Modeling light below tree canopies overestimates net photosynthesis and radiation use efficiency in understory crops by averaging light in space and time

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Abstract

By averaging in time and/or space, models predict less variable light patterns under tree canopies than in reality. We measured light every minute in 24 positions in a grid under different chestnut orchards, for several clear and overcast days. We also modelled this light with a purposely created 3D, spatially explicit, ray-tracing light interception model, where canopy porosity was calibrated to match measured daily light. Finally, we used both the measured and modeled light patterns transmitted under the tree canopies to estimate the daily net photosynthesis ($A_n$) and radiation use efficiency (RUE) of an understory wheat leaf. As expected, modeled light was more uniform than measured light, even at equal daily light. This resulted in large overestimation of daily $A_n$ and RUE of the understory leaf. Averaging light in time increased the overestimations even further. A sensitivity analysis showed that this overestimation remained substantial over the range of realistic values for leaf photosynthetic parameters (i.e. $V_{c,max}$, $J_{max}$, $R_d$) of the understory crop.

Keywords: agroforestry, alley cropping, leaf response curve, shade tolerance, silvoarable, PAR

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1. Introduction

Agroforestry systems (AFS) are increasingly recognized for their potential contribution towards sustainable intensification (Doré et al., 2011). Alley cropping (i.e. silvoarable, crops grown in the alleys between lines of trees), is one of the agroforestry practices most studied and developed in temperate regions (Palma et al., 2007; Liagre et al. 2009) because of its potential to increase yield and income while providing environmental benefits and allowing modern mechanization (Dupraz 2005; Garrity et al., 2010; Luedeling et al., 2011; Cardinael et al. 2015). Field experiments in AFS are time-consuming and expensive because of the long-term nature of trees and the many possible combinations of trees and crops (Knörzer et al., 2011; Lovell et al., 2017). Modeling becomes indispensable as an initial test of the many possible field designs and management strategies, improving our understanding of the complex interaction in AFS (Chimonyo et al., 2015). In particular, process-based models are considered particularly suitable (Bayala et al., 2015; Luedeling et al., 2016).

Light is often the most limiting factor in crop growth in AFS (e.g. Friday and Fownes 2002; Jose et al. 2004; Zamora et al. 2009), therefore a proper representation of light distribution between trees and crops becomes essential for effective modeling (Dufour et al., 2013). Light distribution under trees has been addressed with different levels of complexity in different models (for a review, see Malézieux et al., 2009). Initial models considered trees and crops with a single one-dimensional canopy representation, with strong limitations. Two-dimensional models improved upon this, but only three-dimensional (3D), spatially explicit models are suited to represent the highly variable light distribution when combining trees and crops (Chazdon and Pearcy, 1986; Knapp and Smith, 1987).

Only models that reproduce the exact architecture of trees, at the individual shoot or leaf level (e.g. Dauzat et al. 2001; Mialet-Serra et al. 2001; Casella and Sinoquet 2007; Lamanda et al. 2008) can predict the exact light pattern available under the trees in both time and space. While
possible, this approach is computationally demanding, making it impossible on a large scale. Therefore, the most common 3D models of AFS approximate light interception by tree canopies using:

1) a fixed geometric shape for the canopy (e.g. cylinder, ellipsoid)
2) a homogeneous canopy of a fixed porosity to light
3) averaging the position of the sun over time

These simplifications result in predictions of light patterns under the trees that are always averaged at some level of time and space, not representing the actual variability. For a given total light interception, photosynthesis is reduced under variable light compared to more uniform light (Külheim et al., 2002; Poorter et al., 2016; Kromdijk et al., 2016; Vialet-Chabrand et al., 2017). This is because the photosynthetic response of a leaf to light is curvilinear:

at high irradiance, net photosynthetic assimilation ($A_n$) tends to saturate, reducing the radiation use efficiency (RUE). At very low light, the apparent quantum yield is highest, but RUE decreases due to leaf respiration. RUE is zero at the light compensation point and becomes negative at lower irradiance (Hirose and Bazzaz, 1998; Rosati and DeJong, 2003). Therefore, two minutes at average irradiance can result in greater $A_n$ than one minute at high and one at low irradiance.

