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RESEARCH PAPER

Estimating the contribution of plant traits to light partitioning in simultaneous maize/soybean intercropping

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Abstract

Spatial configuration and plant phenotypic plasticity contribute to increased light capture in relay intercropping, but there is little information on whether these factors also increase light capture in simultaneous intercropping. We developed and validated a three-dimensional functional–structural plant model to simulate light capture in maize and soybean sole crops and intercrop scenarios, using species traits observed in sole crops and intercrops. The intercrop maize phenotype had 2% greater light capture than the sole crop phenotype in a pure stand. The soybean intercrop phenotype had 5–10% lower light capture than the sole crop phenotype in a pure stand. The intercrop configuration increased the light capture of maize by 29% and reduced the light capture of soybean by 42%, compared with the light capture expected from sole crops. However, intercrop configuration only marginally affected total light capture by the intercrop system (+1%). Testing of individual soybean plant traits revealed that plasticity in leaf dimensions was the main reason for differences in light capture by soybean in simulated sole crops and intercrops. The results of this study illustrate a major shift of light capture from shorter species (soybean) to the taller component (maize) in a simultaneous strip intercrop. Plastic plant traits modulate this overall effect, but only marginally.

Keywords: Functional–structural plant modelling, intercrop configuration, light capture, light partitioning, maize/soybean intercropping, phenotype plasticity.

Introduction

Intercropping can improve the utilization of resources and grain yield (Agegnehu *et al.*, 2008; Lithourgidis *et al.*, 2011; Pypers *et al.*, 2011), as well as soil fertility, and reduce soil erosion and occurrence of diseases, insects, and weeds (Leihner *et al.*, 1996; Rao and Mathuva, 2000; Saucke and Ackermann, 2006). Strip intercropping, in which strips of two species are grown side

by side, results in yield benefits due to improved efficiency of resource capture and conversion (Brooker *et al.*, 2015; Stomph *et al.*, 2020). Intercrops of two species with distinct canopy structure and growing periods enhance total light capture by (i) improving soil coverage and reducing the proportion of light reaching the ground, as shown for maize/soybean (Liu *et al.*, 2018), maize/peanut (Awal *et al.*, 2006), and sorghum/peanut intercropping systems (Harris *et al.*, 1987); and (ii) complementary light capture in time and extending the total crop season, such as sorghum/pigeon pea (Natarajan and Willey, 1980), wheat/maize (Wang *et al.*, 2015; Gou *et al.*, 2017), and winter wheat/cotton intercrops (Zhang *et al.*, 2008).

The changed availability of resources in an intercrop can result in plastic responses (Sultan, 1995, 2000) especially at the strip borders, potentially further increasing light capture (Zhu *et al.*, 2016; Evers *et al.*, 2019). Zhu *et al.* (2015) separated the intercropping effect on plant performance into two components: a configuration effect which represents the change in resource capture solely as a result of the mixing of two sole crop phenotypes in a mixed stand; and a plasticity effect, resulting from a changed phenotype in response to the changed resource environment, and quantified both effects each using plant modelling.

A frequently used strip intercropping is the maize/soybean system, and both simultaneous intercropping and relay intercropping of these two species are applied in practice (Xu *et al.*, 2020). Maize (*Zea mays*) and soybean [*Glycine max* (L.) Merr.] differ in physiology, phenology, and plant architecture. Light capture in intercrops depends on row configuration, which causes heterogeneous canopy structure compared with a sole crop (Liu *et al.*, 2017*a*). Therefore, plants in different row positions, such as border rows and inner rows within a strip, have different yield and yield components (Gou *et al.*, 2016; S. Li *et al.*, 2020). Xu *et al.* (2020) found in a worldwide meta-analysis that the average pLER (partial land equivalent ratio) of maize was 0.79 ± 0.02, while that of soybean was 0.56 ± 0.02, indicating that in maize/soybean intercrops, the maize profits more from a reduction of competition due to mixing than the soybean. Liu *et al.* (2018) described how soybean grows as a subordinate crop in the maize/soybean simultaneous intercropping system and its light capture is lower than that of maize.

In the north of China, maize and soybean are grown as simultaneous intercrops in which the two species are sown and harvested at the same time. In such systems, soybeans are shaded by maize for most of their growing period. Consequently, soybean displays plastic responses in its architectural development in order to capture more light (Liu *et al.*, 2017*b*). We have shown experimentally that these plastic responses are not sufficient for the soybean to overcome the maize shading (S. Li *et al.*, 2020). However, the contribution of such plastic responses to overall maize/soybean intercropping light capture cannot be quantified experimentally, and it is also not clear how the changes in traits in the mixed canopy affect the partitioning of radiation between the two species. A key question in this respect is whether changes in soybean phenotype in the mixture as compared with the pure stand can contribute to a higher light capture than would be realized if soybean plants had the exact same traits as in the pure stand. In other words: do soybean plants in the intercrop respond architecturally in ways that mitigate the negative consequences of shading by maize? Knowing the role of single soybean shade avoidance traits in light capture in different configurations could help identify the main traits to diminish soybean negative effects in intercropping and choose an appropriate variety of a subordinate species to adapt to a shading environment and improve crop yield, while maintaining maize variety and management.

