in silico Plants, 2024, **6**, diae002
https://doi.org/10.1093/insilicoplants/diae002
Advance access publication 21 February 2024
Original Research

in silico Plants
OXFORD

Original Research

An evaluation of Goudriaan's summary model for light interception in strip canopies, using functional-structural plant models

Shuangwei Li,[1,2,3] Wopke van der Werf,[3] Fang Gou,[4] Junqi Zhu,[5,] Herman N. C. Berghuijs,[6,7,] Hu Zhou,[1] Yan Guo,[1] Baoguo Li,[1] Yuntao Ma,[1,*,] and Jochem B. Evers[3,]

[1]College of Land Science and Technology, China Agricultural University, Beijing 100193, China
[2]Institute of Agricultural Equipment, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China
[3]Centre for Crop Systems Analysis, Wageningen University, PO Box 430, Wageningen 6700 AK, The Netherlands
[4]Bragato Research Institute, PO Box 845, Blenheim 7240, New Zealand
[5]The New Zealand Institute for Plant and Food Research Ltd, Marlborough Research Centre, PO Box 845, Blenheim 7240, New Zealand
[6]Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Ulls väg 16, Uppsala 75651, Sweden
[7]Plant Production Systems, Wageningen University, P.O. Box 430, Wageningen 6700 AK, The Netherlands

[*]Corresponding author's e-mail address: yuntao.ma@cau.edu.cn

Handling Editor: Xin-Guang Zhu

Abstract. Dealing with heterogeneity in leaf canopies when calculating light interception per species in a mixed canopy is a challenge. Goudriaan developed a computationally simple, though conceptually sophisticated, model for light interception in strip canopies, which can be reasonably represented as 'blocks', such as vineyards and crop rows. This model is widely used, but there is no independent verification of the model. Hence, we developed a comparison of light interception calculations with Goudriaan's model and with detailed spatially explicit three-dimensional functional–structural plant models (FSPM) of maize in which plant architecture can be represented explicitly. Two models were developed, one with small randomly oriented leaves in blocks, similar to Goudriaan's assumption, which we refer to as the intermediate model (IM), and another with a realistic representation of individual plants with stems and leaves having shape, orientation and so on, referred as FSPM. In IM and FSPM, light interception was calculated using ray tracing. In Goudriaan's model, the light extinction coefficient (k), including both its daily and seasonal average values, was generated using the FSPM. Correspondence between the three models was excellent in terms of light capture for different levels of crop height, leaf area and uniformity, with the difference less than 3.3 %. The results are strong support for the use of Goudriaan's summary model for calculating light interception in strip canopies.

KEYWORDS: Functional-structural plant model; geometric model; intermediate model; light interception; model comparison; strip crops.

1. INTRODUCTION

Light interception is one of the fundamental processes underlying plant growth and production in plant communities, as it drives the energy and water balances of the community and physiological and biophysical processes in plants. The fraction of intercepted light is a function of leaf area index (LAI, m^2 leaf area per m^2 ground area), canopy architecture and optical properties of foliage and stems (Guiducci *et al.* 1992). For homogeneous plant canopies, robust estimates of light interception can be obtained with a simple one-dimensional turbid medium model relating light interception and LAI via one coefficient called the light extinction coefficient (k, Lambert–Beer's law). However, this relatively simple model does not accurately describe light interception in more heterogeneous canopies like strip crop canopies with wide paths, such as grapes (Weber and Penn 1995) and apple (Wang *et al.* 2019).

Several geometrical light transmission models have been developed to calculate light interception in spatially heterogeneous strip intercropping systems (Tsubo and Walker 2002; Munz *et al.* 2014). For systems with widely spaced tree rows or strip-planted crops, a simple model for daily light interception that captures key aspects of crop geometry has been developed by Goudriaan (1977). Goudriaan's model is based on a few equations that summarize the average light interception by a strip crop, when assuming that the light originates from a uniform overcast sky. We refer to this model as the 'block model' (BM) as it represents the rows of the canopy as homogeneous blocks, separated by empty paths. The blocks are characterized by height and width and the LAI contained in the block volume. Blocks can increase in height, width and LAI as the crop grows, resulting in a change in light interception by the canopy over time. Goudriaan's BM has been widely used, for instance, to quantify light utilization in mixtures of young jujube trees and cotton (Zhang *et al.* 2014), light availability of cocksfoot in apple orchards (Wang *et al.* 2019), light partitioning in a wheat/maize strip intercropping (Gou *et al.* 2017; Wang *et al.* 2017) and maize/soybean strip intercropping (Liu *et al.* 2017), and to identify the effects of strip width on yields in wheat/maize relay-strip intercropping (van Oort *et al.* 2019). The BM does not consider solar angles as affected by the day of the year, the latitude and the time of day, but integrates over all possible angles of incoming light.

In contrast to the BM approach, functional–structural plant models (FSPM) quantify the dynamics of daily light interception in heterogeneous canopies by considering the daily incoming light from the sky in three-dimensions (3D). FSPM simulates realistic plant and canopy structure, explicitly considering the 3D structure, size, orientation and optical properties of individual leaves and stems (Vos *et al.* 2010), and typically uses a ray tracing algorithm or similar (Chelle and Andrieu 1999; Hemmerling *et al.* 2008) to simulate the 3D distribution of light interception at the level of the leaf. Therefore, FSPM has been applied to heterogeneous canopy types to investigate the effect of plant traits (Barillot *et al.* 2014; Zhu *et al.* 2015; Li *et al.* 2021) and planting patterns (Mao *et al.* 2016) on light interception. FSPM has many parameters that need to be estimated, resulting in a high data demand, and they are computationally demanding. Simpler techniques like the BM approach are less data demanding and their calculation time is extremely short. The downsides of FSPM hold back wide-scale explorations of light interception in row or strip canopies. Thus, it is important to verify whether predictions of the BM and current FSPM agree, and whether both are accurate enough to calculate light interception across a range of plant traits and cropping systems.

An important assumption of the BM approach is a fixed k throughout the simulation. Since the consequences of such assumptions of light distribution and canopy representation for the model accuracy cannot be easily assessed, the goodness of approximation of the BM approach has to our knowledge never been quantified. To facilitate a comprehensive comparison, an intermediate model (IM) was developed featuring a 3D block structure. This structure was designed by randomly distributing leaves within a canopy volume, which is block-shaped and gradually increases in height, width and LAI over time. Like in the FSPM, ray tracing was used to calculate the light interception by crop strips in the IM.

The FSPM approach, due to its faithful representation of plant architecture and 3D distribution of canopy light interception, makes a very useful tool to assess the prediction accuracy of the BM approach. Therefore, the objectives of this study were: (i) to evaluate the validity of the BM for calculating light interception in strip crops; and (ii) to identify the goodness of approximation of the BM approach with different values for the light extinction coefficient k in calculating light interception in uniform and strips maize crops.