Work on sunflecks and shadeflecks supports the idea that accounting for the effects of variable light is important not only in understory plants (Pearcy et al., 1996; Way and Pearcy, 2012) but also in common crops (Lawson et al., 2012; Carmo-Silva et al., 2015, Kromdijk et al., 2016), where most of the leaves are still exposed to variable light levels due to self-shading (Pearcy et al., 1990; Rosati et al., 2004). Accounting for the variability in the patterns of incident light is especially important for understory crops in AFS, where the incident light is filtered through tree canopies. Variability in light patterns in AFS is caused by both large gaps between trees and small gaps within tree canopies (Chazdon and Pearcy, 1986; Knapp and Smith, 1987). For an equal total incident radiation transmitted below the trees, different light patterns likely result in different $A_n$ and RUE.
Here, we hypothesize that averaging of sub-tree canopy light patterns in time and space overestimates $A_n$ and RUE of understory crops in AFS.

2. Materials and Methods

First, we built a 3D, spatially explicit, ray tracing light interception model with a minutely resolution. While ray-tracing models are commonly used in biophysical modeling, most do not have a minutely resolution. We also measured minutely light transmitted during several days to 24 points in a grid under several chestnut (*Castanea mollissima* Blume) orchards of different ages and spacings. Then, we compared measured and modeled values of light transmitted to the understory crop. Finally, we modeled $A_n$ of a wheat leaf in each of the 24 positions as exposed to (1) the actual (i.e. measured every minute) light pattern transmitted under the trees, (2) temporal averages (half-hourly, hourly, and daily) of the measured light, and (3) modeled (minutely, half-hourly, hourly, and daily) light when approximating the tree crowns to ellipsoids or cylinders. A sensitivity analysis was also performed by changing the photosynthetic parameters of the understory crop to simulate variation in leaf physiology.

2.1 Measuring light under tree canopies in the field

We measured the photosynthetically active radiation (PAR) transmitted under the canopies of four adjacent trees in two mature and two young chestnut orchards differing in age, spacing, and row orientation (Table 1). The orchards were located at the Horticulture and Agroforestry Research Center of the University of Missouri, in New Franklin, MO, USA. The mature orchards were 20 years old, and the young orchards were five years old. Tree characteristics (i.e. trunk circumference, bole height, tree height, within-row canopy radius, and between-row canopy radius) were measured on each of the 16 trees (four per orchard) under which PAR was measured (Table S1). Canopy volumes were then calculated approximating the canopy shape to either an ellipsoid or a cylinder. The trees in the mature orchards were heterogeneous in size, with canopy volumes ranging from 56
to 135 m$^3$ in mature orchard A and from 56 to 285 m$^3$ in mature orchard B. In the young orchards, tree canopy ranged from 8 to 25 m$^3$ in young orchard A and from 12 to 29 m$^3$ young orchard B.

In each orchard, 24 PAR sensors (GaAsP photosensors, Hamamatsu, Japan), previously calibrated with a quantum sensor (LI-190; LI-COR Inc., Lincoln, NE, USA) and connected to a datalogger (GP2, Delta-T Devices Ltd, Cambridge, UK), were placed in a grid in the rectangular area between the four adjacent trees. The grid was designed with regular spacing to be representative of the whole area. Measurements were made in September and October 2016, over two-five days in each orchard (Table 1), measuring PAR every minute. Daily PAR incident on each orchard was then computed by summing the minutely values for the whole daylight period.

Measurement days included clear, partly overcast, and heavily overcast days, as indicated by the total daily incident PAR measured outside the orchard with a PAR sensor (LI-190; LI-COR Inc., Lincoln, NE, USA) connected to a datalogger recording PAR every minute (Table 1).