Functional–structural plant (FSP) models can simulate the development over time of the 3D architecture or structure of plants (Guo *et al.*, 2006; Vos *et al.*, 2010). They can help to identify the performance-related traits that might differ due to specific plant–plant interactions and complementarities, and enable theoretical testing of all species and genotype combinations, regardless of the number of plant components and their spatial arrangement in mixed systems (Evers *et al.*, 2019; Gaudio *et al.*, 2019). Several FSP models have provided insights into interactions between plant structure and a single environmental factor such as light and nitrogen (Barillot *et al.*, 2014, 2018; Zhu *et al.*, 2015).

Therefore, the general aim of this study was to quantify the role of plasticity in plant traits on light capture and light partitioning in simultaneously sown maize/soybean intercropping using FSP modelling. To this end, we first quantified the differences in architectural phenotypes between sole crops and intercrops, and used this information to design and calibrate an FSP model in which light capture by pure stands and mixtures of phenotypes with different traits (measured in pure stands and mixtures) was compared. Then, we calculated the relative contributions of plant phenotype plasticity to the light capture. Finally, we analysed the pure relative contributions of individual soybean traits to overall light capture in sole crops and intercrops, which only can be done using a model approach, while keeping maize phenotype constant.

Materials and methods

Here, we first describe the model. Secondly, we describe the field experiments in which measurements were made to estimate model parameters. Third, we describe the parameterization of the model. Fourth, we describe model tests. Finally, we use the model to conduct simulation studies to analyse the effect of plant traits and plant trait plasticity on light capture in pure stands of maize and soybean, and the intercrop of the two species.

Model development

An FSP model (Vos *et al.*, 2010) of maize/soybean intercropping, mainly including organ development and radiation modules, was developed in the GroIMP platform (www.sourceforge.net/projects/groimp)

(Hemmerling *et al.*, 2008). Since our research questions require the accurate calculation of light capture in relation to plant phenotype, the model was designed such that organ dimensions were represented using the measured data as input, and daily light capture was simulated.

Thermal time and plant development

The phenological development of both species was driven by thermal time (°Cd) from sowing to maturity. Daily thermal time was calculated as the fitted daily mean temperature (Equations 1 and 2) from 2013 (Supplementary Fig. S1), which was calculated by actual daily maximum and minimum temperature, minus a base temperature of 8 °C for maize and 10 °C for soybean (Major *et al.*, 1975; Ritchie and NeSmith, 1991):

$$T_m = a + b \times \sin\left(\frac{2\pi(D_y - c)}{365}\right) \tag{1}$$

$$T_{ave} = w \times T_{max} + (1 - w) \times T_{min} \tag{2}$$

Where T_m is the daily maximum or minimum temperature (T_{max} or T_{min}, °C), D_y is the day of year, T_{ave} is the daily mean temperature (°C), a is the largest temperature of the year (°C), b is the scale, c is the day of the year where temperature is largest, and w is the relative weight of maximum temperatures in the calculation of average temperature.

Organ expansion

The beta growth function was used to describe the expansion of all organs (both in length and in width) versus organ age (Yin *et al.*, 2003):

$$L_t = L_{max}\left(1 + \frac{t_e - t}{t_e - t_m}\right)\left(\frac{t}{t_e}\right)^{\frac{t_e}{t_e - t_m}} \quad (0 \leq t_m < t_e) \tag{3}$$

Where L_t is the organ length or width (cm/mm) at organ age t (°Cd) and L_{max} is the final organ length/width (cm/mm). t_e is the age when the final organ length/width was reached (°Cd) corresponding to the elongation duration from organ appearance to maturity; t_m is the organ age at which growth rate is maximal (°Cd).

Elongation duration of leaf and internode, and the leaf life span for maize and soybean were optimized to minimize the root mean square error (RMSE) between the observed and simulated leaf area per plant and plant height. Leaf and internode elongation duration used the same value across treatments both for maize (150 °Cd for internode and 200 °Cd for leaf) and for soybean (200 °Cd for internode and 350 °Cd for leaf). Leaf life span also used the same value across treatments for maize (1150 °Cd) whereas different values were used for soybean (1015 °Cd in sole crop and 1085 °Cd in intercrop). Leaf number was set to 21 for maize and 25 for soybean both in sole crop and intercrop. Branches were not simulated due to the low percentage of plants with branches (10% in sole crop and 8% in intercrop, with one or two small branches in those cases) and the small area of leaves on those branches (<200 cm², which is <5% of the whole plant area).

