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Scaling-up productivity (NPP) using light or water use efficiencies (LUE, WUE) from a two-layer tropical plantation

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Abstract Net primary productivity (NPP) is a key driver of ecosystem C balance. Scaling NPP up to larger areas requires indirect methods: (a) for examble epsilon models based on light use efficiency (LUE = NPP/APAR, where APAR is the absorbed photosynthetically active radiation by green elements of canopy, or else models based on water-use-efficiency (WUE = NPP/E, where E = evapo-transpiration); (b) remote sensing tools to estimate the fraction of APAR (*f*APAR) from vegetation indexes, or to estimate E. However, LUE and WUE are suspected to vary in space (edapho-climatic conditions, planting density) and time (seasonality, age), which needs to be documented before scaling up. Moreover, the application of this scaling approach to agroforestry systems with a stratified canopy may be difficult, since each layer contributes to the overall ecosystem light- and water-use efficiencies. The seasonal and inter-annual variabilities of LUE and WUE was assessed in a very simple bi-layer tropical coconut grove displaying minimum climatic and LAI variations, distinguishing the upper layer of coconuts, the herbaceous under-storey and the whole stand (subscripts C, H and S, respectively). We monitored NPP biometrically during 3 years above and below ground, together with microclimate and E_S above the canopy (eddy-covariance), transpiration (T_C) by sapflow, and $f\text{APAR}_C$ by LAI-2000 combined with canopy light absorption models. The partitioning of APAR, NPP and E was very close to the rule-of-thumb of canopy coverage by upper-layer (75%). Also the mean annual value of LUE_S (1.7 g_{DM} $\text{MJ}^{-1}_{\text{PARi}}$) or mean WUE_S (3.7 g_{DM} $\text{kg}^{-1}_{H_2O}$) were mainly driven by the upper-layer of coconuts. However, the under-storey experienced around twice as much seasonal variations of NPP, E, LUE and WUE than the upper-storey. Given that NPP_S varied by only 23% over the year, the high seasonal variations of WUE_S (240%) and LUE_S (250%) were mostly driven by the variations of APAR_S (230%) and were adjusted successfully using climate, age and density data, as a first step to estimate NPP on larger scales using climate, GIS and remote-sensing.

Keywords *Cocos nucifera* L. · Flux partitioning · Seasonal and inter-annual variations · Scaling up · Radiation use efficiency

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Introduction

Net primary productivity (NPP), defined as the organic matter produced over a specified interval (Clark et al. 2001) i.e. biomass build-up and litter production (mortality), is a key driver for ecosystem C balance, for Clean Development Mechanism (Roupsard et al. 2008b; UNFCCC 2008), and for agronomical (yield) applications. NPP is currently being investigated on a global scale, through meta-analyses of field data (e.g. Scurlock and Olson 2002; Luyssaert et al. 2007). 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, for young and middle-aged classes, and for the belowground compartment.

Scaling NPP spatially from the stand up to the landscape or the region requires indirect methods such as those involving a combination of remote-sensing and modelling approaches (Gower et al. 1999; Goetz et al. 2000; Turner et al. 2006; Friend et al. 2007). These approaches rely either on process-based models (Moran et al. 1996; Nouvellon et al. 2001; Inoue and Olioso 2006) or, more commonly, on simpler models requiring a limited number of input parameters, such as the widely used parametric ε-models, based on the light use efficiency (LUE,epsilon), defined as the ratio NPP/APAR, where APAR is the absorbed photosynthetically active radiation by the green elements of the cover (Monteith 1972; Gower et al. 1999; Nouvellon et al. 2000). A major assumption in these models is that NPP can be related linearly to APAR, the slope (LUE) being a constant: it is generally assumed that photosynthesis of the cover (gross primary productivity, or GPP) responds linearly to APAR through space (according to the leaf area index, LAI) and through time (according to seasons) and that NPP remains a constant fraction of GPP.

LAI is also a key variable for NPP models. The direct method for estimating LAI destructively or using litter-traps remains a reference for local studies, but suffers from important limitations during the process of up-scaling, since the allometric coefficients used to estimate LAI can vary according to numerous ecological factors. Remote sensing can be used to estimate regionally the fraction of absorbed PAR (*f*APAR) from vegetation indexes (e.g. Normalized difference vegetation index, NDVI, Asrar et al. 1984). It was proven useful to classify the vegetation according to LAI, after inverting simple Beer-law interception models which are linking the fraction of intercepted light to extinction coefficient and plant area index, or after using more detailed refined models dealing with leaf angle distribution and clumping (Nilson 1971), ideally distinguishing the green elements from the whole cover and leading to true LAI. Hence, *f*APAR from NDVI is often calibrated against *f*IPAR assed in the field by optical methods (e.g. LAI 2000 or hemispherical photography). Both approaches are spatially explicit, although they share similar limitations for inferring the true LAI from the previously described models, and NDVI is known to saturate for high values of LAI. Remote-sensing can also be used to estimate evaporation, E, from energy balance or from models (Moran et al. 1996; Allen and Bastiaanssen 2005). Thus, alternatively to LUE models, models based on water-use-efficiency (WUE = NPP/E, where E = evapo-transpiration) can be used to upscale NPP.

In most attempts to scale up NPP, the spatial, temporal (seasonal) variations of LAI, LUE and WUE, the age of the systems, the separation of green and non-green elements of the cover and the quality of climatic data are reported to be critical (Zaehle et al. 2006; Zhao et al. 2006). For instance, in a coniferous forest, Lagergren et al. (2005) observed important variations of LUE seasonally and interannually, according to temperature and vapour pressure deficit (VPD). Applications of remote sensing for agroforestry systems even suffer from supplementary impediments: first, it is suspected that distinct contribution of the layers for the reflected signal can be detrimental for classification, although recent development of light detection and ranging (LIDAR) might help documenting spatially their complex vertical structure (Hilker et al. 2008; Sherril et al. 2008); second, NPP, C balance, remote sensing and parametric models remain scarce for agroforestry systems (Mattamachado and Jordan 1995; Binkley and Ryan 1998; Mobbs et al. 1998; Sundarapandian et al. 1999; McGrath et al. 2000; Das and Chaturvedi 2005); last, field data for calibration of simulated fluxes should be partitioned ideally between the upper and the under-storey, which is extremely rare.

