between 1.6 and 4 mm d^{-1} (factor of 2.6; similar to radiation), whereas for coconut it was mitigated down to a factor of 1.7, probably as a consequence of stomatal regulation of transpiration during conditions of high VPD (Roupsard et al., 2006). On a yearly basis,T represented 69% of E.

$E_g = E_s - T_c$, computed only for non-rainy days only, fluctuated seasonally by a factor of more than sixteen, confirming that the under-storey was much more affected by the microclimate and superficial soil water conditions than the upper-layer. As a yearly average, it represented only 31% of E_s, which is realistic.

LUE

As a yearly average (Fig. 2a), LUE was very similar (around 0.3 g_{DM} mol_{PAR}^{-1}) for both layers (coconut and grass). Seasonally, LUE varied similarly for stand and coconut layers by a factor of 3, i.e. between 0.17 and 0.52 g_{DM} mol_{PAR}^{-1}. However, for grass, the factor was six.

Large seasonal variations of LUE might appear detrimental to estimations of NPP by ε-process models. In order to cope with that limitation, we attempted to interpret and model the seasonal variations of LUE. LUE_S was plotted against PAR_i and NPP_s in Fig. 3a. When the same variables were standardized from 0 to 1 in order to remain comparable (data not shown), the respective slopes ranged from -1.06 to +0.48, i.e. by a factor of around 2.2 in absolute value, indicating that LUE_s was much more relying on PAR_i than on NPP_s. This was consistent with rather low seasonal variations for NPP. The coefficient of determination of the relationship (R^2) was not presented here, considering that neither NPP_s nor PAR_i were independent from LUE_s (auto-correlated variables).

For every layer, LUE appeared to be maximum during the cool season (Fig. 2a), when PAR_i was minimum, the sun elevation (β) was lower, and the fraction of diffuse radiation (*f*DIF) was higher. We propose here (Fig. 3c) a multiple linear regression model of LUE using only factors that can be remotely sensed or computed from climate files, in the form:

$$LUE = a \cdot PAR_i + b \cdot fDIF + c \cdot \sin\beta + d \qquad (2)$$

where a, b, c and d are parameters, adjusted empirically using the least square method.

Ninety-five percent of the variability of LUE_s was predicted using this simple empirical model, with a RRMSE of only 8%.

WUE

As a yearly average (Fig. 2b), WUE was quite similar (around 3.7 and 4.0 g_{DM} kg_{H2O}^{-1}) for stand and coconut, respectively. For grass, it was only 2.4 g_{DM} kg_{H2O}^{-1}. Also seasonally, WUE varied quite similarly for stand and coconut layers by a factor of 2 to 2.8. However, for grass, the factor was five. For every layer, WUE appeared to be maximum during the cool season (Fig. 2b), when PAR_i was minimum.

WUE_s was plotted against E_s and NPP_s in Fig. 3b. When the same variables were standardized from 0 to 1 in order to remain comparable (data not shown), the respective slopes ranged from -0.84 to +0.53, i.e. by a factor of around 1.6 in absolute value, indicating that WUE_s was much more relying on E_s than on NPP_s. Again, the coefficient of determination of the relationship (R^2) was not presented here.

We propose a multiple linear regression model of WUE, using only factors that can be remotely sensed or computed from climate files (Fig. 3d), in the form:

$$WUE = a \cdot PAR_i + b \cdot VPD + c \cdot \sin \beta + d \tag{3}$$

Eighty-three percent of he variability of WUE_s was predicted by using this simple empirical model, with a RRMSE of 11%.

Conclusions

Although the upper-layer and the under-storey received rather constant fractions of the incoming radiation, the variability in NPP, evapo-transpiration, LUE and WUE appeared much larger for the under-storey, which we interpret to originate from occasional very low amounts of light and also occasional drought in the superficial soil layers, worsened by shallow rooting of grass, as compared to coconuts. The under-storey thus appeared to be less bulked than the over-storey for major physiological variables. This observation appears somewhat counter-intuitive and would deserve comparison with other multi-layer or agroforestry systems.