Profile of mature organ morphological traits along the plant stem

The distribution of final blade length and final petiole length ($L_{i,r}$) along the main stem was described using the Cauchy distribution function (Buck-Sorlin, 2002; Evers *et al.*, 2005):

$$L_{i,r} = \frac{L_{i,m}}{1 + \left(\frac{r - r_{i,m}}{b_i}\right)^2} \tag{4}$$

Where i is B for blade and P for petiole, $L_{i,m}$ is the maximum final organ length (cm), b_i is a scale parameter, and $r_{i,m}$ is phytomer rank at the maximum final organ length.

A linear model was used to describe the relationship between blade width ($L_{B,w}$) and length ($L_{B,r}$):

$$L_{B,w} = a_1 \times L_{B,r} + b_1 \tag{5}$$

Where $L_{B,r}$ is the final blade length at phytomer rank r (cm), a_1 is the slope (cm cm^{-1}), and b_1 is the intercept of the linear model.

Maize leaf shape was fitted by the function in Evers *et al.* (2010), and soybean leaf shape was fitted using the following relationship (Equation 7; Supplementary Fig. S2):

$$W_m = \left(\frac{-x(x - 2L_m)}{L_m^2}\right)^{C_m} \tag{6}$$

$$W_s = \left(\frac{x}{L_s}\left(\frac{1-x}{1-L_s}\right)^{\frac{1-L_s}{L_s}}\right)^{C_m} \tag{7}$$

Where W_m and W_s are the normalized margin to midrib distance (where normalization is achieved by dividing by half the greatest leaf width) of maize and soybean as a function of normalize leaf length (x). x is the distance from leaf tip to the measured point divided by final leaf length. L_m and L_s are the distance of the point of maximum margin–midrib distance to the leaf tip of maize and soybean as a function of the final length ($0.5 < L_m < 1$ and $0.5 < L_s < 1$), and C_m and C_s are the maize and soybean curvature coefficient ($0 < C_m < 1$ and $0 < C_s < 1$).

A logistic equation was used for final internode length for maize:

$$I_{m,r} = \frac{I_m}{1 + e^{-k_1(r - r_1)}} \tag{8}$$

Where $I_{m,r}$ is the maize final internode length at phytomer rank r (cm), I_m is the maximum internode length (cm), r_1 is the phytomer rank of the inflection point, and k_1 is the slope.

A broken stick function was used for soybean final internode length:

$$I_{s,r} = \begin{cases} a_2 r + b_2, & r < r_0 \\ \dfrac{I_{l,m}}{1 + \left(\frac{r - r_{l,m}}{b_l}\right)^2}, & r \geq r_0 \end{cases} \tag{9}$$

Where $I_{s,r}$ is the soybean final internode length at phytomer rank r (cm), r_0 is the breakpoint, a_2 and b_2 are the slope and intercept of the linear regression, $I_{l,m}$ is the maximum final internode length (cm), b_l is a scale parameter, and $r_{l,m}$ is phytomer rank at the maximum final internode length.

Internode diameter along the stem was described by a decreasing logistic equation (Gu *et al.*, 2014):

$$D_r = D_m - \frac{D_m}{1 + e^{-k_2(r - r_2)}} \tag{10}$$

Where D_r is the final internode diameter at rank r (mm), D_m is the theoretical maximum internode diameter at the base of the plant (mm), k_2 is the slope, and r_2 is the inflection point.

Maize leaf declination angle distribution along the stem was described by a negative exponential equation:

$$\beta_{m,r} = a_3 e^{-b_3 r} + c \tag{11}$$

Where $\beta_{m,r}$ is the maize leaf declination angle at rank r (°), $a_3 + c$ is the value when r would be 0, b_3 is the scale, and c is the asymptote when r gets larger.

Soybean petiole declination angle distribution along the stem was described by the Cauchy distribution function:

$$\beta_{s,r} = \frac{\beta_{A,m}}{1 + \left(\frac{r - r_{A,m}}{b_A}\right)^2} \tag{12}$$

Where $\beta_{s,r}$ is the soybean petiole declination angle at rank r (°), $\beta_{A,m}$ is the maximum declination angle (°), b_A is a scale parameter, and $r_{A,m}$ is phytomer rank at the maximum declination angle.

Radiation calculation

The daily course of incident radiation intensity was calculated using latitude and day of year to achieve the pure effect of the intercrop designs and plant phenotypes, not affected by variation in weather data (Supplementary Fig.