2.2 Light interception model

Most 3D canopy light interception models do not run on a minutely time scale. Therefore, to compare PAR measured every minute with modeled PAR, we built a model capable of modeling light at any time scale. The model is built using the R statistical computing software version 3.5.1 (R Core Team, 2018). The model utilizes a horizontal scene, onto which trees can be placed, and a hemispherical sky discretized into one-degree by one-degree grid cells. The location of the sun and the proportions of direct and diffuse radiation are first calculated using the solaR package (Perpiñán, 2012) using a supplied date, time, and latitude. The proportions of direct and diffuse radiation are calculated following the method of Collares-Pereira and Rabl (1979). Direct radiation is allocated to the sky cell where the sun is located, and diffuse radiation is allocated uniformly across the entire sky. If a day is deemed completely overcast (two days in this study), then both direct and diffuse radiation are allocated uniformly across the entire sky.
Tree canopies are placed onto the scene using an x and y location, upper and lower heights of the crown, a uniform canopy porosity (Table 1), and crown radii: two independent radii for an ellipsoid or one uniform radius (i.e. the average of the radii measured in two directions) for a cylinder (Table S1). For a given point of interest on the scene floor, a line is drawn between each sky grid cell and the point. The radiation transmitted to the point is the sum of the radiation of all sky grid cells, with the radiation from a given sky cell reduced by the canopy porosity if its line intersects a tree canopy. Tree canopies are assumed to reduce radiation uniformly regardless of the path length of a radiation ray through the canopy. The effect of tree trunks was assumed negligible during the months of the experiment, as all trees had full foliage (Dupraz et al. 2018). Sensors in the field were placed in a grid within the rectangle between four adjacent trees, avoiding the border of the orchard, to avoid edge effects. Similarly, the model for each orchard included two additional rows of trees in all directions; the dimensions of additional trees in each orchard were taken as the mean of the four primary trees in that orchard.

The purpose of the study was not to assess whether the model could correctly estimate total daily PAR transmitted under the trees, but rather to investigate whether the intra-daily variability of the PAR pattern affects estimation of daily $A_n$ and RUE of an understory crop leaf. Therefore, we set the canopy porosity for each orchard and canopy shape that provided the best match of measured and modeled daily PAR averaged across the 24 sensors (Fig. 1; Table 1). By matching measured and modeled daily PAR, any difference in estimated daily $A_n$ can be attributed to different daily patterns of PAR transmitted under the canopy. The model and the data files are available on GitHub: https://github.com/kevinwolz/Rosati_etal_2019.

2.3 Modeling daily $A_n$ with measured and modeled light

The daily $A_n$ for an understory crop leaf was estimated by using the Farquhar model (Farquhar et al., 1980) with parameters for winter wheat ($Triticum aestivum$; Guo et al., 2015). Wheat was selected because it is the most common crop grown in temperate alley cropping.
experiments to date (Wolz and DeLucia, 2018). Instantaneous $A_n$ was estimated from instantaneous PAR via eight different approaches: using measured or modeled data, each as measured each minute, or averaged over half-hour, hour, or all daylight hours. Daily $A_n$ for each sensor was then obtained for each calculation approach by summing instantaneous $A_n$ over each day (for further details on this approach see Rosati et al., 2003; 2004). The daily $A_n$ obtained with measured minutely PAR was assumed to be the most realistic, thus all other approaches were compared to this $A_n$. Daily RUE was then calculated by dividing daily $A_n$, obtained with the different PAR data, by its respective daily incident PAR.

2.4 Sensitivity analysis

To ensure that results were relevant beyond the specific leaf physiology of winter wheat measured in Guo et al. (2015), a sensitivity analysis of the overestimation of daily $A_n$ in the understory crop to the Farquhar et al. (1980) photosynthesis model parameters was performed. This was done by estimating daily $A_n$ using a range of values for the three key Farquhar et al. (1980) model parameters: (1) $V_{c,max}$, the maximum RuBP saturated rate of carboxylation ($\mu$mol m$^{-2}$ s$^{-1}$), (2) $J_{max}$, the maximum rate of electron transport used in the regeneration of RuBP ($\mu$mol m$^{-2}$ s$^{-1}$), and (3) $R_d$, the mitochondrial respiration rate in the day ($\mu$mol m$^{-2}$ s$^{-1}$). The ranges explored for $V_{c,max}$ and $R_d$ were taken from the ranges measured in winter wheat by Sun et al. (2015). Since $V_{c,max}$ and $J_{max}$ are known to be highly correlated across plant species and plant functional types (Wullschleger 1993, Walker et al. 2014), the values explored for $J_{max}$ were calculated from the $V_{c,max}$ values and the relationship demonstrated by Walker et al. (2014).