2. MATERIALS AND METHODS

We used three models (Fig. 1): a BM based on Goudriaan's definition (Goudriaan 1977), a maize strip crop FSPM (Li *et al.* 2021) and an IM that uses the ray tracing method in the same way as the FSPM, but represents the canopy as block structures, similar to the BM. This IM is highly similar in its basic assumptions to the BM, both in terms of the radiation model (Uniform overcast sky) and the canopy structure (randomly oriented leaves within block-shaped volumes). Therefore, the results of the BM and IM are expected to agree closely if both models perform well. By comparing the results of the BM and the IM, we can infer whether substantial differences in light interception result from differences between the two models in the representation of incoming light and its interception. By comparing the results of the IM and the FSPM, we can infer to which extent the simplified block structure of the IM canopy, ignoring plant architecture, affects calculated light interception. To achieve the first objective, the BM was tested by comparing its output to that of the IM for a range of different canopy traits. To achieve the second objective, the importance of canopy structure in an FSPM context was assessed by comparing the output of the IM and FSPM, and quantifying the contribution of plant architecture when using the ray tracing method.

2.1 The BM

2.1.1 Radiation model

The BM assumes that the angle of incidence of incoming light is hemispherically distributed (Uniform Overcast Sky, UOC, Monteith and Unsworth 1990), that is, homogeneous radiance from the entire sky (Goudriaan 1977). This assumption enables spatial integration over all directions without the need to consider time of day. The day length was set to 12 h and the atmospheric transmissivity was set to 0.25 (Allen *et al.* 1998), which gives a constant daily global radiation of 14.8 MJ m^{-2} at ground level according to a solar constant of 1367 W m^{-2}.

2.1.2 Canopy model

A strip crop is a canopy with strips consisting of one or more crop rows (strip width: R in m). The strips are separated by empty paths (path width: P in m) (Fig. 1C). Goudriaan (1977) and Pronk *et al.* (2003) proposed to calculate the fraction of light intercepted by a strip crop as a weighted average of two extremes: light interception by a fully 'compressed' canopy, consisting of one wide strip and one wide path, and light interception by a homogeneous canopy, in which the LAI of the blocks is homogeneously distributed over the strips and the paths (Goudriaan 1977; Pronk *et al.* 2003; Gou *et al.* 2017; see also Supporting Information—Supplementary Method). The model has been implemented in R (R Core Team 2022). The BM requires as inputs the height $H(t)$, strip width $R(t)$, path widths $P(t)$ and leaf area index $LAI(t)$ of the canopy, and the value of

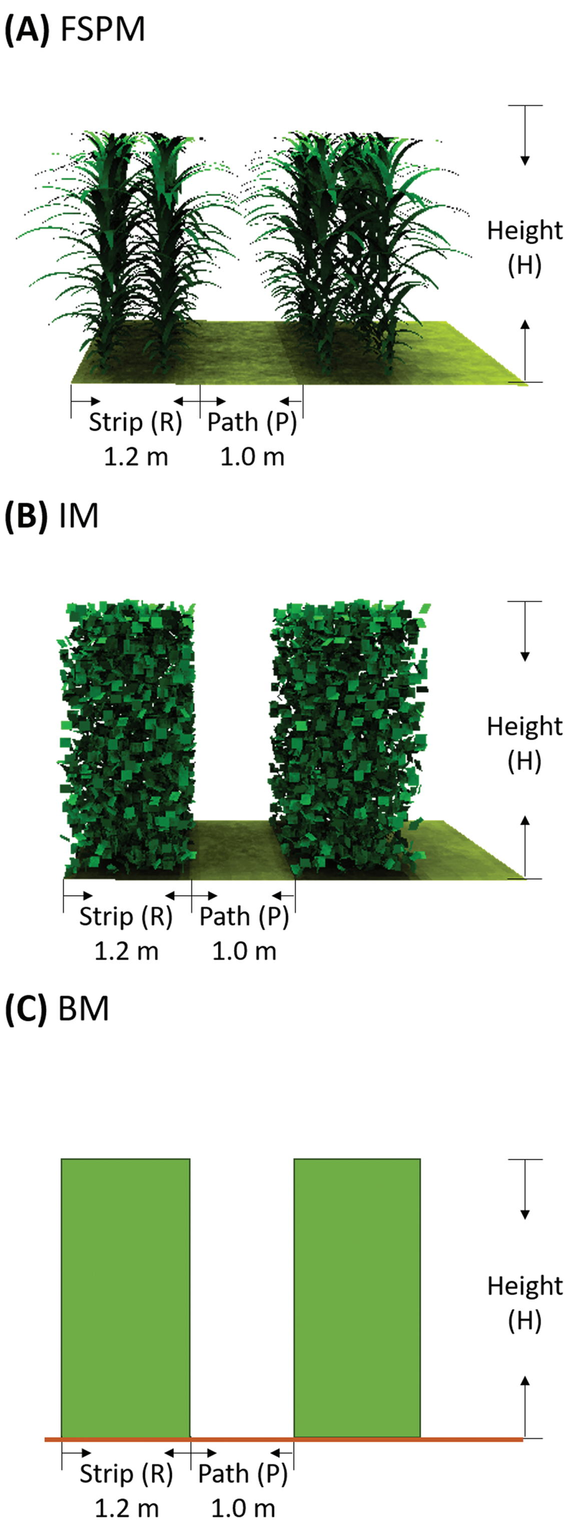

Figure 1. Cross sections through the strip crop canopy in a FSPM (A), IM (B) and BM (C) at 72 days after emergence. The simulations were run with 2 × 10 plants (one maize strip) in the FSPM. The strip width in the IM and BM was 1.2 m, which is two times the row distance of 60 cm in the FSPM. The strip height in the IM and BM includes the height of tassel in FSPM, but the tassel is not visualized. The plots in the FSPM and IM were copied 40 times in both *x* and *y* directions using the replicator functionality of GroIMP to calculate light interception by the centre plants and minimize border effects with respect to the incoming light. The BM was implemented in the R programming language.

the parameter *k*, which can be modelled as a constant (k_{av}) or as a time varying parameter ($k(t)$).

2.2 The FSPM

2.2.1 Radiation model

In the FSPM, the distribution of light interception was simulated by reverse Monte-Carlo ray tracing algorithm in the GroIMP platform (Hemmerling *et al.* 2008). Diffuse radiation was approximated using an array of 46 directional light sources, which were positioned in a hemisphere according to the TURTLE model and with incoming light from all angles (Den Dulk 1989; Dauzat *et al.* 2001). We assumed the same daylength (12 h), atmospheric transmissivity (0.25), solar constant (1367 W m^{-2}) and resulting global radiation (14.8 MJ m^{-2}) as in the BM. The reflectance and transmittance of leaf blades for photosynthetically active radiation (PAR) were set to 0.0923 and 0.0127 for maize (Zhu *et al.* 2015). Only green leaf blades were included in the simulated scene. Dead leaves, internodes and other organs were not included to use as much as possible the same canopy representation with only leaves in all three models.