S3) (Spitters, 1986; Evers *et al.*, 2010). Direct incoming radiation was simulated using an array of 24 directional light sources, representing the daily course of the sun based on latitude and day of the year (Evers *et al.*, 2010; Buck-Sorlin *et al.*, 2011). Diffuse radiation was approximated using an array of 72 directional light sources, which were positioned in a hemisphere in six circles with 12 light sources each (Evers *et al.*, 2010). This dome representing the sources of diffuse radiation was randomly rotated at each time step and the relative light intensity of each source depended on its location in the dome. Light capture was simulated by the reverse Monte-Carlo ray tracing algorithm in GroIMP (Hemmerling *et al.*, 2008).

For all simulations, day 125 was the starting day, day 255 was the ending day, and 40.13°N was set as the latitude to determine the angle of the light sources. The atmospheric transmissivity was set to 0.363 based on the global radiation data between May and September during these two years. The fraction of diffuse radiation in daily radiation was set to 0.619 (Zhou *et al.*, 2004). The reflectance and transmittance of leaf blades for PAR were set to 0.079 and 0.082 for soybean (Kasperbauer, 1987), and as 0.0923 and 0.0127 for maize (Zhu *et al.*, 2015). Maize leaf sheaths were not considered separately due to a lack of measurements. Internodes were defined as opaque objects, and their reflectance was set as the sum of the transmittance and reflectance of the blade.

Field experiments

To provide the plant phenotypic traits data for constructing an FSP model, field experiments were conducted in 2012 and 2013 at Shangzhuang experimental station, Beijing, China (40°08′N, 116°11′E). Shangzhuang has a temperate, semi-humid, continental monsoon climate.

The strip intercropping pattern used in this study consisted of two rows of maize alternated with three rows of soybean, which is normally used by farmers in northwest China due to high system performance. Additionally, both species were grown as sole crops. In the intercrop, the border rows were labelled M1 and M2 for maize, and S1 and S3 for soybean, while S2 was the inner row for soybean (Fig. 1). For both the sole and intercrop design, maize and soybean were planted at 20 cm distance within the row, 60 cm between maize rows and 30 cm between soybean rows. In the intercrop, the distance between maize and soybean strips was 50 cm. Therefore, the plant density was 8.3 plants m^{-2} for maize and 16.7 plants m^{-2} for soybean in the sole crops and within the intercrop strips.

Overall, plant density per m^2 of intercrop area was 4.5 plants m^{-2} for maize and 6.8 plants m^{-2} for soybean, giving relative densities (density in intercrop divided by density in sole crop) of 0.55 for maize (RD_m) and 0.41 for soybean (RD_s). The area of each plot was 11 m×33 m. The row orientation was north–south in both years.

Maize cultivar 'Zhengdan 958' and soybean cultivar 'Zhonghuang 30' were both sown on 7 May in 2012 and on 5 May in 2013. There were 2–3 seeds per hole at sowing, and only one plant per seeding hole was kept after emergence. Harvesting was on 20 September in both years. Based on local practice for maize and soybean, chemical fertilizers were applied in both years and in both sole crops and the intercrop at uniform rates across treatments of 100 kg N ha^{-1}, 130 kg P$_2$O$_5$ ha^{-1}, and 100 kg K$_2$O ha^{-1} before sowing. The 50 kg N ha^{-1} treatment was only top-dressed in sole maize and intercropped maize at the maize V8 stage (i.e. eight leaves with collar visible). Following local management, water was given to avoid soil water stress impact on crop growth. Meteorological data during the crop growing season were taken from the weather station (Rainroot, China) at the experimental site.

Measurements

In situ observations and destructive measurements were made on individual plants of both species in each treatment in 2013 to obtain plant architectural parameters. Observations were conducted from plant emergence onwards. Leaf tip appearance was observed every week for each phytomer rank on nine plants per plot in the sole crop and three plants in each row in the intercrop. The observed plants were selected randomly after plant emergence. Phyllochron (i.e. the thermal time between successive leaf tip appearances) was estimated per plant as the slope obtained from a linear regression of thermal time versus leaf number (°Cd per leaf). The declination angle of each leaf/petiole (i.e. the small angle between the stem and leaf/petiole) was measured on four plants in sole crops and two plants in each row in the intercrop, using a digital protractor at full leaf expansion. Phyllotaxis, the angles between consecutive leaves along a stem, was measured using a digital protractor from the top of the maize plant (Supplementary Table S1). Phyllotaxis was not measured in soybean but was assumed to conform to 137°, commonly observed in plants (Niklas, 1988).