We propose here to document LUE and WUE, their seasonal variations and their partitioning for a very simple bi-layer system, composed by a coconut upper-storey and an herbaceous under-storey, both growing continuously in tropical optimal conditions, with high fertility, without seasonal drought, with very low variations of LAI and temperature, moderate variations of VPD, the seasonality of which is driven by radiation. This study is proposed in order to facilitate spatial and temporal scaling up of NPP in similar coconut groves, and to provide a simple example of scaling up of NPP for other agroforestry systems. Some major prospect of calibrating remote-sensing tools in coconut groves would be to map *f*APAR or APAR directly, and to verify how they vary among plots differing by age, density (given by land registers), cultivars, fertilisation, drought etc. The monitoring of APAR can be agronomically meaningful for studying modifications of APAR after foliar attacks, hurricanes or drought events (e.g. El-niño). Also, it must be stressed that around 46% of coconut NPP is for fruits, and this compartment is very flexible as compared to vegetative compartments (Navarro et al. 2008), suggesting that a monitoring of NPP through remote-sensing tools might find applications in the prediction of yield on large scales.

The aim of this article is: (a) to monitor seasonal and inter-annual variations of NPP, E, APAR, LUE and WUE in both strata of a mature coconut grove (coconut palm + herbaceous under-storey); (b) to explain and model the variations of LUE and WUE; (c) to propose a method for scaling NPP of agroforestry systems from plot up to region, using GIS only or remote-sensing tools.

Materials and methods

Location, stand and climate

The "Cocoflux" experiment was contributing to the FLUXNET database of eddy covariance sites (FLUXNET 2008). The coconut plantation was located in Santo, Vanuatu, South Pacific (15°26.6′ S, 167°11.5′ E). The stand of 8 ha had been row-planted in 1983 with the Vanuatu red dwarf × Vanuatu tall (VRD × VTT) high-yielding hybrid coconut variety (Labouisse et al. 2005), and the experiment lasted from 2002 to 2004. Adult (around 20 YAP) coconut tree canopies covered around 75% of the ground. The herbaceous under-storey included 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 herbs were managed by slashing every 2–3 months but were left untouched in the windrow. The true leaf area index (LAI), obtained by destructive sampling was 2.95 ± 0.15 SD for the coconut layer (Roupsard et al. 2008a, b), and 2.6 ± 0.14 SD for the herbs, i.e. a total of 5.6 ± 0.29 SD, remarkable for little seasonal variations.

The climate was "tropical wet", according to the World climate classification of Köppen (Peel et al. 2007). During the experiments (three complete years, 2002–2004), climate variables were logged above the coconut canopy (22 m). Annual rainfall for two decades (1983–2003) was 2,763 mm year^{-1}, peaking during the warm and rainy season (December–April), with an average of 327 mm month^{-1}. A cooler and drier season occurred from June to September, with an average of 119 mm month^{-1}. Incident photosynthetically active radiation (PAR$_\mathrm{i}$) was measured with home-made PAR-probes (Dauzat and Eroy 1997) calibrated against commercial ones. PAR varied seasonally by a factor of 2.3, peaking during the warm and wet season. Air temperature displayed very low seasonal variations, 24.8 ± 1.4°C. The daily maxima for vapour pressure deficit (VPD) did not exceed 12 hPa. Soil volumetric water content remained above 0.49 $\mathrm{m^3_{H_2O}\ m^{-3}_{soil}}$ when considering the total soil profile (0–250 cm), i.e. close to field capacity. These recordings suggest that seasonality was mainly driven by radiation. The growth conditions (favourable soil texture, high fertility, absence of seasonal water shortage) were considered to be optimum for coconut cultivation (Roupsard et al. 2006) and rather simple for interpreting eventual seasonal variations of LUE or WUE.

NPP of coconut tree (NPP$_\mathrm{C}$) and herbs (NPP$_\mathrm{H}$)

The NPP experiment has been reported previously by Navarro et al. (2008). Briefly, for every plant organ monitored, net primary productivity (NPP) was the sum of dry mass build-up (ΔDM) and of mortality or litter production (L), as follows:

$$\mathrm{NPP} = \Delta DM + \mathrm{L}. \qquad (1)$$

The tree sampling was stratified, based on a preliminary stand survey of tree height and nut load distributions. Ten trees were monitored non-destructively (January 2002–December 2005, 19–22 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, based on destructive samplings (10 other representative trees felled for biomass; sub-samples dried in a ventilated oven at $T° = 70°\mathrm{C}$ to constant weight). Belowground tree NPP was assessed by large rhizotrons combined with sequential trenching, in order to assess root lifespan and turnover.

Above-ground herbaceous NPP was assessed by successive harvests ($N = 8$), during 18 months between 2002 and 2004, 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, $\mathrm{NPP_H}$ 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).

According to Navarro et al. (2008), $\mathrm{NPP_S}$ agreed very well on a yearly basis with the difference between GPP (the ecosystem photosynthesis) and R_a (the autotrophic respiration), where GPP was obtained by eddy-covariance (the sum of diurnal net ecosystem exchange and nocturnal ecosystem respiration, after filtering nocturnal ecosystem respiration for friction velocity >0.4 and adjusting it for actual diurnal temperatures). This result supported that $\mathrm{NPP_S}$ was realistic.

Radiation measurements and models

Light interception and absorption by coconut and herbaceous layers

Micro-climate variables were logged at reference height (22 m on top of the eddy covariance tower) as described by Roupsard et al. (2006). The cloudiness was computed using the ratio between global and clear-sky solar radiation (FAO 1998), it ranged from 0.5 during the warm season to 0.75 during the cool season). The fraction of diffuse radiation was computed according to the ratio between global and extra-terrestrial radiation, as proposed by Spitters et al. (1986). *f*IPAR (the fraction of intercepted PAR, i.e. the complement of PAR transmittance below the canopy) has been reported at the scale of the coconut cover (green + non-green elements) using a LAI-2000 Plant Canopy Analyser by Roupsard et al. (2008a). $f\mathrm{APAR_C}$ (the fraction of absorbed PAR), has been computed at the scale of the green elements (leaflets) of the coconut canopy, using a combination of Sun-shade and 3D architectural models, hence taking into account the actual leaf angle distribution function (LADf) of coconut leaflets, the actual clumping index (Ω), the sine of solar elevation ($\sin\beta$), and the fraction of diffuse light. Herbaceous *f*APAR ($f\mathrm{APAR_H}$) was computed here from the next equations:

$$f\mathrm{IPAR_H} = 1 - \mathrm{e}^{(-k_\mathrm{H}\cdot\mathrm{LAI_H})} \tag{2}$$

$$f\mathrm{APAR_H} = \alpha \cdot f\mathrm{IPAR_H} = 0.95 \cdot f\mathrm{IPAR_H} \tag{3}$$

$$\mathrm{APAR_H} = f\mathrm{APAR_H} \cdot \mathrm{PAR_i} \cdot (1 - f\mathrm{IPAR_C}). \tag{4}$$