2.2.2 Canopy model

Since our research questions require that the FSPM can simulate the light interception of maize grown in rows, we used an FSPM of maize strip cropping (Li *et al.* 2021), developed in the GroIMP platform (www.sourceforge.net/projects/groimp) (Hemmerling *et al.* 2008) (Fig. 1A). Maize phenological development, organ expansion and organ size along the plant stem were all represented faithfully. Data for parameterization of the model were collected in field experiments in 2012 and 2013 at Shangzhuang experimental station, Beijing, China (40°08′ N and 116°11′ E). The strip crop pattern used consisted of two rows of maize. Maize was planted at 0.2 m distance within the row, 0.6 m between maize rows and 1.6 m between maize rows in neighbouring strips (Fig. 2). Destructive measurements on plant green leaf area were made at 15–20-day intervals starting at 30 days after emergence. Four plants were taken from each row to measure plant height (i.e. the distance from the soil surface to the top of the plant) and whole-plant green leaf area. Two plants were sampled in each row to measure final leaf length and width, final internode length and diameter for each phytomer rank at maize tasselling (VT) stage (i.e. tassel completely visible). Whole-plant leaf area was measured using a LI-COR LI-3100 leaf area metre (LI-COR, Inc., NB, USA). Details on data collection and parameterization of maize plant architecture in FSPM, and its validation, are presented in Li *et al.* (2021).

2.3 The IM

The IM, also implemented in GroIMP, used the same method to calculate the distribution of light interception and the same radiation model settings and leaf optical properties as the FSPM. To mimic the canopy representation of the BM, a strip crop design, composed of small square leaves, was constructed similar to Morales (2017) (Fig. 1B). The number of leaves per m^2 strip in the IM canopy was calculated as the canopy LAI, divided by the

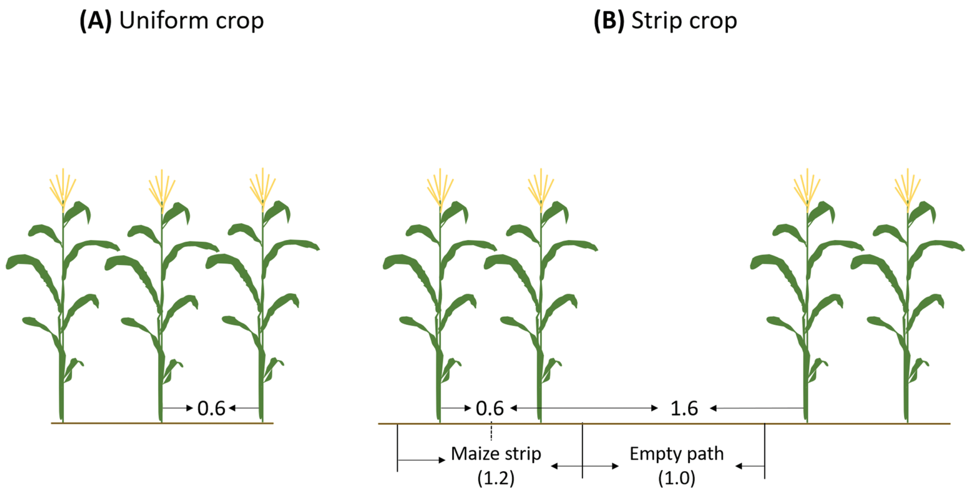

Figure 2. Row configurations of uniform crop (A) and maize strip crop (B, 2 rows of maize alternated with an empty path) (Unit: m).

size of a single leaf, which was set to 100 cm^2. The leaves were randomly distributed within the canopy using a spherical distribution, which means the x, y and z coordinates are each drawn from uniform distribution. The leaf elevation angle distribution was spherical and the azimuth angle was uniform with respect to the North.

2.4 Simulation approach

The FSPM was used to generate the canopy characteristics height, $H(t)$ (m), strip width, $R(t)$ (m), path, $P(t)$ (m), leaf area index, $LAI(t)$ (m^2 m^{-2}) and the light extinction coefficient, $k(t)$ and its average value over time, k_{av}. The simulated values of $H(t)$, $R(t)$, $P(t)$, $LAI(t)$, $k(t)$ and k_{av} were then used as inputs for the BM and IM (Table 1). This modelling approach ensured that there was correspondence between the three models in these major canopy characteristics, while differences in calculated light interception could still result as a consequence of differences in canopy structure between the models and the representation of the incoming light and its interception by the canopy. The daily values of k ($k(t)$) were calculated from the relationship between $LAI(t)$ and light interception in the FSPM, by solving k from Lambert–Beer's equation (Monsi and Saeki 2005):

$$k(t) = -\frac{\ln(1 - f_{\text{int}}(t))}{\text{LAI}(t)}, \qquad (1)$$

where $f_{int}(t)$ is the fraction of light intercepted by the canopy. We also calculated the average k value over the whole season from Equation (1) because usually Goudriaan's summary model is used assuming a fixed value of k (k_{av}). Plant architecture affects the light interception of the plants, which means that the k values could change over the whole growing season. To evaluate the change of k value, both early and late growing stages were defined. Early growth stage was defined from seed emergence to the maximum LAI value (71 days after emergence), and late growth stage was defined from the maximum LAI value to the harvest time. In an equivalent way, daily and average values for k were also calculated from the output of the IM to evaluate the performance of BM (objective 1).

2.4.1 *Simulations for objective 1*

Scenario 1: To evaluate the validity of the BM for calculating light interception in strip crops, we first compared output of the BM and the IM for a range of different strip widths and initially for a scenario with black leaves without reflection or transmission. In the simulation, the LAI was set to a very high value of 80 m^2 m^{-2}, which results in full absorption at a reasonable computation time, in both the BM and IM to make the blocks impermeable to light such that the results would be determined by the interaction between the radiation model and the block structure in the IM, without an effect of LAI (Table 2). Leaves in the IM were randomly positioned in the canopy volume and horizontally oriented, and a theoretical k value of 1.0, which is appropriate for black horizontal leaves (Goudriaan 2016), was used to calculate light interception in the BM. The sum of strip width and path width in the BM and IM was set to 2.2 m, and the strip width was set to 0.2 m, 0.6 m, 1.0 m, 1.4 m, 1.8 m and 2.2 m, where a strip width of 2.2 m represents a uniform crop.

Scenario 2: After scenario 1, we moved to a more realistic situation in which we evaluated the BM including leaf optical properties, canopy height, and realistic values of LAI. The leaves were randomly distributed within the canopy block using a spherical distribution. The leaf angle distribution was spherical. The reflectance and transmittance of small leaves for PAR were now set to 0.0923 and 0.0127, the same as in the FSPM. Simulations were done for five different canopy heights: 0.5 m, 1.0 m, 1.5 m, 2.0 m and 2.5 m (Table 2) and for 129 LAI values from 0 m^2 m^{-2} to 3.9 m^2 m^{-2}, in order to investigate how the fraction of light interception changes with LAI for a certain plant height. Strip width was set to 1.2 m and path width was set to 1.0 m. LAI was expressed as m^2 leaf area per unit area of the whole field.