Important seasonal variations in LUE and WUE might appear as an impediment for inferring NPP from remote sensing of *f*IPAR and of evapo-transpiration. However the simple empirical models proposed here can cope with such a seasonal variability, as the only use variables that can be remotely-sensed and yield reasonably well.

Surprisingly, the yearly average of LUE remained rather similar for the stand and for each of its layers. It would be of interest to understand if this observation would be confirmed in plantations displaying different densities. In this case, it might simplify the problem of estimating LUE in two-layer stands by remote sensing.

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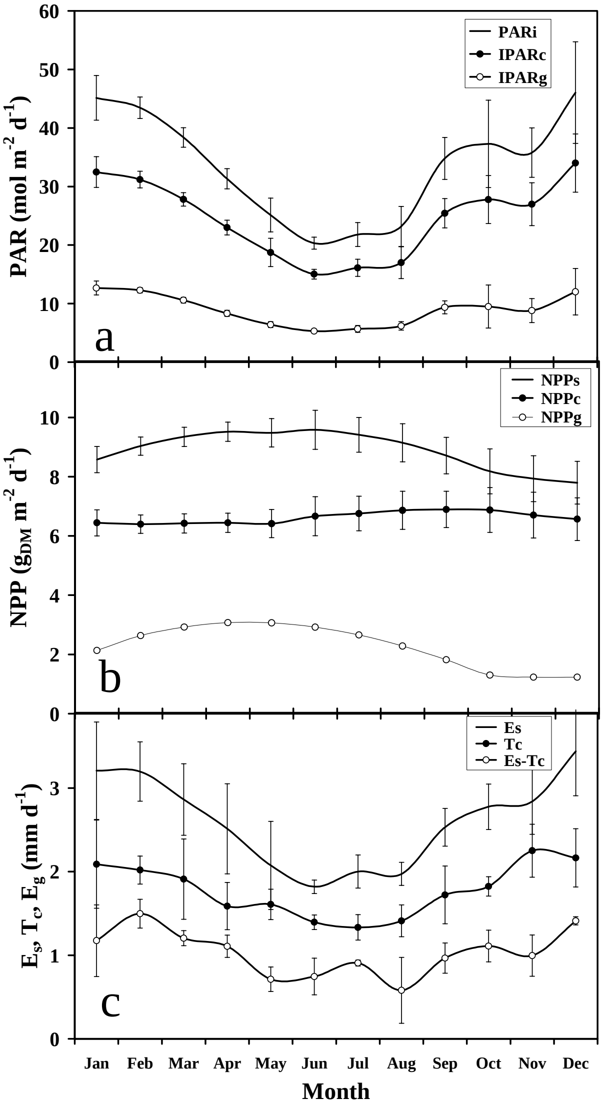

Fig. 1: Seasonal and interannual variations of available photosynthetically active radiation (PAR), Net Primary Productivity (NPP) and evapo-transpiration (E, T) in a two-layer coconut + grass plantation. **a**/ Incident PAR (PAR_i), PAR intercepted by the coconut canopy ($IPAR_c$) and PAR transmitted to the under-storey ($IPAR_g$); **b**/ NPP; **c/** Evapo-transpiration of the whole stand (E_s: eddy-covariance), transpiration of the coconut trees (T_c: sapflow) and evapo-transpiration of the under-storey ($E_g = E_s - T_c$ only for non-rainy days, *i.e.* no rain interception). Subscripts: s: stand; c: coconut layer; g: grass under-storey. One symbol is a mean monthly average and error bars are SD for three years (2002, 2003, 2004). NPP of grass was observed for 18 months only and extrapolated. Coconut + grass plantation, VARTC-Vanuatu, 2002-2004.