Destructive measurements on plant green leaf area were made every 15–20 d in all treatments from 30 d after emergence. Four plants were
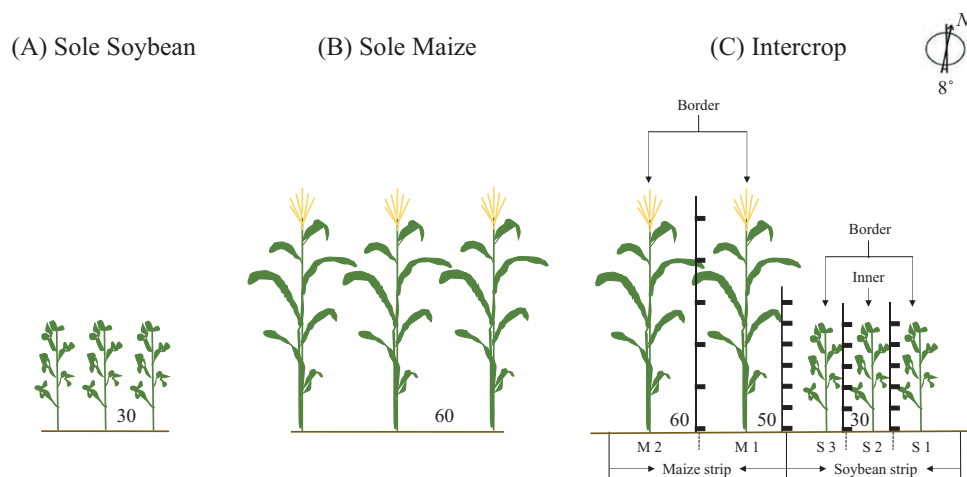
Fig. 1. Row configurations of sole soybean (A), sole maize (B), and a maize/soybean intercrop (C, two rows of maize alternated with three rows of soybean) (unit: cm). In the intercrop, M1, M2, S1, and S3 are border rows while S2 is an inner row. The positions for the light intensity measurements for intercrop canopy are indicated in (C). The interval between two vertical measurements was 40 cm in the middle between maize rows and 20 cm at other positions.

taken in each sole crop plot and in each row of each species in the inter-crop plot 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 per plot in sole crops and in each row in intercrop plots to measure final leaf length and width, final internode length and diameter, and final petiole length for each phytomer rank at maize VT stage (i.e. tassel completely visible). Length and width of each soybean leaflet were measured, and the mean value of the final leaflet size at each phytomer rank was used as the final leaf dimension for the rank. Leaf shape was assessed by measuring width at 5 cm intervals along the length of the leaf in maize and every 5 mm on soybean leaflets along the length of each of 7–10 fully grown leaves, chosen randomly. Whole-plant leaf area was measured using a LI-COR LI-3100 leaf area meter (LI-COR, Inc., Lincoln, NB, USA) in both years to calibrate and validate the change of leaf area over time in the FSP model. Soybean plants in the field had a strong main stem and in some cases produced small branches on the lower phytomers. Therefore, the percentages of branching plants, branch number, and leaf area on those branches were recorded separately.

The photosynthetically active radiation (PAR) intensity at different horizontal and vertical positions of the intercrop canopy (Fig. 1C) was measured on 28 August 2012 by using an LP-80 linear quantum sensor (AccuPAR, Decagon, USA) from 07.00 h to 17.00 h every 2 h. The external light sensor of the linear quantum sensor was always placed 20 cm above the maize. Four horizontal positions were measured (Fig. 1C): one between the maize rows, one between the maize and soybean strip, and two between the soybean rows. For the vertical PAR profile between the two maize rows, measurements were made at 40 cm intervals to the top of the maize canopy. For the three other horizontal locations, measurements were made at 20 cm intervals to the top of the soybean canopy.

The plant traits from 2013 were used to derive model parameters for the sole crop and intercrop phenotypes. The leaf area and plant height from both 2012 and 2013, and relative light intensity in the intercrop canopy from 2012 were used to identify the effect of plant traits on model performance in different years and to test the model.

Model parameterization

The phyllochron was analysed using a linear mixed model (lme) in the 'nlme' package in R (R Core Team, 2020), with plot and plant (nested in plot) as random effects. The parameters C_m, L_m, C_s, and L_s for defining leaf shape were estimated by minimizing the RMSE using the 'solver' function in Microsoft Excel 2016. Nested models (mle2) in the 'bblme' package of R were used for analysing the distribution of final internode dimensions, final leaf dimensions, petiole angle, and final petiole length.

The equations were fitted to data of the three row positions (sole crop, intercrop border row, and intercrop inner row) (Supplementary Table S2). Multiple model versions were fitted representing different assumptions on equality of parameters in different row positions. Specifically, the data were fitted: (i) using three lines—one line for each row; (ii) using two lines—one line for sole crop and the other line for intercrop border row and intercrop inner row; and one line for the sole crop and the intercrop inner row, and the other line for the intercrop border row; and (iii) using one line—for the data of all rows combined. For parameters in the equations, we also had different assumptions under the assumptions for plant traits in different row positions. For example, if there were three parameters in the equation, we had four assumptions: (i) the three parameters were the same values in different row positions; (ii) only one parameter was the same value in different row positions; (iii) there were two parameters the same in different row positions; and (iv) all the three parameters had different values in different row positions.