3. Results

Even though we set the canopy porosity so that total daily modeled and measured PAR below the orchard were matched (Fig. 1), the difference in the daily patterns between measured and modeled minutely data was dramatic.
Fig. 1 Average modeled vs. measured daily PAR incident on the understory crop across the orchard floor after calibration of the canopy porosity in each orchard. Point shapes represent the different orchards, and point color represent the two modeled canopy geometries (ellipsoid: black; cylinder: grey).

While generally following the same trends, measured data was much more variable, whereas modeled data maintained smooth curves since the modeled light is passing through unrealistically homogeneous canopies (Fig. 2). Since the results were nearly identical when modeling canopy shape as a cylinder or as an ellipsoid, the rest of results are shown only for one shape (i.e. ellipsoid).
Fig. 2 Representative example time series of measured and modeled minutely PAR from one sensor under the canopy in the Young A orchard on a clear day. The shaded area shows the PAR incident on the orchard above the tree canopy. Modeled data is shown for (a) ellipsoidal and (b) cylindrical tree canopies.

Ao always increased with daily incident PAR, both when estimated with measured or with modeled PAR, and when estimated using the minutely PAR data, or the half-hour, hour and daily PAR averages (Fig. 3). However, Ao was always greater at any PAR value when estimated with modeled PAR, both for minutely PAR and at any time averaging level except for daily averages,
where it was the same by default design of the modeling (i.e. when using a single PAR value for a
day, there is no difference in daily pattern between modeled and measured data, and the response
curve takes the shape of the instantaneous response curve). Daily $A_n$ estimated with modeled PAR
was also less variable at any given daily PAR. Daily RUE was similarly overestimated with
modeled data and more scattered with measured data (Fig. 4).
Fig. 3 Measured and modeled daily $A_n$ as a function of daily incident PAR. Modeled data is for ellipsoidal tree canopies. Each point represents one of the 24 sensor locations for one of the 11 orchard-date combinations measured in the field. Daily $A_n$ is calculated using incident PAR averaged at the (a) minutely, (b) half-hourly, (c) hourly, and (d) daily level.
Fig. 4 Measured and modeled daily RUE as a function of daily incident PAR. Modeled data is for ellipsoidal tree canopies. Each point represents one of the 24 sensor locations for one of the 11 orchard-date combinations measured in the field. Daily RUE is calculated using incident PAR averaged at the (a) minutely, (b) half-hourly, (c) hourly, and (d) daily level.
Compared to daily $A_n$ estimated using the actual (i.e. measured minutely) PAR, modeled minutely PAR overestimated daily $A_n$ by an average of 26% across all orchards (top right panel; Fig. 5). When temporally averaging the light as well, in addition to the spatial averaging of light inherent in the model (i.e. uniform canopy porosity), the overestimation increased: Half-hourly (28%) and hourly (29%) approaches were only marginally worse, but calculating daily $A_n$ using mean daily modeled PAR resulted in overestimation by 46%. Using temporal averages of measured PAR overestimated daily $A_n$ less than with the corresponding modeled PAR, except for daily averages, with daily $A_n$ overestimations of 7%, 11% and 49% respectively for half-hourly hourly and daily averages (Fig. 5).
Fig. 5 Comparison between daily $A_n$ calculated from measured minutely PAR (x-axis) and daily $A_n$ calculated from measured/modeled PAR in each temporal averaging window. Each point represents the mean of the 24 sensor locations for one of the 11 orchard-date combinations measured in the field.

The overestimations of daily $A_n$ resulted in similar overestimations of daily RUE (Fig. 6).
Fig. 6 Comparison between daily RUE calculated from measured minutely PAR (x-axis) and daily RUE calculated from measured/modeled PAR in each temporal averaging window. Each point represents the mean of the 24 sensor locations for one of the 11 orchard-date combinations measured in the field.