We used the measured time-course of herbaceous leaf biomass (weighted for the clear interrow, row and windrow), the measured average leaf mass:area ratio (LMA) of $45.2 \pm 3.3\ \mathrm{g_{DM}\ m_{leaf}^{-2}}$, the derived time-course for $\mathrm{LAI_H}$, assuming a spherical LADf (extinction coefficient for PAR, $\mathrm{k_H} = 0.5$), no clumping ($\Omega = 1$), and absorption at full light interception (α) of 0.95 (Monsi and Saeki 1953). Light intercepted by the stand ($\mathrm{IPAR_S}$) was subsequently estimated as the algebraic sum of $\mathrm{IPAR_C}$ and $\mathrm{IPAR_H}$, and similarly for absorbed light ($\mathrm{APAR_S}$).

Depending on the availability of remote-sensing multispectral tools for estimating *f*APAR or not, LUE may be more useful for estimating NPP when based on IPAR than on APAR. Both types of LUE where thus presented below.

Evapo-transpiration

Evapo-transpiration results have been reported in detail by Roupsard et al. (2006). Eddy-covariance measurements were performed continuously above the canopy (22 m), yielding the evapo-transpiration of the stand, $\mathrm{E_S}$. Tree transpiration ($\mathrm{T_C}$) was measured by thermal dissipation (Granier 1985), on the ten trees monitored for NPP, and using home-made probes specifically calibrated in the laboratory, and validated in the field.

It is assumed here that during non-rainy days, $\mathrm{E_S} - \mathrm{T_C}$ yields $\mathrm{E_H}$, the evapo-transpiration of the under-storey (herbs + soil). 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_H dataset, leaving around 50% of data.

Statistical analysis

Variables were analysed in order to test the significance of seasonal variation (12 months) and of annual variation (3 years). One monthly average represented one replication. Normality and distribution of residues were checked. Variances were homogeneous (Bartlett's test) and the variables did not require transformation. Univariate ANOVAs were computed with the SAS statistical package using the general linear model (Proc GLM).

Results and discussion

The uncertainties of indirect estimations of NPP using LUE have been extensively reviewed by Gower et al. (1999). In the present study, we addressed their main concerns: true PAR_i was actually measured above the canopy; the relationship between intercepted and absorbed radiation was documented for the green elements of the coconut; leaf angle distribution, clumping and fraction of diffuse light were taken into account when computing *f*APAR by the sun-shade model; NPP was measured above and below-ground, including mortality and turnover; upper and under-storey were taken into account; the monitoring lasted 3 years, thus integrating inter-annual variations of climate and phenology; the influence of environmental factors was minimized by choosing this wet tropical example.

PAR interception and absorption

Incident PAR (PAR_i) showed seasonal variation (Fig. 1a; Table 1) by a factor of 2.3 between 4.6 MJ_{PAR} m^{-2} day^{-1} (cooler season) and 10.4 MJ_{PAR} m^{-2} day^{-1} (warm season), due to variations of solar angle (vertical in November and in February) and of cloudiness. PAR intercepted by the coconut cover ($IPAR_C$, green + non-green elements) was 74% of PAR_i (Table 1), which was close to the rule-of-thumb, considering that the coconut covered around 75% of the soil. PAR absorbed by the coconut leaflets ($APAR_C$, green elements only) was 60% of PAR_i, $APAR_H$ was 18% and $APAR_S$ was 78%. For low solar elevations (mornings, evenings and cooler season), PAR available for the under-storey could

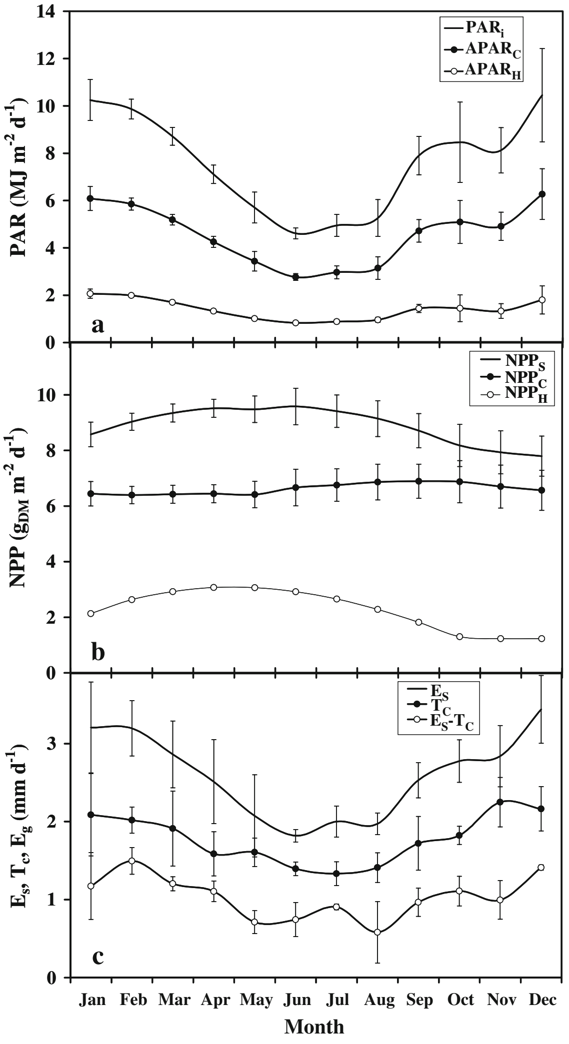

Fig. 1 Time-course of photosynthetically active radiation (PAR), Net primary productivity (NPP) and evapo-transpiration (E, T) in a two-layer coconut + herbs plantation. **a** Incident PAR (PAR_i), PAR absorbed by the coconut canopy ($APAR_C$) and PAR absorbed by the under-storey ($APAR_H$); **b** NPP; **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 ($E_H = E_S - T_C$ only for non-rainy days, i.e. no rain interception). Subscripts: *S*, stand; *C*, coconut layer; *H*, herbaceous under-storey. One symbol is a monthly average and error bars are SD for 3 years of monitoring. NPP of herbs was observed for 18 months only and extrapolated. Coconut + herbs plantation, VARTC-Vanuatu, 2002–2004