Akaike's information criterion (AIC) was used to determine which model version was best supported, with small AIC values representing better overall fits: models with AICs less than 2 apart (ΔAIC<2) are more or less equivalent, and in this situation the simple model is better; those with AICs 4–7 apart are clearly distinguishable; and models with AICs >10 apart are definitely different (Bolker, 2008). The plant traits were thought to be different or the same according to the selected model. The fitted parameter values are listed in Table 1.

Evaluation of model performance

Due to different light and temperature environment in the two years, simulations were run using the plant population density of the field experiment (8.3 plants m^{-2} for maize and 16.7 plants m^{-2} for soybean in the sole crops and within the intercrop strips) and temperature data in the two years to evaluate model performance with respect to plant leaf area and plant height datasets of sole crops and intercrops, and relative light intensity of the intercrop canopy in 2012. In the model, maize plant height was defined as the sum of internodes and tassel length. Due to the more complex architecture of soybean compared with maize, soybean plant height was defined as the distance from the ground to the highest point of the plant in the 3D scene. Tile sensors were set to 0.1 m×0.1 m in the model to estimate light intensity in different intercrop canopy heights (40 cm for maize row and 20 cm for soybean row). The relative light intensity was calculated as the ratio between light intensity within the canopy and the value above the canopy in the field and in the model.

Simulations were run for a scene of 6×10 plants for sole crops and 5×10 plants for intercrop (one maize strip and one soybean strip in intercrops). These plots were copied 10 times in both the *x* and *y* direction using the replicator functionality of GroIMP to minimize border effects with respect to the incoming light. The RMSE was used to assess the correspondence between simulated and observed values for leaf area per plant, plant height, and PAR in the intercrop canopy:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (P_i - O_i)^2} \qquad (13)$$

Where P_i and O_i are the simulated and observed values. *n* is the number of simulated or observed values.

Simulation experiment on the contribution of intercrop configuration and plant traits to light capture

To quantify the contribution of intercrop configuration and plant traits to light capture, two sets of situations were simulated in this study: (i) a sole crop configuration with phenotypes from either the sole crop or the intercrop border and inner rows to quantify the effect of traits of the intercrop phenotype on light capture in the absence of the heterogeneous intercrop configuration; and (ii) an intercrop configuration with sole and intercrop phenotypes to quantify the effect on light capture of intercrop phenotype of one or both species in an intercrop configuration compared with the sole crop phenotype. Each scenario was run 10 times to account for variation in the model due to random effects of the ray tracing algorithm and the randomly chosen initial plant orientation. Temperature data from 2013 were used in these scenarios.

To calculate the effects of configuration and plasticity, an expected light capture was introduced and used as a reference value. L_{exp} represents the light capture expected in an intercrop based on the relative densities of both species, in case both the intercrop configuration and plasticity would not have any effect on the light capture per plant (Zhu *et al.*, 2015):

$$L_{exp} = L_{exp,m} + L_{exp,s} = L_{s,sm} \times RD_m + L_{s,ss} \times RD_s \qquad (14)$$

Where $L_{exp,m}$ and $L_{exp,s}$ are expected light capture (MJ m^{-2}) of maize and soybean in intercrop with phenotypes in sole configuration, $L_{s,sm}$ and $L_{s,ss}$ are the light intercepted (MJ m^{-2}) by maize and soybean with sole phenotypes in sole configuration, and RD_m and RD_s are the relative density of maize and soybean, defined as the ratio between the density in sole and in intercropping.

Table 1. The list of fitted parameter values for organ length/width in sole crop maize (SM), intercrop maize (IM), sole crop soybean (SS), intercrop soybean in border row (IS$_B$) and inner row (IS$_I$) by using observed data from the 2013 growing season