The sensitivity analysis (i.e. estimating $A_n$ with a range of photosynthetic model parameter values for the understory crop) showed that modeling and averaging PAR resulted in large
overestimation of $A_n$ for any realistic values of the Farquhar et al. (1980) model parameters (i.e. $V_{c,max}$, $J_{max}$ and $R_d$: Fig. 7).
Fig. 7 Sensitivity analysis of the overestimation of daily $A_n$ (A) and RUE (B) in the understory crop calculated as in figure 5 and 6, but at varying $V_{c,max}$, $J_{max}$ and $R_d$ parameters of the Farquhar et al. (1980) photosynthesis model. The vertical dotted line represents the parameter values used in all other figures.
4. Discussion

Our hypothesis was that, by averaging the PAR transmitted under the tree canopy in space (i.e. by approximating canopy shapes and assuming uniform canopy porosity) and time, crop models overestimate \( A_n \) and RUE of understory crops. The results fully supported the hypothesis. Daily \( A_n \) estimated with measured minutely PAR was always lower than the \( A_n \) estimated using the modeled PAR, even when modeling PAR for every minute (Fig. 3). Averaging in time further increased the overestimation, both for modeled and measured PAR. By comparing daily \( A_n \) estimated with measured and modeled PAR at the different time resolutions, the overestimations were shown to be large (Fig. 5). This resulted in similar overestimation of RUE (Fig. 4 and 6). The sensitivity analysis showed that this overestimation remained substantial across realistic values of the Farquhar et al. (1980) photosynthesis model parameters for the understory crop (Fig.7).

It has long been known that averaging of light in space and/or time overestimates \( A_n \) (Sinclair et al., 1976; Spitters, 1986). In previous work (Rosati et al., 2003), we also found that averaging measured PAR over one hour resulted in overestimation of daily \( A_n \) of different leaves within a tree canopy. However, in a tree or indeed any overstory canopy, most of the photosynthesis is contributed by the outer-canopy, better-exposed leaves, which receive a more uniform irradiance. Understory crops are instead exposed to more variable light patterns even on their outer-canopy leaves. Therefore, quantifying the overestimation of \( A_n \) with averaging of light is likely more important. This is the first time that the overestimation is quantified for an understory crop exposed to the PAR transmitted by the overstory canopy, a typical agroforestry situation.

Additionally, our data allowed us to analyze the overestimation due to time and space averaging. Figure 5 shows that daily \( A_n \) was overestimated by about 7% when averaging measured PAR data to half-hour intervals, by 11% when averaging hourly, and by 49% when averaging over the entire daylight period. Therefore, time averaging, even at intervals as short as half-hour, results in important overestimations of daily \( A_n \). However, the overestimation was much greater at any time
averaging step, when using modeled PAR (i.e. approximating tree canopies to regular shape and
assuming uniform canopy porosity). When using the modeled PAR at minutely time steps, the
overestimation was 26%, more than two or three times the overestimation observed with hourly or
half-hourly averages of measured data, respectively.

Given that the overestimation results from averaging variable PAR, these results suggest that,
at least under the conditions of this experiment, approximating tree canopies to regular shape and
assuming uniform canopy porosity results in averaging PAR to a larger extent than hourly time
averaging. In fact, it appears clearly that modeled PAR remains at almost constant values for up to
three hours, while measured PAR is much more variable (Fig. 2). This suggests that approximating
tree canopies to a regular shape and assuming uniform canopy porosity results in greater model bias
than setting half-hourly or hourly time steps to save computational effort. This could be due, at least
in part, to the fact that our model assumed a regular canopy shape and a uniform canopy porosity,
neglecting both clumping (and gaps), and the actual canopy depth crossed by light rays, which
depends on where the ray passes (i.e. canopy center or margins). Simple geometrical shapes are
very rough approximations of real tree shapes, and leaves are clustered within shoots (Cohen et al.
1995; Falster and Welstoby, 2003). Finer geometry descriptions have divided the canopy either in
sub-volumes (Mariscal et al. 2000) or voxels (Knyazikhin et al. 1996; Sinoquet et al. 2005). Leaf
area distribution within sub-volumes may be considered uniform or described by statistical
functions (Wang and Jarvis 1990; Cescatti 1997). Finer canopy descriptions result in dramatic
increases in computation time (Mialet-Serra et al. 2001; Roupsard et al. 2008) and, while improving
model predictions (Sinoquet et al. 2005), light patterns are still averaged at some levels of space and
time. Based on the present results, averaging, even at the scale of relatively short time and/or space
intervals, results in important overestimations of daily An.