In all cases, the plots in the IM and FSPM were copied 40 times in both the x and y directions using the replicator functionality of GroIMP to minimize border effects with respect to the incoming light. Each simulation in IM was run three times to account for variations in the model coming from the ray tracing algorithm.

Table 1. Main attributes of the FSPM, IM and BM.

Model	FSPM	IM	BM
Radiation model	TURTLE	TURTLE	n/a
Light absorption	Ray tracing	Ray tracing	Lambert–Beer's law
Canopy	Individual plants	Block	Block
Representation of leaves	Realistic shape composed of polygons	10 × 10 cm squares	n/a
Leaf position	Modelled for each part of a leaf	3-D uniform	n/a
Leaf orientation	Modelled for each part of a leaf	Spherical distribution	n/a
Leaf optical properties	Reflectance and transmittance as measured	Reflectance and transmittance as measured	n/a
k	k is output	n/a	k is input
Canopy structure	Plants in rows	Block	Block
Light condition	Uniform overcast sky (UOC) with isotropic light distribution		
Other	The same incoming PAR, LAI, plant height, strip width, path width		

Table 2 List of parameters used in the IM, the BM and the FSPM when doing simulations for two different objectives.

Model	Scenario 1		Scenario 2		Scenario 3		
	IM	BM	IM	BM	FSPM	IM	BM
Incoming daily global radiation (MJ m^{-2})	14.8	14.8	14.8	14.8	14.8	14.8	14.8
Leaf elevation angle distribution	Horizontal	n/a	Spherical	n/a	Modelled for each part of a leaf	Spherical	n/a
Leaf azimuth angle distribution	Uniform	n/a	Uniform	n/a	Modelled for each part of a leaf	Uniform	n/a
Light extinction coefficient (k)	output	1.0	output	0.76 (from IM)	output	output	Seasonal k (0.76) and daily k (from FSPM)
Leaf area index (m^2 m^{-2})	80	80	0–3.9 (from FSPM)		from FSPM (0–7.1 in uniform crop and 0–3.9 in strip crop)		
Canopy height (m)	0–2.6 (from FSPM)		0.5, 1.0, 1.5, 2.0, 2.5		0–2.6 (from FSPM)		
Strip width (m)	0.2, 0.6, 1.0, 1.4, 1.8, 2.2		1.2	1.2	3 in uniform crop and 1.2 in strip crop		
Path width (m)	2.0, 1.6, 1.2, 0.8, 0.4, 0		1.0	1.0	0 in uniform crop and 1.0 in strip crop		

2.4.2 Simulations for objective 2

Scenario 3: In practical applications of the BM for calculating light interception, a constant value of k is used. In the simulations of this study, we generated k values from the FSPM so that we could obtain both time-varying, daily values of k ($k(t)$) and seasonal average value of k (k_{av}). The light extinction coefficient was generated in an FSPM with maize rows at 0.6 m row distance and 0.2 m plant distance in the row. We then compared light interception of the BM, the IM and the FSPM for strip canopies when using either a time varying value of k or a constant value of k (*viz.* the seasonal average from the FSPM) to calculate light interception in the BM. In the IM and the FSPM, light interception was based on ray tracing and the optical properties and position and orientation of the leaves, hence k is not an input to these models. In the strip crop setup, there were two rows in each strip, with empty paths between two crop strips during the whole growing season. The distance between two rows within a strip was 0.6 m, and there was 1.6 m distance between the centres of the two border rows of neighbouring strips (Fig. 2). To make sure the three models represent a similar canopy, the strip width was 1.2 m and path width was 1.0 m in both BM and IM (Table 2). Daily values of plant height and LAI from the FSPM were used as input for the BM and IM. Either seasonal average or daily k values from FSPM were used as input in the BM.

In the FSPM, simulations of 6 × 10 plants (6 rows and 10 plants in each row) were run for the uniform crop and 2 × 10 plants (2 rows and 10 plants in each row) for the strip crop. The plot size was set to 2.2 m × 2.0 m in the FSPM and IM. These plots were copied 40 times in both the x and y directions using the replicator functionality of GroIMP to minimize border effects with respect to the incoming light. Each simulation was run five times. The goodness of approximation of the BM was quantified as the difference in light interception between the BM and FSPM. The effect of plant architecture was calculated as the light interception difference between FSPM and IM. The effect of ray tracing was calculated as the difference in light interception between IM and BM with the same canopy settings.

2.5 Evaluation of model performance

The root mean squared error (RMSE) was used to assess the correspondence between observed and simulated values for leaf area per plant and plant height in the FSPM:

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2}, \qquad (2)$$

where O_i is the observed value for measurement i, P_i is the simulated value of measurement i and n is the number of observed values.

2.6 Statistical analysis

All data analysis was done using R (version 4.1.0) (R Core Team 2022). Nested models in 'bbmle' package were used to analyse the differences in the seasonal average k value in LAI and fraction of light interception between the IM and FSPM, and between the early and late growing season. Akaike's information criterion (AIC) was used to determine the grouping of the model data that was best supported (Li *et al.* 2021), with small AIC values representing better overall fits (Bolker 2008). One-way analysis of variance (ANOVA) and least significant differences (LSD) test from the 'stats' and 'agricolae' package in R were employed to evaluate the differences among the FSPM, IM and BM (with daily k and seasonal average k) under uniform crop and strip crop at the 5 % ($P = 0.05$) level. The 'ggplot2' package in R programming language (Wickham 2009) was used to produce figures. The accumulated light interception over the growing season is presented as means ± S.E.

3. RESULTS

3.1 Leaf area and plant height generated by FSPM

The FSPM adequately represented the architectural development of maize in a strip crop, represented by plant height and leaf area during the growing season (Fig. 1A and Fig. 3). Simulated leaf area per plant showed a characteristic pattern of increase during leaf production and extension, and decrease during leaf ageing and shedding (Fig. 3A). Overall, there was satisfactory correspondence between simulated and observed values, with RMSE values of 0.06 m^2 for leaf area per plant and 0.08 m for plant height.

3.2 Investigating *k* values using FSPM and IM

Changes in leaf size, leaf angle, leaf distribution and leaf shape during the season resulted in a variation in k value over time (Fig. 4). The daily k decreased with the growth of leaves and increased with leaf senescence (Fig. 4B). When LAI was higher than 6 m^2 m^{-2}, 98 % of light was absorbed in the FSPM, leading to a k of 0.59. However, all light was intercepted in the IM when LAI was higher than 6, leading to a lowest daily k of 0.65. The seasonal average k value was 0.76 in both the FSPM and IM during the whole growing season under diffuse light conditions.