Table 1 Statistics on seasonal and inter-annual variability of the main variables, monitored during 36 months between 2002 and 2004

Variable	Unit	Mean	SD	CV	Monthly min.	Monthly max.	Seasonal factor of magnitude	F value (d*F* = 11)	*P*	Seasonal effect	Annual min.	Annual max.	Inter-annual factor of magnitude	F value (d*F* = 2)	*P*	Interannual effect
NPP_C	$g_{DM}\ m^{-2}\ day^{-1}$	6.62	0.58	0.09	6.40	6.89	1.08	0.35	0.6470	NS	6.33	7.14	1.13	19.11	0.0001	***
NPP_H	$g_{DM}\ m^{-2}\ day^{-1}$	2.72	0.70	0.26	1.23	3.07	2.50	NM	NM	NM	2.27	2.27	1.00	NM	NM	NM
NPP_S	$g_{DM}\ m^{-2}\ day^{-1}$	8.89	0.58	0.06	7.80	9.58	1.23	3.72	0.0034	**	8.60	9.42	1.09	4.92	0.0134	*
E_S	$kg_{H_2O}\ m^{-2}\ day^{-1}$	2.60	0.40	0.15	1.82	3.44	1.89	5.82	0.0002	**	2.29	2.87	1.25	2.87	0.0710	NS
T_C	$kg_{H_2O}\ m^{-2}\ day^{-1}$	1.75	0.26	0.15	1.33	2.25	1.69	3.68	0.0037	**	1.63	1.98	1.22	4.80	0.0148	*
$E_S - T_C$	$kg_{H_2O}\ m^{-2}\ day^{-1}$	1.03	0.22	0.21	0.58	1.50	2.58	4.56	0.0009	**	0.92	1.09	1.19	1.17	0.3235	NS
PAR_i	$MJ_{PAR}\ m^{-2}\ day^{-1}$	7.46	0.75	0.10	4.61	10.45	2.27	19.93	0.0001	***	7.23	7.88	1.09	0.39	0.6823	NS
$fIPAR_C$_g + ng	–	0.74	0.03	0.04	0.72	0.75	1.05	0.67	0.7514	NS	0.73	0.75	1.04	3.77	0.0335	*
$IPAR_C$_g + ng	$MJ_{PAR}\ m^{-2}\ day^{-1}$	5.49	0.48	0.09	3.41	7.72	2.26	25.53	0.0001	***	5.26	5.72	1.09	0.31	0.7357	NS
$IPAR_H$_g + ng	$MJ_{PAR}\ m^{-2}\ day^{-1}$	1.43	0.26	0.18	0.83	2.02	2.43	7.75	0.0001	***	1.24	1.49	1.20	0.94	0.3996	NS
IPARS_g + ng	$MJ_{PAR}\ m^{-2}\ day^{-1}$	6.92	0.66	0.10	4.59	9.62	2.09	22.10	0.0001	***	6.70	7.29	1.09	0.35	0.7069	NS
$fAPAR_C$_g	–	0.60	0.01	0.02	0.59	0.60	1.02	0.67	0.7489	NS	0.60	0.61	1.01	3.78	0.0334	*
$APAR_C$_g	$MJ_{PAR}\ m^{-2}\ day^{-1}$	4.47	0.42	0.09	2.77	6.27	2.26	22.76	0.0001	***	4.31	4.70	1.09	0.34	0.7137	NS
$APAR_H$_g	$MJ_{PAR}\ m^{-2}\ day^{-1}$	1.36	0.25	0.18	0.83	2.07	2.48	7.75	0.0001	***	1.24	1.49	1.20	0.94	0.3995	NS
$APAR_S$_g	$MJ_{PAR}\ m^{-2}\ day^{-1}$	5.83	0.63	0.11	3.60	8.15	2.26	17.90	0.0001	***	5.64	6.18	1.10	0.43	0.6541	NS
WUE_C	$g_{DM}\ kg^{-1}_{H_2O}$	3.94	0.69	0.17	3.04	5.12	1.68	3.20	0.0083	**	3.34	4.49	1.34	6.61	0.0038	**
WUE_H	$g_{DM}\ kg^{-1}_{H_2O}$	2.33	0.47	0.20	0.87	4.14	4.74	14.79	0.0001	***	2.32	2.34	1.01	0.00	0.9989	NS
WUE_S	$g_{DM}\ kg^{-1}_{H_2O}$	3.65	0.53	0.15	2.22	5.28	2.38	10.43	0.0001	***	3.18	3.96	1.24	1.90	0.1653	NS
LUE_C_IPAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.30	0.15	0.11	0.90	1.96	2.17	3.20	0.0083	**	1.26	1.35	1.07	6.61	0.0038	**
LUE_H_IPAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.79	0.26	0.14	0.85	3.50	4.14	14.79	0.0001	***	1.77	2.00	1.13	0.00	0.9989	NS
LUE_S_IPAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.40	0.14	0.10	0.89	2.26	2.54	10.43	0.0001	***	1.39	1.43	1.03	0.16	0.8492	NS
LUE_C_APAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.60	0.17	0.11	1.09	2.41	2.21	21.34	0.0001	***	1.56	1.65	1.06	0.17	0.8421	NS
LUE_H_APAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.89	0.27	0.14	0.85	3.50	4.14	34.89	0.0001	***	1.77	2.00	1.13	0.17	0.8421	NS
LUE_S_APAR	$g_{DM}\ MJ^{-1}_{PAR}$	1.66	0.16	0.10	1.06	2.67	2.51	35.53	0.0001	***	1.65	1.68	1.02	0.02	0.9821	NS

Coconut plantation, VARTC-Vanuatu

NM not measured; *_IPAR* variable calculated based on IPAR; *NS* non significant; *_APAR* variable calculated based on APAR; *, **, *** significant, very significant, highly significant, respectively; *_g + ng*: green + non-green elements; *_g*: green elements become rather low. However, the magnitude of seasonal variations of PAR_i, $APAR_C$, $APAR_H$ and $APAR_S$ remained comparable (factor around 2.3). Although seasonal variations of PAR and all its derivates were very highly significant, they were generally not significant inter-annually (Table 1).