Plant traits	Attributes	Maize				Soybean					
		SM		IM		SS		IS$_B$		IS$_I$	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Phyllochron[a]	Slope (°Cd)	53	0.8	53	0.8	40	1.9	48	1.6	48	1.6
Blade length (Equation 4)	$L_{B,m}$ (cm)	109.66	1.00	109.66	1.00	11.24	0.17	9.63	0.19	9.63	0.19
	b_B	6.06	0.12	6.06	0.12	14.05	1.28	14.05	1.28	14.05	1.28
	$r_{B,m}$	13.15	0.06	13.15	0.06	15.76	0.63	15.76	0.63	15.76	0.63
Blade width (Equation 5)	a_1	0.06	0.00	0.06	0.00	0.50	0.06	0.50	0.06	0.50	0.06
	b_1	3.29	0.15	3.79	0.29	3.15	0.60	2.03	0.20	3.15	0.60
Petiole length (Equation 4)	$L_{P,m}$ (cm)					33.12	0.69	37.89	1.03	33.12	0.69
	b_P					9.95	0.53	7.83	0.58	9.95	0.53
	$r_{P,m}$					17.79	0.20	17.79	0.20	17.79	0.20
Internode length (Equations 8 and 9)	a_2					-0.15	0.16	-0.05	0.05	-0.05	0.05
	b_2					2.81	0.79	2.81	0.79	2.81	0.79
	r_0					6.30	3.83	6.30	3.83	6.30	3.83
	l_m or $l_{I,m}$ (cm)	16.74	0.23	16.74	0.23	5.22	0.28	7.80	0.32	7.80	0.32
	r_1 or b_I	7.60	0.10	7.60	0.10	7.50	0.50	7.50	0.50	7.50	0.50
	k_1 or $r_{I,m}$	1.16	0.14	1.16	0.14	16.13	0.41	15.26	0.49	15.26	0.49
Internode diameter (Equation 10)	D_m (mm)	17.19	0.54	19.98	0.49	8.42	0.13	6.71	0.22	7.62	0.20
	r_2	17.92	0.40	16.99	0.23	22.72	0.29	22.72	0.29	22.72	0.29
	k_2	0.37	0.03	0.37	0.03	1.11	0.33	0.37	0.32	0.32	0.32
Declination angle (Equations 11 and 12)	a_3 or $\beta_{A,m}$ (°)	49.15	4.50	28.37	3.71	41.79	2.90	58.35	4.74	58.35	4.74
	b_3 or b_A	0.27	0.04	0.27	0.04	16.95	5.50	9.44	5.60	9.44	5.60
	c or $r_{A,m}$	14.12	1.90	17.88	1.38	10.50	0.46	10.50	0.46	10.50	0.46

[a] Phyllochron is the slope of linear regression between thermal time and leaf number.

In the sole crop configuration, the effect of plasticity was calculated as the light capture difference caused by setting all traits from the sole crop trait value to the intercrop trait value. In the intercrop, the effect of plasticity was calculated as the light capture difference caused by setting all traits of a species from the sole crop trait value to their intercrop trait value while keeping the other species traits as intercrop traits. The effect of intercrop configuration was calculated as the light capture difference between a scenario in which both species have the sole crop trait values and the expected light capture (L_{exp}) of the intercrop.

Contribution of individual soybean architectural traits to light capture

From the experimental data and parameter optimization, six soybean traits showed substantial differences between the sole crop and the intercrop: final internode length, final leaf dimensions, leaf life span, petiole declination angle, final petiole length, and phyllochron. We determined the effects on light capture of changes in single traits and in combinations of traits in sole crop and intercrop designs. The scenario with all sole crop trait values was the reference case in the sole crop, and the scenario with all intercrop trait values was the reference case in the intercrop setting. The light capture for soybean in intercrops was expressed as MJ m^{-2} total intercrop area. Maize was set to the intercrop phenotype, as the objective here was to analyse the contribution of soybean traits to the performance of soybean in a realistic maize/soybean intercrop setting. Each scenario was run 10 times. Temperature and plant phenotype data from 2013 were used in these scenarios.

In the sole crop configuration for soybean, the expected contribution of each intercrop plant trait to light capture by soybean as a sole crop was calculated as the change in light capture resulting from setting one trait from its sole trait to the intercrop trait value. In the intercrop, the contribution of each sole crop trait of soybean to light capture by soybean was calculated as the change in light capture caused by setting one trait from the intercrop trait value to the sole trait value.

The relative contribution of the plasticity in each individual trait to light capture over the whole growing season in intercrops was calculated as the difference in light capture between a null model with all traits set to the intercrop value (L_{null}) and a model with this trait set to the sole crop value (L_i), divided by the difference in light capture between the null model (L_{null}) and the model with all six selected traits having the sole crop value (L_{all}) (Zhu *et al.*, 2015):

$$C_i = 100 \times \frac{L_i - L_{null}}{L_{all} - L_{null}} \tag{15}$$

Where C_i represents the relative contribution of sole crop trait i (i.e. internode length, leaf dimensions, leaf life span, petiole angle, petiole length, and phyllochron) to the increased light capture of soybean in an intercrop as compared with all traits from an intercrop.

Statistical analysis

All statistical analysis was made using R version 4.0.2 (R Core Team, 2020). Least significant differences (LSDs) were calculated using the 'agricolae' package to assess pairwise differences in light capture at the 5% (P=0.05) level. The 'ggplot2' package (Wickham, 2009) was used to produce figures. The values presented in the figures are means ±SEs.

Results

Plant traits in intercropping and sole cropping

Phyllochron

Maize phyllochron, the thermal time interval between successive leaf tip appearances, was the same (53±0.8 °Cd) in both the intercrop and the sole crop (Fig. 2A). Intercropping

increased soybean phyllochron, but there was no difference between border rows and inner rows (Fig. 2B). In the model, soybean phyllochron was set to 40 °Cd in the sole crop and 48 °Cd in the intercrop.