3.3 Evaluation of the simplified light interception method in a BM (objective 1)

Scenario 1: Under the extreme assumptions of horizontal black leaves and the LAI of 80 m^2 m^{-2}, the fraction of light interception calculated by the BM was close to that of the IM for canopy heights greater than 0.5 m. For lower canopies, the fraction of light interception was slightly lower in the BM than in the IM (Fig. 5). But for a homogeneous canopy (strip width = 2.2 m), the fraction of the light interception was 1 at all heights for both the IM and the BM (Fig. 5). The fraction of light interception increased with strip width for a fixed total width of the strip plus path. These results show that simulation of light interception in strip crops is sensitive to strip width, path width and canopy height. It also shows that the simpler light interception approach in the BM has similar performance compared to the more demanding and complex radiation modelling of the IM approach for all canopy heights except those lower than 0.5 m.

Scenario 2: With realistic leaf optical properties, the fraction of light intercepted by the strip crop increased with both LAI and canopy height (Fig. 6). The fraction of light intercepted was lower in the BM than in the IM for LAI < 1, but higher for LAI > 2. In other words, the response of light interception to

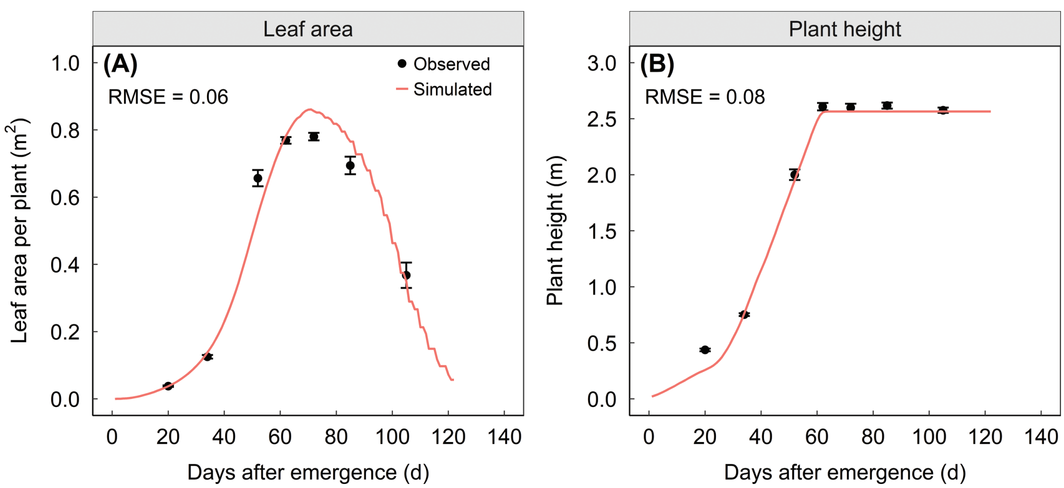

Figure 3. Maize leaf area per plant (A) and plant height (B) in a strip crop predicted by functional-structural plant model (FSPM), compared to observed data from field experiment. Dots represent with error bars represent means ± S.E. of the observations ($n = 7$).

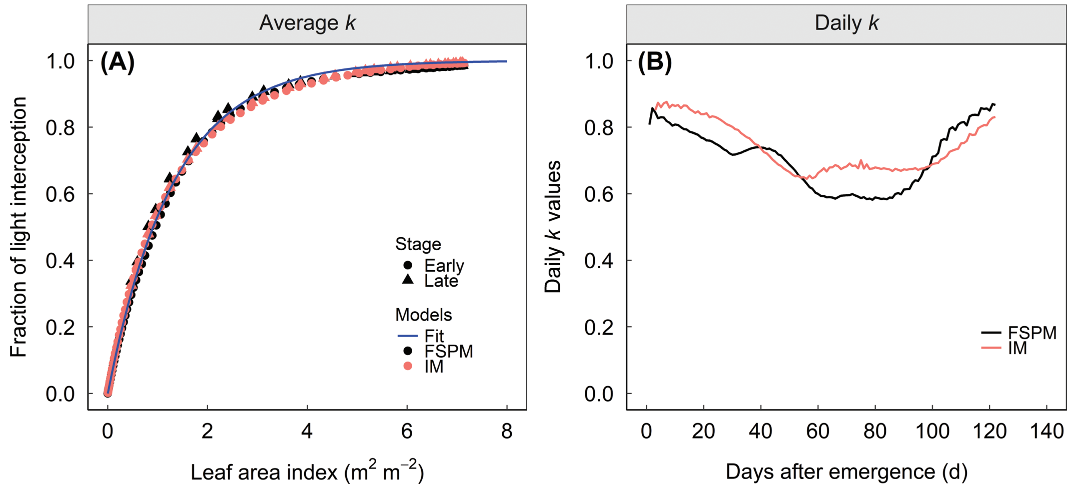

Figure 4. The relationship between the fraction of light interception and LAI (A) and seasonal daily *k* (B) of uniform maize in the FSPM and the IM under fully diffuse light conditions. Early growth stage was defined from seed emergence to the maximum LAI value (71 days after emergence), and late growth stage was defined from the maximum LAI value to the harvest time. Seasonal average *k* was 0.76 in both the FSPM and the IM.

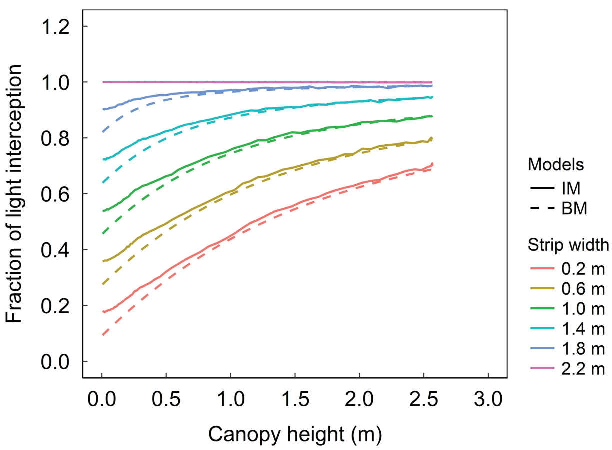

Figure 5. Comparison of fraction of light intercepted by black leaves in a strip crop with different strip width (0.2 m, 0.6 m, 1.0 m, 1.4 m, 1.8 m and 2.2 m for a total strip + path width of 2.2 m) calculated by the IM and BM under fully diffuse light conditions. A theoretical *k* value of 1.0 (Goudriaan 2016) was used to calculate light interception in the BM. The sum of strip width and path width was fixed to 2.2 m; therefore, the simulation with strip width for 2.2 m represents the case of a uniform crop.