Net primary productivity (NPP)

Considering the coconut NPP (NPP_C), a major assumption of the epsilon models (Monteith 1972) is the proportionality between photosynthesis and absorbed PAR at the level of the cover, without the saturation that usually occurs at leaf scale: this assumption was verified here, from the linear relationship we obtained between GPP_S and PAR_i (linear regression with $r^2 = 0.75$; data not shown). However, we found no seasonal proportionality between NPP_C and PAR (Fig. 1a, b) or NPP_C and GPP, i.e. no constant LUE. Seasonally, NPP_C was varying essentially according to NPP of the nuts (very little variation in NPP of vegetative organs), although NPP_C did not vary much (factor 1.08, Fig. 1b, Table 1) and peaked around September–October, i.e. 6 months after the peaks of PAR and of photosynthesis (GPP, data not shown): this delayed pattern between GPP and NPP has already been interpreted (Mialet-Serra et al. 2005, 2008; Navarro et al. 2008) considering the flowering phenology, the dynamics of nut growth (nut C demand), the stocks and dynamics of the reserve compartment. The determinants of yield were investigated further here, trying to relate yield with NPP_C, NPP of the nuts or with PAR. Yield in coconut is the copra harvest, i.e. the harvest of the dry albumen within the nut, which is the product of nut yield by the copra content. Although on average, NPP of nuts and nut harvest were the same (around 3.1 g_{DM} m^{-2} day^{-1}, i.e. 46% of NPP_C), we found here that nut harvest and copra content displayed larger seasonal fluctuations than NPP of the nuts, and a time-lag of another 6 months (Fig. 2a, b) with it. The copra yield (average around 3.4 t_{DM} ha^{-1} $year^{-1}$) fluctuated thus apparently better in phase with PAR (Fig. 2b) than NPP_C did. However, this simple finding should not overlook the 1-year delay between flowering and nut harvest (6 months to reach maximum nut NPP, 6 other months to ripen). Moreover, the correlation between yield and PAR was not significant. As a whole, it appeared that coconut yield expressed a pattern even more complex than NPP_C or NPP of nuts. Accordingly, we did not attempt here to model yield for the purpose of up-scaling it from plot to region: this would require more extended investigations, notably on the expression of reproductive phenology in various growing conditions.

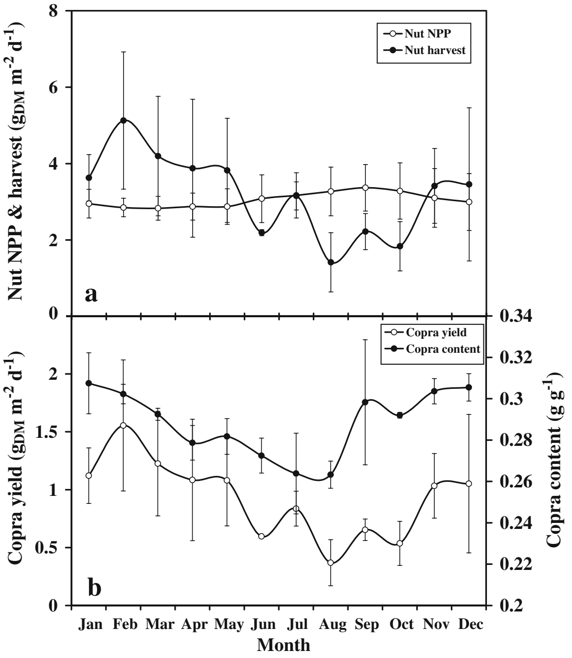

Fig. 2 Time-course of coconut yield (copra) components **a** net primary productivity of the nut compartment and nut harvest and **b** nut copra content and copra yield. One symbol is a monthly average and error bars are SD for 3 years. Coconut + herbs plantation, VARTC-Vanuatu, 2002–2004

Compared with radiation, the temporal variation of stand (NPP_S) productivity (Fig. 1b; Table 1) was reduced (factor 1.2). NPP_H was not in phase with PAR either. The under-storey was prone to important seasonal NPP limitations with confounding effects, originating from schedule of slashing, low incoming radiation during the cool season, and casual superficial soil water depletion (which did not affect the coconut trees, rooted down to 3 metres). As a yearly average, NPP_C represented 74% of NPP_S, close to the rule-of-thumb. The seasonal variations of NPP_S were highly significant (Table 1) and were more influenced by the under-storey (NPP_H: seasonal variation with a factor 2.5), than by coconuts. Hence, although the under-storey may represent a limited fraction of the annual productivity of the ecosystem (around 26%), it can potentially influence much its seasonal variations when the upper-storey does not fluctuate much.

Evapo-transpiration

The time-course of stand evapo-transpiration (Fig. 1c; Table 1) varied seasonally between 1.8 and 3.4 mm day^{-1} (factor of 1.9, consistently to radiation), whereas coconut transpiration (T_C) varied only by a factor of 1.7, probably a consequence of stomatal regulation of transpiration during conditions of higher evaporative demand (Roupsard et al. 2006). On a yearly basis, T_C represented 68% of E, close to the rule-of-thumb. $E_H = E_S - T_C$, computed only for non-rainy days fluctuated seasonally by a factor of 2.6, confirming that the under-storey was more variable than the upper-layer (slashing events, microclimate and superficial soil water conditions). The inter-annual effect was low or nil for evapo-transpiration variables.