For instance, Zhao et al. (2003) accounted for some of these aspects in their model and found
the modeled and measured light to be very similar when averaged over half-hour. In this model the
actual canopy thickness crossed by each ray was considered, and gaps in the canopy where
accounted for by calculating the statistical probability of a ray to pass through the canopy without intercepting a leaf (based on hemispherical photographs). However, this did not yield the actual light available on a given point and time, but rather the “expected average radiation flux on the point”. Therefore, while variations in canopy porosity and gap probability were considered, light was still averaged compared to reality. Additionally, canopy shape was still approximated to a regular geometric shape and leaf orientation was assumed to be spherical. Therefore, while better representation of canopy porosity is noteworthy, it probably did not allow measured and modeled transmitted light to match at the instantaneous time scale. Unfortunately, data were presented only as half-hourly averages. At this scale, our results show $A_n$ as overestimated by 7% when using measured PAR, and by 26% when using modeled PAR.

Talbot and Dupraz (2012) also attempted to consider non-uniform canopy porosity, by accounting for clamping with a clumping coefficient, but concluded that this did not improve model predictions of transmitted light. However, this resulted from the fact that the clumping coefficient was too dependent on the canopy volume adjustments procedure. They concluded that their model was not suited to account for the effects of architectural specificities of individual trees. Their results, therefore, do not suggest that more realistic modeling of light transmittance through the canopy is not important, but only that other limitations, particularly the approximation of canopy shape to regular geometric shapes, override possible improvements via other approaches.

Some light models use an explicit stand description at scale of shoot or leaf (Dauzat et al. 2001; Mialet-Serra et al. 2001; Casella and Sinoquet 2007; Lamanda et al. 2008). Models that account for individual leaves are the most likely to predict light patterns under the tree canopy that closely match the actual patterns, but these models are very demanding in terms of the number of parameters needed and computational effort. Consequently, they are not suitable for field agroforestry simulations (many trees), over long time scales.

When using modeled PAR, estimated daily $A_n$ was not only higher but also less variable than when using measured PAR, resulting in a narrower range of $A_n$ values at any daily PAR (Fig.
This trend is also evident for RUE (Fig. 4). In other words, for a given daily incident PAR, measured light results in more variable daily $A_n$ and RUE than for modeled light. This is because a given daily PAR can be obtained with long exposure at uniformly low irradiance or with short alternating exposure at high and low irradiance. In the first case, daily $A_n$ and RUE are higher, while in the second case they are lower, despite having the same daily PAR, because fluctuating irradiance negatively impact time-integrated photosynthesis at equal total irradiance (Külheim et al., 2002; Poorter et al., 2016; Kromdijk et al., 2016; Vialet-Chabrand et al., 2017). By averaging in space and time, modeling PAR reduces the difference in variability in the incident PAR (i.e. more variable light is more affected by averaging than less variable light, which is already closer to an average value), thus not only overestimating daily $A_n$ and RUE but also reducing their variability at any given daily PAR.