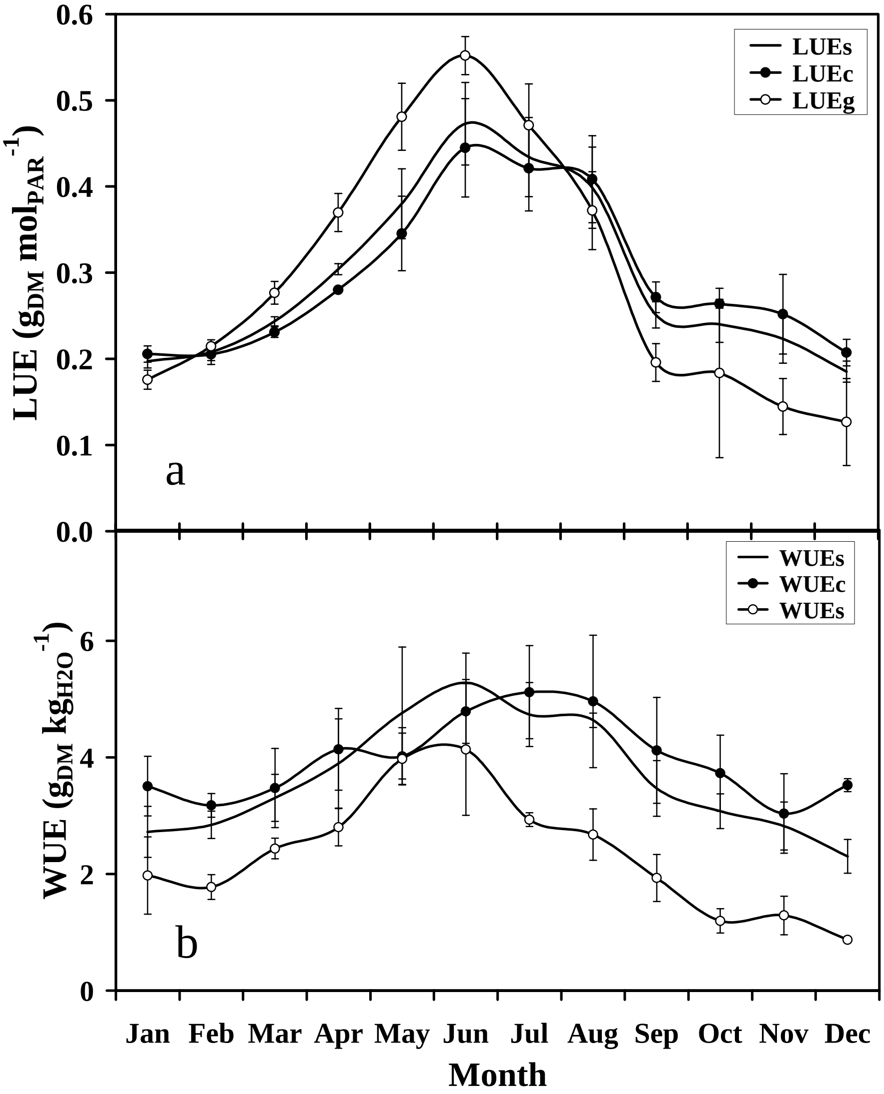

Fig. 2: Seasonal and interannual variations of **a/** light-use-efficiency (LUE) and **b/** water-use-efficiency (WUE) in a two-layer coconut + grass plantation. Subscripts: s: stand; c: coconut layer; g: grass under-storey. One symbol is a mean monthly average and error bars are SD for three years (2002, 2003, 2004). Coconut + grass plantation, VARTC-Vanuatu, 2002-2004.