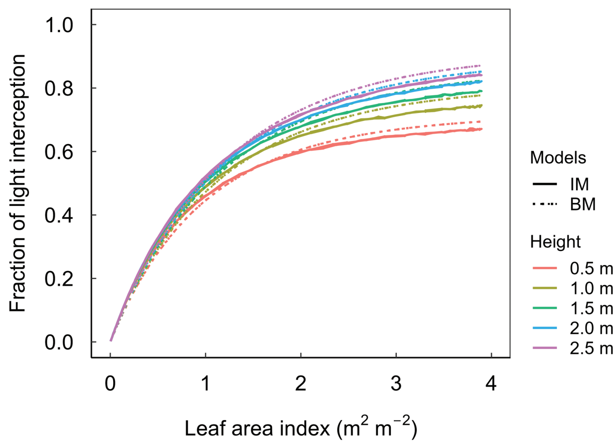

Figure 6. Comparison of the fraction of light intercepted by a strip crop with leaves with normal optical properties, calculated by IM and BM under fully diffuse light conditions. The BM used a light extinction coefficient (k) of 0.76, calculated by applying inverse Lambert–Beer's law to light interception generated with the IM. The strip width was 1.2 m and the path width 1.0 m.

LAI had greater initial slope in the IM than in the BM, but the plateau reached by the BM was slightly higher than that of the IM. The BM and IM had similar fractions of light interception when the LAI was between 1 and 2. When the leaf self-shading is low, that is, the black leaves scenario and LAI < 2 in leaves with optical properties scenario, the fraction of light interception was higher in IM than in BM, and vice versa.

3.4 Accuracy of a BM when simulating light interception in strip and uniform crops (objective 2)

Scenario 3: In a uniform crop, the accumulated light interception over the growing season was 671.8 ± 0.6 MJ m^{-2} in the FSPM, which was only marginally different from that in the IM (674.2 ± 0.1 MJ m^{-2}) (Fig. 7A). The LSD value at 5 % level was 1.48 and *P* value was 0.013 in the uniform crop. The BM had similar accumulated light interception as the FSPM when daily *k* values from the FSPM were used (671.8 ± 0.6 MJ m^{-2}), while it had a significantly higher accumulated light interception (676.9 ± 0.6 MJ m^{-2}) than the FSPM when an average *k* (0.76) was used in the BM (Fig. 7A). The daily fractions of light intercepted in the BM with average *k* was higher during the middle growing season than that in other models (Fig. 8A).

In a strip crop, there was no significant difference in total light interception between the BM with an average *k* (0.76) and the FSPM; however, the BM with daily *k* had 3.1 % lower light interception than the FSPM (Fig. 7B). The LSD value at

5 % level was 2.36 and P value was 0.002 in the strip crop. The BM (average k) and IM had a slightly lower light interception in the middle growing season than the FSPM (Fig. 8B). The BM with daily k estimated light interception very well in the early and late growing season, but underestimated the light interception in the middle growing season. Absence of plant architecture slightly reduced light interception from 522.4 ± 1.3 MJ m^{-2} in the FSPM to 517.3 ± 0.2 MJ m^{-2} in the IM (−1.0 %). The BM light algorithms decreased light interception by 0.4 % to 2.2 % (BM vs. IM).

4. DISCUSSION

Despite the simplifying assumptions made in the BM regarding the representation of the canopy and the calculation of light interception, the estimated light interception was close to the estimates made with more complex and realistic models that use ray tracing and 3D representation of plant architecture. The difference between the BM (computationally simplest) and FSPM (computationally most complex) was 3.1 % at most for the total seasonal light interception (Fig. 7). Leaf optical properties, strip width, canopy height and LAI affected the correspondence between the three models (Figs 5 and 6). Plant architecture had no effect on seasonal average k (0.76 in both FSPM and IM), but the IM had higher daily k values than the FSPM during the early and middle season, and lower daily k values during the later growth season (Fig. 4). The effect of average k and daily k (from the FSPM) on the whole season light interception in BM was tested and the difference to FSPM was less than 3.3 %. The detailed representation of plant architecture (FSPM) thus resulted in a slightly lower light interception in the early and late growing season; however, increased light interception in the middle growing season compared to the IM (Fig. 8B). Overall, these differences were small enough to conclude that the BM model suffices for the calculation of light interception by maize grown in strips.

For heterogeneous canopies consisting of a crop strip and empty path, light interception in the BM was smaller than in the IM, especially for low canopies (<0.5 m) (Fig. 5). However, leaves are not black, which means that they reflect and transmit some of the light that they received. Therefore, the BM overestimated light interception, especially when LAI > 2 m^2 m^{-2}, which may be because the BM approach only considers light scattering from bottom and upper leaf layers (Fig. 6, Larsen and Kershaw 1996; Goudriaan 2016).

A limitation of this study is that the results are applicable under the assumption of BM, such as uniform overcast sky and uniform leaf distribution. The crop strip canopy in the field is often with anisotropic leaf inclination and azimuth, varying plant spacing and crop height, and under changing diffuse light fraction, which may lead to different results, compared to BM. Ponce de León and Bailey (2019) found that Lambert–Beer's law could estimate light interception accurately for canopies with isotropic leaf orientation and relatively high leaf density, but the accuracy decreased with increasing plant spacing. Goudriaan gave a sophisticated conceptual model to calculate light interception in strip crop, even though the model still underestimate light interception for shorter plants with small leaf area, and overestimate light interception for taller plants with large leaf area (Fig. 6). In a maize strip crop, plants occupy the space of empty path to intercept more light during the middle of the growing season. Therefore, the light interception during the whole growing season is acceptable. A BM with k as a constant is often used to calculate light interception in a crop strip canopy. Even though leaves are distributed in blocks, a BM with seasonal average k still simulates light interception very well in a maize strip crop, compared to an FSPM. But a BM with seasonal daily k decreased light interception by 3.1 %. (Figs 7B and 8B). Therefore, seasonal daily k is not necessary for calculating light interception by a strip crop canopy and an average k value is sufficient. In the future, the comparison method could be used to quantify the effects of leaf angle