Light-use-efficiency

At the level of the plot

Annual averages of LUE calculated on an APAR basis were similar (around 1.6 g_{DM} MJ^{-1}_{APAR}) for coconut, and stand, and were 1.9 for herbs (Table 1). Reviewing LUE results among vegetation functional groups, Gower et al. (1999) reported that for non-crop C_3 plants, LUE ranged essentially between 1 and 2 g_{DM} $MJ^{-1}_{APAR.}$ Our estimates of coconut grove LUE fell in this range, between natural tropical evergreen broadleaved ecosystems (around 0.5 g_{DM} MJ^{-1}_{APAR}) and planted ones (ranging from 1.5 to 2.5 g_{DM} $MJ_{APAR}{}^{-1}$), and were similar to the values reported by Dufrêne et al. (1990) and Ruimy and Saugier (1994) for oil palm (1.6–1.83 g_{DM} MJ^{-1}_{APAR}). LUE_C clearly drove LUE_S in this bi-layer system where upper-layer represented 75% of coverage, suggesting that it would be worth testing this result under other configurations (age, density, etc.).

Seasonal LUE reports are scarce, most studies using epsilon-models operate yearly, or use a maximum value for LUE which is modulated seasonally by climate variables. Alternatively, process-models may be preferred when dealing with seasonal variations, but they generally require more parameters (Le Maire et al. 2005), which are highly difficult to document on a spatial scale. In spite of rather steady conditions for LAI, soil water availability, temperature and VPD, LUE varied highly significantly seasonally for stand and coconut layers by a factor around 2.5 (Fig. 3a; Table 1), i.e. between 1.06 and 2.7 g_{DM} MJ^{-1}_{APAR}. For herbs, the factor was 4.1. It must be stressed here that three important variables contributing directly to LUE, i.e. NPP_C, *f*IPAR and *f*APAR did not vary significantly seasonally, and they were the only ones not to vary in the dataset (Table 1): hence LUE was mainly driven by PAR_i seasonally. Although the inter-annual variations of NPP_C and NPP_S were significant (Table 1), they were not significant for PAR or LUE and their derivates in general. A seasonally variable but inter-annually invariable LUE is thus a rather original result, which does complete the general assumption that LUE can be assumed constant for ecosystems or biomes on an annual basis.

For every layer, LUE appeared to be maximum during the cool season (Fig. 3a), when PAR_i was

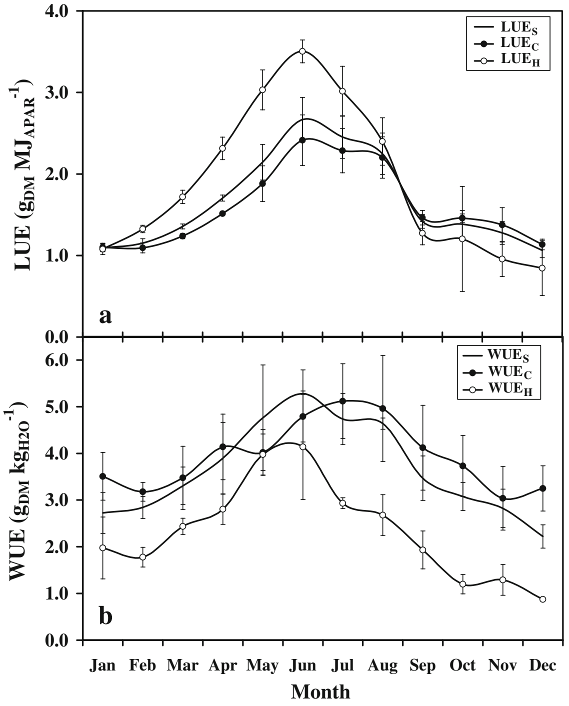

Fig. 3 Time-course of **a** light-use-efficiency (*LUE*) calculated with absorbed PAR (LUE_{APAR}) and **b** water-use-efficiency (*WUE*) in a two-layer coconut + herbs plantation. Subscripts: *S* stand; *C* coconut layer; *H* herbaceous under-storey. One symbol is a monthly average and error bars are SD for 3 years. Coconut + herbs plantation, VARTC-Vanuatu, 2002–2004

minimum, the sun elevation (β) was lower, and the fraction of diffuse radiation (fDIF) was higher for the 3 years considered.

Scaling up from plot to region without fAPAR

When remote-sensing multispectral tools are not available, i.e. $f\text{APAR}_\text{S}$ is not available, we propose a method for estimating LUE, using only climate variables (essentially radiation) and field informations (like land registers, aerial photographs, panchromatic imagery), on the density and age of plantations. We propose here (Fig. 4a) a multiple linear regression model of LUE using only factors that can be computed from climatic data, in the form:

$$\text{LUE}_\text{S} = a_\text{S} \cdot \text{PAR}_\text{i} + b_\text{S} \cdot f\text{DIF} + c_\text{S} \cdot \sin\beta + d_\text{S} \quad (5)$$

where PAR_i is the incident PAR, fDIF is the fraction of diffuse light, β is the sun elevation angle from horizontal, a_S, b_S, c_S and d_S are parameters fitted empirically using the least square method and given in Table 2. From Fig. 4a, 95% of the variability of LUE_S was predicted using this simple empirical model, with a relative root mean square error (RRMSE) of only 8%. Independent variable PAR_i was the major contributor to this adjustment, followed by $\sin\beta$ and then by fDIF, as presented in Table 3, comparing the RRMSE of various combinations. This model performed much better than when using solely IPAR_S as an independent variable (data not shown). Substituting IPAR_s–PAR_i did not improve the model further (Table 2). We propose that this model could be applied in order to derive seasonal and annual LUE_S of similar coconut groves, solely from climatic variables that can be obtained on a temporal and spatial scale using either weather station or world climatic databases (e.g. Worldclim, Hijmans et al. 2005) and fed into a GIS. Given the high LAI of the system (around 5.6), $f\text{IPAR}_\text{S}$ might be assumed close to 0.91 in order to obtain rough estimations of NPP_S of similar coconut groves.