No current models used in agroforestry account for this variation in $A_n$ and RUE with different sub-canopy light patterns, because all models do some averaging of light in space and/or time. The present results suggest that the light estimation approach used by these models is likely to result in overestimation of $A_n$ and RUE for understory crops. Some models, however, do not use mechanistic approaches (e.g. Farquhar et al. 2018) to estimate $A_n$ in the understory crop, but rather convert daily incident PAR into biomass growth using empirical RUE coefficients. These RUE coefficients are typically measured under field conditions or modeled, calibrated, and validated with field measurements. However, our results show that RUE varies greatly not only with daily PAR, but also with the daily PAR pattern, which, as discussed above, results in quite variable daily $A_n$ and RUE even at equal daily PAR (Fig. 4). The variation of RUE with daily PAR is well established, and the shape of the RUE response curve to daily PAR (Fig. 4) closely resembles the one we previously published (Rosati et al. 2004) or the one often used in modeling (e.g. STICS component in the Hi-SAFe agroforestry model; Brisson et al. 2009, Dupraz et al. 2019). However, in these models, the RUE of the crop is calibrated under full-sun conditions, with a more uniform PAR pattern compared to that experienced under tree canopies. The present work suggests that,
when such calibrations in open fields are used in the crop component of agroforestry models, they are likely to overestimate the $A_n$ and RUE of the crop under the trees. In this work, with chestnut orchards with different tree ages and spacing, $A_n$ of the understory crop was overestimated by 26-46% (Fig. 5), and RUE by 22-38% (Fig. 6).

The impact of these results on global biophysical models is difficult to predict. Most crop-only models are applied only in full-sun situations, and most forest models do not model photosynthesis directly. Nevertheless, considering that agroforestry is practiced on almost half of all agricultural area worldwide (Nair et al. 2009), and there is increasing interest in mixed tree-crop land uses, it will be critical to consider these results to correctly develop global biophysical agroforestry models.

5. Conclusions

The current results suggest that modeling understory crop $A_n$ and RUE is quite challenging for several reasons. First, the daily PAR incident over the understory canopy varies from place to place during the same day, therefore the modeling must be done separately for different positions, receiving different daily PAR. Some models account for this by estimating the PAR incident under the trees at various space scales, then using this PAR to run the crop sub-model for each area unit (e.g. STICS crop model in the Hi-sAFe agroforestry model, Dupraz et al., 2019). However, the daily PAR transmitted in each area under the trees estimated by the models is not realistic, being more uniform than in reality, thus probably resulting in overestimated crop RUE.

Ideally, therefore, crop RUE should be calculated under real agroforestry situations, using experimental agroforestry setups. While possible, this complicates model calibration, especially considering, as discussed above, that different agroforestry situations result in different light patterns of daily PAR, resulting in substantially different possible RUE values for a given daily PAR (i.e. high variability of RUE for any daily PAR value, Fig. 4). With varying whether conditions (i.e. frequency of sunny and overcast days), seasons (i.e. duration and intensity of
radiation), tree age (i.e. canopy size) and relative shade patterns, and position under the trees, the transmitted PAR pattern under the trees can vary greatly even for an equal daily total PAR, resulting in variable RUE values. Therefore, estimating the correct RUE in agroforestry models might be more challenging than previously thought. Possible solutions to overcome these modeling challenges are desirable.
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latitude on the light availability for intercrops in an agroforestry alley-cropping system. 


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Table 1. Tree spacing, row orientation, daily incident PAR in the different measuring days, and calibrated tree porosity for the four chestnut orchards used to measure the transmitted PAR on 24 positions under the canopies, during several days per orchard.

<table>
<thead>
<tr>
<th>Orchard</th>
<th>Tree spacing (m)</th>
<th>Row orientation (°E of N)</th>
<th>Daily incident PAR above orchard canopy (mol m$^{-2}$)</th>
<th>Calibr. tree canopy porosity</th>
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<td>Within rows</td>
<td>Between rows</td>
<td></td>
<td>Ellipsoid</td>
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<td>8.2</td>
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<td>36.5, 38.6</td>
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<td>8</td>
<td>131</td>
<td>31.6, 23.7, 27.3, 30.8, 30.9, 8.3</td>
</tr>
<tr>
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<td>36.4, 37.2</td>
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<td>9.3, 14.4, 31.6, 34.0, 34.4</td>
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Table S1 Tree parameters for the 16 trees used in each of the four orchards.

<table>
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<tr>
<th>Orchard</th>
<th>Trunk Circumfer. (cm)</th>
<th>Bole Height (m)</th>
<th>Canopy Height (m)</th>
<th>Canopy Diameter (m)</th>
<th>Canopy Volume (m$^3$)</th>
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<tr>
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<td>Cylin</td>
<td>Ellips</td>
<td>Cylin</td>
<td>Ellips</td>
<td>Y</td>
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