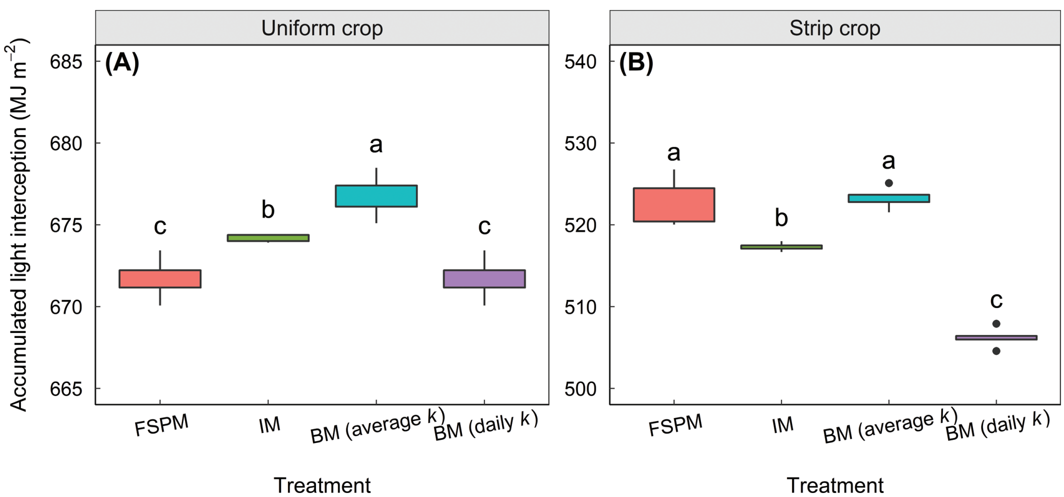

Figure 7. Accumulated light interception over the growing season in a uniform crop (A) and a strip crop (B) under fully diffuse light. Each simulation was run five times in BM, IM and FSPM. Daily values of plant height and LAI from the FSPM were used as input for the BM and IM. Seasonal average k (0.76) and daily k value from FSPM were used in the BM. LSD (5%) = 1.48 in the uniform crop and 2.36 in the strip crop. P = 0.013 in the uniform crop and 0.002 in the strip crop. n = 5 for each treatment.

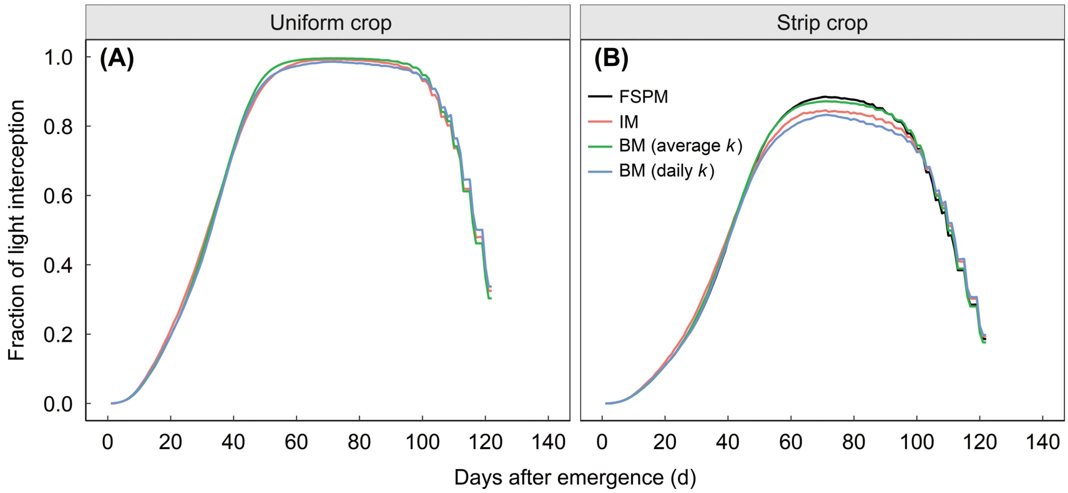

Figure 8. Fraction of light intercepted by a uniform crop (A) and a strip crop (B) under fully diffuse light. Seasonal average k (0.76) and daily k value from functional-structural plant model (FSPM) were used in the BM.

orientation, crop species, plant spacing, row orientation and diffuse light to the accuracy of BM, which are not considered in this study.

This is one of the few studies to evaluate the accuracy of the BM approach in calculating light interception in a strip crop. Gijzen and Goudriaan (1989) showed that BM calculated light absorption and photosynthesis only little reduced compared to a closed canopy when path width <30 % of the row height under diffuse light. The turbid medium approach allowed an acceptable estimation of the light interception by the canopy with the incident radiation is estimated at the height of the canopy (Edouard *et al.* 2022). The results suggest that for relatively simple uniform and heterogeneous maize canopies, a detailed 3D approach that requires many parameters and computational time, may not be necessary. More complex canopies such as intercrops, which contain multiple species of different height and different growth patterns, more realistic modelling approaches like FSPM may still be necessary (Barillot *et al.* 2014; Zhu *et al.* 2015; Louarn *et al.* 2020; Li *et al.* 2021).

5. CONCLUSIONS

The BM approach is well suited to calculate light interception in heterogeneous canopies, compared to model with actual plant architecture and ray tracing methods for light calculation, such as FSPM. Even though the BM did not need a daily k value to estimate light interception well, an analysis of different k values is needed to see whether more accurate k values need to be used. Our findings illustrate the influence of plant architecture, LAI, canopy height and strip width on the effectiveness of the BM in estimating light capture. Further investigation into the application of the BM across various canopy architectures is necessary to assess the general applicability of the model to heterogeneous canopies. Our results indicate that for simple heterogeneous canopies under diffuse light conditions, the straightforward BM approach proves adequate.

SUPPORTING INFORMATION

The following additional information is available in the online version of this article –

Supplementary Method: Canopy model for block model.

ACKNOWLEDGEMENTS

We acknowledge the financial support of the China Scholarship Council (CSC201706350202). J.B.E. and W.W. acknowledge funding from the European Union's Horizon 2020 Programme for Research and Innovation under grant agreement no. 727217 (ReMIX: Redesigning European cropping systems based on species MIXtures). We thank Alejandro Morales for sharing the code for the IM.

CONTRIBUTIONS BY THE AUTHORS

Methodology, S.L., W.W., J.B.E., Y.M., H.Z., Y.G. and B.L.; data analysis, S.L., W.W., J.B.E. and Y.M.; model construction, S.L., J.B.E., F.G., J.Z. and H.N.C.B.; writing, S.L., W.W., J.B.E., F.G., J.Z., H.N.C.B. and Y.M.; experiment and conduct H.Z., Y.G., B.L. and Y.M. All authors contributed to discussion and interpretation of data of the manuscript.

CONFLICT OF INTEREST STATEMENT

None declared.

FUNDING

This work was jointly supported by the Science and Technology projects from Inner Mongolia (CCPTZX2023K03), Pinduoduo-China Agricultural University Research Fund (PC2023B01004), and the Beijing Digital Agriculture Innovation Consortium Project (BAIC10-2024).

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

LITERATURE CITED

Allen RG, Pereira LS, Raes D, Smith M. 1998. *Crop evapotranspiration-guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56, Vol.* 300. Rome: FAO, p. D05109.

Barillot R, Escobar-Gutiérrez AJ, Fournier C, Huynh P, Combes D. 2014. Assessing the effects of architectural variations on light partitioning within virtual wheat-pea mixtures. *Annals of Botany* 114:725–737. doi:10.1093/aob/mcu099.

Bolker BM. 2008. *Ecological models and data in R*. Princeton, NJ: Princeton University Press.

Chelle M, Andrieu B. 1999. Radiative models for architectural modelling. *Agronomie* 19:225–240. doi:10.1051/agro:19990304.