However, predictions using this empirical model are suspected to become unreliable under dissimilar conditions (other tree densities, age, drought, fertility, cultivar, other characteristics of the under-storey). Addressing the difficult question of age and density, Roupsard et al. (2008a) proposed empirical relationships between the fraction of intercepted PAR ($f\text{IPAR}_\text{C}$) and a wide combination of tree ages (6–40 YAP, i.e. when trees are actually mature and yield fruits) or planting densities (95–180 trees ha^{-1}, the most usual density being 143–160). Their linear model linking $f\text{IPAR}_\text{C}$ with both age and density performed well ($r^2 = 0.87$; RRMSE = 0.07), irrespective of cultivars and countries. Assuming that LUE_C values reported here are quite representative of mature coconut trees individuals growing in fertile conditions and without drought and will not vary much according to age, density or cultivars, it is proposed a more general model for predicting seasonal or annual LUE_C and NPP_C, according solely to climatic variables, age (YAP) and density (D) from a GIS, following Eq. 6–8:

$$\text{LUE}_\text{C} = a_\text{C} \cdot \text{PAR}_i + b_\text{C} \cdot f\text{DIF} + c_\text{C} \cdot \sin\beta + d_\text{C} \quad (6)$$

$$f\text{IPAR}_\text{C} = e_\text{C} \cdot D + f_\text{C} \cdot \text{YAP}^2 + g_\text{C} \cdot \text{YAP} + h_\text{C} \quad (7)$$

$$\text{NPP}_\text{C} = \text{LUE}_\text{C} \cdot \text{PAR}_\text{i} \cdot f\text{IPAR}_\text{C} \quad (8)$$

where a_C, b_C, c_C and d_C were fitted, e_C, f_C, g_C and h_C were reported by Roupsard et al. (2008a), all given in

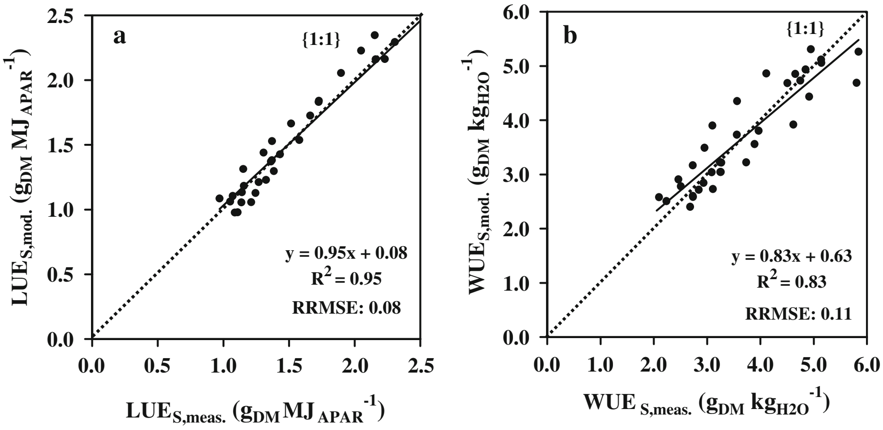

Fig. 4 Empirical modelling of the seasonal variations of stand **a** light-use-efficiency (LUE_s) and **b** water-use-efficiency (WUE_s) as a function of climatic variables (see text). One symbol is a monthly average for 3 years. Coconut + herbs plantation, VARTC-Vanuatu, 2002–2004

Table 2 Empirical adjustments for the main variables

Dependent variable	Independent variables													Source
		PAR_i	IPAR	APAR	*f*Dif	sin(β)	VPD	Density	Age^2	Age	*f*IPARC_g + ng	Constant	RRMSE	
	Units	MJ_{PAR} m^{-2} day^{-1}	MJ_{PAR} m^{-2} day^{-1}	MJ_{PAR} m^{-2} day^{-1}	–	–	hPa	tree ha^{-1}	$year^2$	year	–	–	–	–
f$IPAR_C$_g + ng	–							0.00315	−0.00059	0.02657		0.00968	0.070	Roupsard et al. (2008a) and Eq. 7
f$IPAR_S$_g + ng	–	0.91460										0.09510	0.010	This study
f$APAR_C$_g	–										0.31770	0.36530	0.100	This study
LUE_C_IPAR	g_{DM} MJ_{PAR}^{-1}	0.06170			2.98464	−5.58539						2.26755	0.103	This study, Eq. 6
LUE_C_IPAR	g_{DM} MJ_{PAR}^{-1}		−0.05891		1.63317	−3.59763						2.72190	0.092	This study
LUE_H_IPAR	g_{DM} MJ_{PAR}^{-1}	−0.42747			−5.15930	−9.14718						13.55145	0.138	This study
LUE_H_IPAR	g_{DM} MJ_{PAR}^{-1}	−0.40645			−0.89972	−16.08526						12.37880	0.160	This study
LUE_S_IPAR	g_{DM} MJ_{PAR}^{-1}	−0.02469			1.44433	−6.67224						4.60504	0.078	This study, Eq. 5
LUE_S_IPAR	g_{DM} MJ_{PAR}^{-1}		−0.03282		1.36589	−6.57043						4.63699	0.078	This study
LUE_C_APAR	g_{DM} MJ_{PAR}^{-1}	0.03344			3.19337	−5.98282						2.88070	0.087	This study
LUE_C_APAR	g_{DM} MJ_{PAR}^{-1}			0.02078	2.90370	−5.61088						2.99838	0.102	This study
LUE_H_APAR	g_{DM} MJ_{PAR}^{-1}	−0.44999			−5.43083	−9.62879						14.26494	0.138	This study
LUE_H_APAR	g_{DM} MJ_{PAR}^{-1}			0.28330	1.06457	−11.80116						7.49660	0.141	This study
LUE_S_APAR	g_{DM} MJ_{PAR}^{-1}	−0.07225			1.24950	−6.99555						5.53541	0.074	This study
LUE_S_APAR	g_{DM} MJ_{PAR}^{-1}			−0.04908	1.67141	−7.65809						5.41010	0.075	This study
WUE_C	g_{DM} $kg_{H_2O}^{-1}$	−0.1938				−9.21343	0.444					8.746502	0.127	This study
WUE_H	g_{DM} $kg_{H_2O}^{-1}$	0.09804				−20.6046	−0.21					14.69102	0.248	This study
WUE_S	g_{DM} $kg_{H_2O}^{-1}$	−0.2827				−10.3557	0.192					10.96677	0.116	This study, Eq. 9

The dependent variables (*first column*) can be computed using a linear combination of the independent variables (*first line*). Coconut plantation, VARTC-Vanuatu, 2002–2004

_g + ng: green + non-green elements; _IPAR, variable calculated based on IPAR; *_g*: green elements; _APAR, variable calculated based on APAR; RRMSE, relative root mean square error

Table 3 Relative contribution of independent variables to model predictions, as assessed by comparing the RRMSE (relative root mean square errors)

Dependent variable	Independent variables				Source
	PAR$_i$	PAR$_i$ + *f*Dif	PAR$_i$ + sin(β)	PAR$_i$ + *f*Dif +sin(β)	
LUE$_S$_IPAR	0.118	0.116	0.083	0.078	This study, Eq. 5

Dependent variable	Independent variables				Source
	PAR$_i$	PAR$_i$ + VPD	PAR$_i$ + sin(β)	PAR$_i$ + VPD + sin(β)	
WUE$_S$	0.311	0.130	0.124	0.116	This study, Eq. 9

Coconut plantation, VARTC-Vanuatu, 2002–2004

Table 2. The latter model is proposed for scaling up LUE$_C$ and NPP$_C$ in broader conditions, coping with the problem of varying age and density. For herbs, wherever LAI$_H$ is known, it is possible to compute *f*IPAR$_H$ and also calculate LUE$_H$ from Table 2. It is highly promising that in Fig. 3a, LUE$_C$ was not very different from LUE$_S$, however, we suspect that this peculiar finding should not be extrapolated without verification to dissimilar ages or densities.