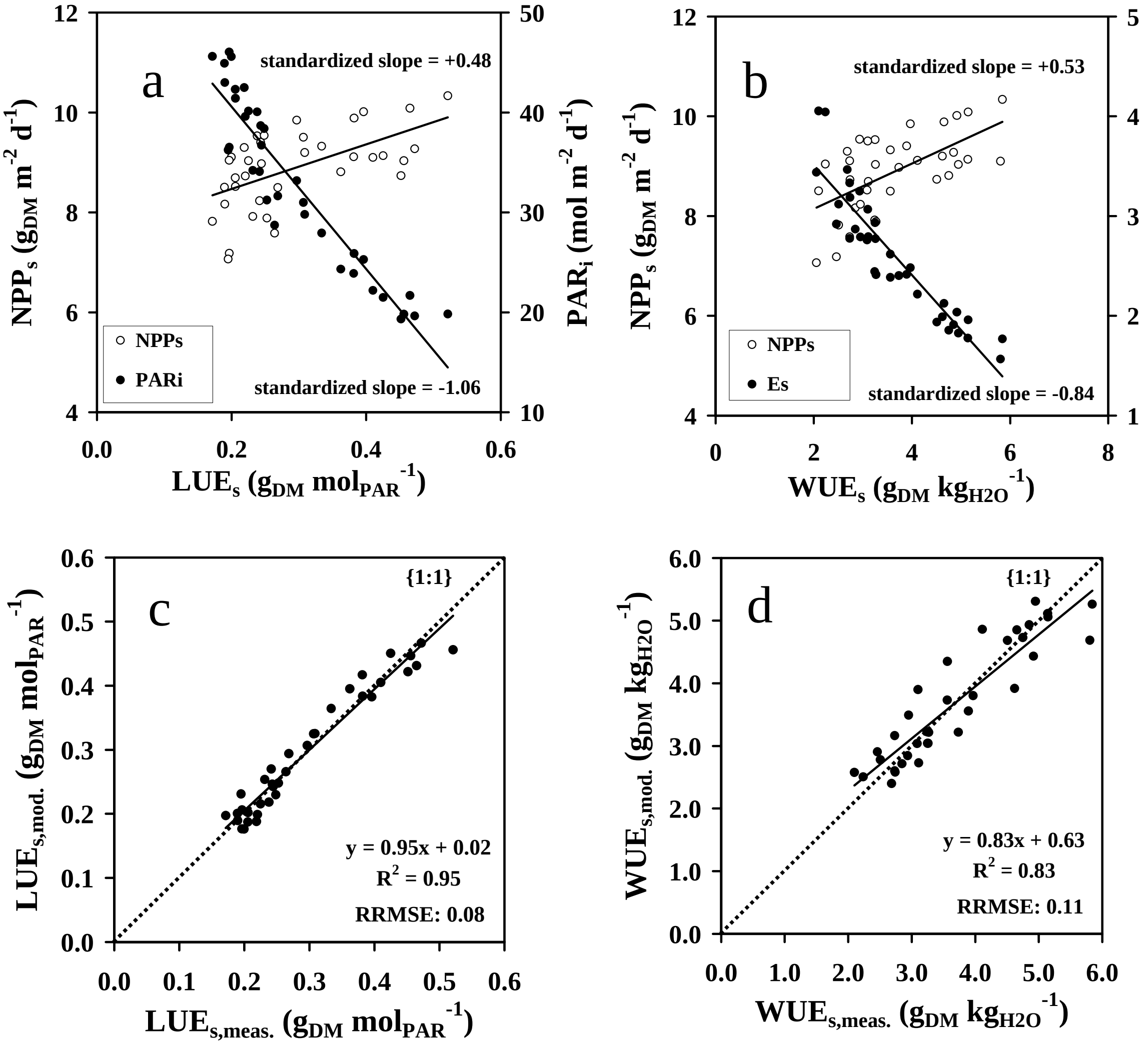

Fig. 3: Correlations between **a/** light-use-efficiency (LUE$_S$) and NPP$_s$ or incident PAR (PAR$_i$); **b/** water-use-efficiency (WUE$_S$) and NPP$_s$ or evapo-transpiration (E$_s$); **c/** and **d/** empirical modelling of the seasonal variations of LUE$_s$ and WUE$_s$, respectively, as a function of variables that can be remotely sensed (see text). "Standardized slope" is referring to slopes obtained after all variables from Fig. 3a and 3b were standardized from 0 to 1, in order to remain comparable. Subscript "s": stand. One symbol is a mean monthly average (2002, 2003, 2004). Coconut + grass plantation, VARTC-Vanuatu, 2002-2004.