Dauzat J, Rapidel B, Berger A. 2001. Simulation of leaf transpiration and sap flow in virtual plants: model description and application to a coffee plantation in Casta Rica. *Agricultural and Forest Meteorology* 109:143–160. doi:10.1016/S0168-1923(01)00236-2.

Den Dulk JA. 1989. *The interpretation of remote sensing, a feasibility study*. Thesis, Wageningen University, Wageningen, The Netherlands. ISBN: 90-9002707-6.

Edouard S, Escobar-Gutiérrez AJ, Van Iseghem M, Barillot R, Louarn G, Combes D. 2022. Is the turbid medium-based approach pertinent for estimating light interception when simulating the growth of a crop in an agri-photovoltaic system? *Biosystems Engineering* 224:131–142. doi:10.1016/j.biosystemseng.2022.10.006.

Gijzen H, Goudriaan J. 1989. A flexible and explanatory model of light distribution and photosynthesis in row crops. *Agricultural and Forest Meteorology* 48:1–20. doi:10.1016/0168-1923(89)90004-X.

Gou F, van Ittersum MK, Simon E, Leffelaar PA, van der Putten PEL, Zhang L, van der Werf W. 2017. Intercropping wheat and maize increases total radiation interception and wheat RUE but lowers maize RUE. *European Journal of Agronomy* 84:125–139. doi:10.1016/j.eja.2016.10.014.

Goudriaan J. 1977. *Crop micrometeorology: a simulation study. Simulation Monographs*. PUDOC, Wageningen, 249.

Goudriaan J. 2016. Light distribution. In: Hikosaka K, Niinemets Ü, Anten APR, eds. *Canopy photosynthesis: From basics to applications*. Dordrecht: Springer, 3–22.

Guiducci M, Antognoni A, Benincasa P. 1992. Effect of water availability on leaf movement, light interception and light utilisation efficiency in several field crops. *Riista di Agronomia* 27:392–397.

Hemmerling R, Kniemeyer O, Lanwert D, Kurth W, Buck-Sorlin G. 2008. The rule-based language XL and the modelling environment GroIMP illustrated with simulated tree competition. *Functional Plant Biology* 35:739–750. doi:10.1071/FP08052.

Larsen DR, Kershaw Jr JA. 1996. Influence of canopy structure assumptions on predictions from Beer's law. A comparison of deterministic and stochastic simulations. *Agricultural and Forest Meteorology* 81:61–77. doi:10.1016/0168-1923(95)02307-0.

Li S, van der Werf W, Zhu J, Guo Y, Li B, Ma Y, Evers JB. 2021. Estimating the contribution of plant traits to light partitioning in simultaneous maize/soybean intercropping. *Journal of Experimental Botany* 72:3630–3646. doi:10.1093/jxb/erab077.

Liu X, Rahman T, Yang F, Song C, Yong T, Liu J, Zhang C, Yang W. 2017. PAR interception and utilization in different maize and soybean intercropping patterns. *PLoS One* 12:e0169218. doi:10.1371/journal.pone.0169218.

Louarn G, Barillot R, Combes D, Escobar-Gutiérrez AJ. 2020. Towards intercrop ideotypes: Non-random trait assembly can promote overyielding and stability of species proportion in simulated legume-based mixtures. *Annals of Botany* 126:671–685. doi:10.1093/aob/mcaa014.

Mao L, Zhang L, Evers JB, Henke M, van der Werf W, Liu S, Zhang S, Zhao X, Wang B, Li Z. 2016. Identification of plant configurations maximizing radiation capture in relay strip cotton using a functional–structural plant model. *Field Crops Research* 187:1–11. doi:10.1016/j.fcr.2015.12.005.

Monsi M, Saeki T. 2005. On the factor light in plant communities and its importance for matter production. *Annals of Botany* 95:549–567. doi:10.1093/aob/mci052.

Monteith JL, Unsworth MH. 1990. *Principles of environmental physics*, 2nd ed. Edward Arnold.

Morales A. 2017. *Dynamic photosynthesis under a fluctuating environment: a modelling-based analysis*. Thesis, Wageningen University, Wageningen, The Netherlands. ISBN: 978-94-6343-045-6.

Munz S, Graeff-Hönninger S, Lizaso JI, Chen Q, Claupein W. 2014. Modeling light availability for a subordinate crop within a strip-intercropping system. *Field Crop Research* 155:77–89. doi:10.1016/j.fcr.2013.09.020.

Ponce de León MA, Bailey BN. 2019. Evaluating the use of Beer's law for estimating light interception in canopy architectures with varying heterogeneity and anisotropy. *Ecological Modelling* 406:133–143. doi:10.1016/j.ecolmodel.2019.04.010.

Pronk AA, Goudriaan J, Stilma E, Challa H. 2003. A simple method to estimate radiation interception by nursery stock conifers: a case study of eastern white cedar. *NJAS: Wageningen Journal of Life Sciences* 51:279–295. doi:10.1016/S1573-5214(03)80020-9.

R Core Team. 2022. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Tsubo M, Walker S. 2002. A model of radiation interception and use by a maize–bean intercrop canopy. *Agricultural and Forest Meteorology* 110:203–215. doi:10.1016/S0168-1923(01)00287-8.

van Oort PAJ, Gou F, Stomph TJ, van der Werf W. 2019. Effects of strip width on yields in relay-strip intercropping: a simulation study. *European Journal of Agronomy* 112:125936. doi:10.1016/j.eja.2019.125936

Vos J, Evers JB, Buck-Sorlin GH, Andrieu B, Chelle M, de Visser PHB. 2010. Functional-structural plant modelling: a new versatile tool in crop science. *Journal of Experimental Botany* 61:2101–2115. doi:10.1093/jxb/erp345

Wang Z, Cao Q, Shen Y. 2019. Modeling light availability for crop strips planted within apple orchard. *Agricultural Systems* 170:28–38. doi:10.1016/j.agsy.2018.12.010

Wang Z, Zhao X, Wu P, Gao Y, Yang Q, Shen Y. 2017. Border row effects on light interception in wheat/maize strip intercropping systems. *Field Crops Research* 214:1–13. doi:10.1016/j.fcr.2017.08.017

Weber J, Penn J. 1995. Creation and rendering of realistic trees. In: Proceedings of the 22nd Annual Conference on Computer Graphics and Interactive Techniques. ACM, 119–128.

Wickham H. 2009. *ggplot2: elegant graphics for data analysis*. New York: Springer.

Zhang D, Zhang L, Liu J, Han S, Wang Q, Evers J, Liu J, van der Werf W, Li L. 2014. Plant density affects light interception and yield in cotton grown as companion crop in young jujube plantations. *Field Crops Research* 169:132–139. doi:10.1016/j.fcr.2014.09.001.

Zhu J, Van der Werf W, Anten NPR, Vos J, Evers JB. 2015. The contribution of phenotypic plasticity to complementary light capture in plant mixtures. *The New Phytologist* 207:1213–1222. doi:10.1111/nph.13416.