Those simulations would be worth testing in dissimilar coconut groves, especially in ranging conditions of fertility, drought and management of the under-storey, and especially with the help of *f*APAR obtained from remote sensing.

Scaling up NPP using remote sensed fAPAR

When using remote-sensing, *f*APAR subtitutes *f*IPAR and green elements substitute full cover (green + non-green) since vegetation indexes only estimate *f*APAR from green elements. In addition, only whole-stand *f*APAR$_S$ is sensed. Table 2 gives adjustments of LUE$_S$ according to APAR$_S$, which can be used to estimate NPP$_S$. Again, we suspect that the latter adjustment of LUE$_S$ would be only valid for similar plantations. For dissimilar plantations, Roupsard et al. (2008a) proposed a process-based method to relate *f*IPAR$_C$ (green + non-green elements) and *f*APAR$_C$ (green elements), given in Table 2. Hence APAR$_C$ can be simulated in every situation where age or density vary, and compared to APAR$_S$ derived from remote-sensing. We propose that the difference would be assumed to be close to APAR$_H$.

Water-use-efficiency, WUE

WUE can be calculated at leaf level, as the ratio of photosynthesis to evaporation, as an intrinsic WUE (WUE$_i$) being the ratio of photosynthesis to stomatal conductance at leaf level or as the so-called "inherent WUE" (WUE$^*_i$), the ratio of (GPP.VPD) to E at ecosystem level. Here, we were dealing with 'integrated' WUE, the ratio of NPP to evapo-transpiration for the purpose of scaling up NPP. All those approaches and scales are generally linked together (Farquhar et al. 1989; Roupsard et al. 1998; Beer et al. 2008).

As a yearly average (Fig. 3b; Table 1), integrated WUE was quite similar (around 3.7 and 3.9 g_{DM} $kg^{-1}_{H_2O}$) for stand and coconut, respectively. For herbs, it was only 2.3 g_{DM} $kg^{-1}_{H_2O}$. In a review of inherent WUE (WUE$^*_i$), Beer et al. (2008) also reported higher maximal values for forest than for herbaceous ecosystems, and 'Cocoflux' belonged to the sites with highest values of WUE$^*_i$, likely a consequence of elevated soil moisture at field capacity and LAI.

Also seasonally, WUE varied highly significantly for stand and coconut layers by a factor of 1.7–2.3, however, their homothecy was not as flawless as for LUE. For herbs, the factor was 4.7. For each layer, WUE reached maximum values during the cool season (Fig. 3b), when radiation and evapo-transpiration were minimum. Inter-annual variability was not significant, excepted for coconut.

We propose a multiple linear regression model of WUE, using only factors that can be derived from climate files (Fig. 4b; Table 2), in the form:

$$\mathrm{WUE_S} = a'_\mathrm{S} \cdot \mathrm{PAR_i} + b'_\mathrm{S} \cdot \mathrm{VPD} + c'_\mathrm{S} \cdot \sin\beta + d'_\mathrm{S} \quad (9)$$

Eighty-three percent of the variability of $\mathrm{WUE_S}$ was accounted for using this simple empirical model, with a RRMSE of 11%. The independent variable $\mathrm{PAR_i}$ was the major contributor to this adjustment, followed by VPD and then by $\sin\beta$, as presented in Table 3, comparing the RRMSE of various combinations.

For the purpose of deriving $\mathrm{NPP_S}$ from $\mathrm{WUE_S}$, $\mathrm{E_S}$ can be estimated from remote-sensing (Moran et al. 1996; Allen and Bastiaanssen 2005). Alternatively, simple climatic models using net radiation and air temperature (Priestley and Taylor 1972) from which the alpha coefficient can be adjusted using remote-sensing (Fisher et al. 2008b) proved to be more efficient than process-models for predicting $\mathrm{E_S}$ in a wide range of tropical forests or plantations (Fisher et al. 2008a), including the “Cocoflux” site ($r^2 > 0.9$ using the latter model). For separating the two layers, it will be further proposed an adaptation of the original two-layer (crop + bare soil) evapo-transpiration model developed by Shuttleworth and Wallace (1985).

Conclusions

The suspected variability of LUE and WUE in time and space generally appears as an impediment for scaling up NPP from simple parametric models. Moreover, in multi-strata or agroforestry systems, the remotely sensed signals used for landscape classification or *f*APAR cannot be easily de-convoluted into separate information by layer, although recent tools help document the vertical structure (LIDAR). We proposed here a calibrated method for partitioning LUE and WUE by layer in simple coconut groves with herbaceous under-storey and for scaling up NPP in time and space, using solely climate variables, age and planting density, or else using *f*APAR derived from remote-sensing.

The upper-layer covered 75% of the ground and contributed to around this amount for NPP, intercepted light and transpiration, which was close to the rule-of-thumb and would be worth testing under dissimilar planting densities and in different agroforestry systems. 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 (around two times) higher for the under-storey. The herbaceous under-storey thus behaved less steadily than the perennial over-storey for major physiological variables. This surprising result may appear rather counter-intuitive for agroforestry systems. It would deserve comparison with other situations, especially when the under-storey is a deep-rooted perennial itself (e.g. shaded coffee or cocoa), or in dry conditions.

Seasonally variable, but inter-annually invariable LUE and WUE are original results, which do complete the general assumption that LUE and WUE can be assumed constant for ecosystems or biomes on an annual basis.

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