Leaf traits

Intercropping had no effect on leaf length of maize, but slightly increased the leaf width/length ratio (Fig. 3A, B). Soybean had reduced leaf dimensions in the intercrop compared with the sole crop, but no difference was found between border rows and inner rows (Fig. 3C, D). Intercropping decreased soybean petiole length in border rows on phytomers under rank 13, whereas it increased petiole length for phytomers with ranks between 16 and 22, compared with the intercrop inner row and the sole crop (Fig. 3E). There was no difference in petiole length between the intercrop inner row and the sole crop.

Internodes

There was no difference in the length of maize internodes between the sole crop and the intercrop (Fig. 4A), but there were differences in stem diameter in ranks under 14, with larger internode diameter in the intercrop than in the sole crop at low and middle ranks (sixth to the14th) (Fig. 4B). Sole maize internode diameter was at most 86% of that in intercropping at the same rank.

Soybean internodes were longer in the intercrop than in the sole crop, but there was no difference in internode length between border rows and inner rows (Fig. 4C). Internodes of all ranks were thinner in intercropped soybean than in sole soybean. Row position affected soybean internode diameter significantly, with thinner internodes in border rows. Internodes were 25% wider at the base of sole soybean than in border rows of intercropped soybean and 11% wider than in inner rows of the intercrop.

Declination angle

Maize declination angle decreased with phytomer rank. Furthermore, leaf declination angle was smaller (more erect)

in the intercrop than in the sole crop at ranks below the sixth, whereas the opposite occurred at higher ranks (Fig. 5A). Soybean petiole declination angle was larger in the intercrop than in the sole crop, especially at some middle ranks (fourth to 18th), while row position did not affect the declination angle (Fig. 5B).

Evaluation of model performance

The model adequately visualized the architectural development of maize and soybean plants, including representation of plant height and leaf area dynamics during the growing season (exemplified for intercrops in Fig. 6). Simulated leaf area per plant showed a characteristic pattern of increase during leaf production and extension, and of decrease during leaf ageing and shedding (Fig. 7). For maize in the sole crop and intercrop, the maximum leaf area per plant was slightly overestimated by the model (Fig. 7A, C). Overall, there was satisfactory correspondence between simulated and observed leaf area per plant, with RMSE ranging from 0.03 m^2 for soybean to 0.08 m^2 for maize across planting patterns. The RMSE for plant height varied from 0.05 m for soybean to 0.09 m for maize across treatments (Fig. 8).

The relative light intensity increased with the height in the canopy (Fig. 9). Simulated and observed relative light intensity at different heights of the canopy in intercropping showed good agreement at maize R3 stage (milk stage), with RMSE ranging from 0.03 to 0.05, even though the model slightly underestimated the relative light density under 1 m at 30 cm from the left maize border row (Fig. 9A).

Contribution of crop configuration and plant phenotype to light capture

The simulated light capture over the growing season was 784.6±1.1 MJ m^{-2} in sole maize and 687.1±0.2 MJ m^{-2} in sole soybean (Fig. 10A). When the intercrop phenotype of maize was
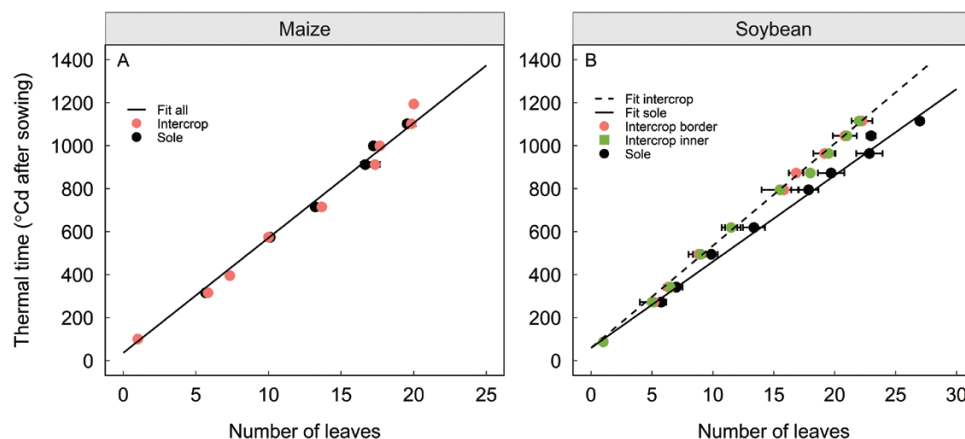

Fig. 2. Thermal time as a function of the number of visible leaves with maize (A) and soybean (B) in sole crop and intercrop during the 2013 growing season. Values are the means ±SE (*n*=9 in the sole crop, 6 in border rows, and 3 in the inner row).
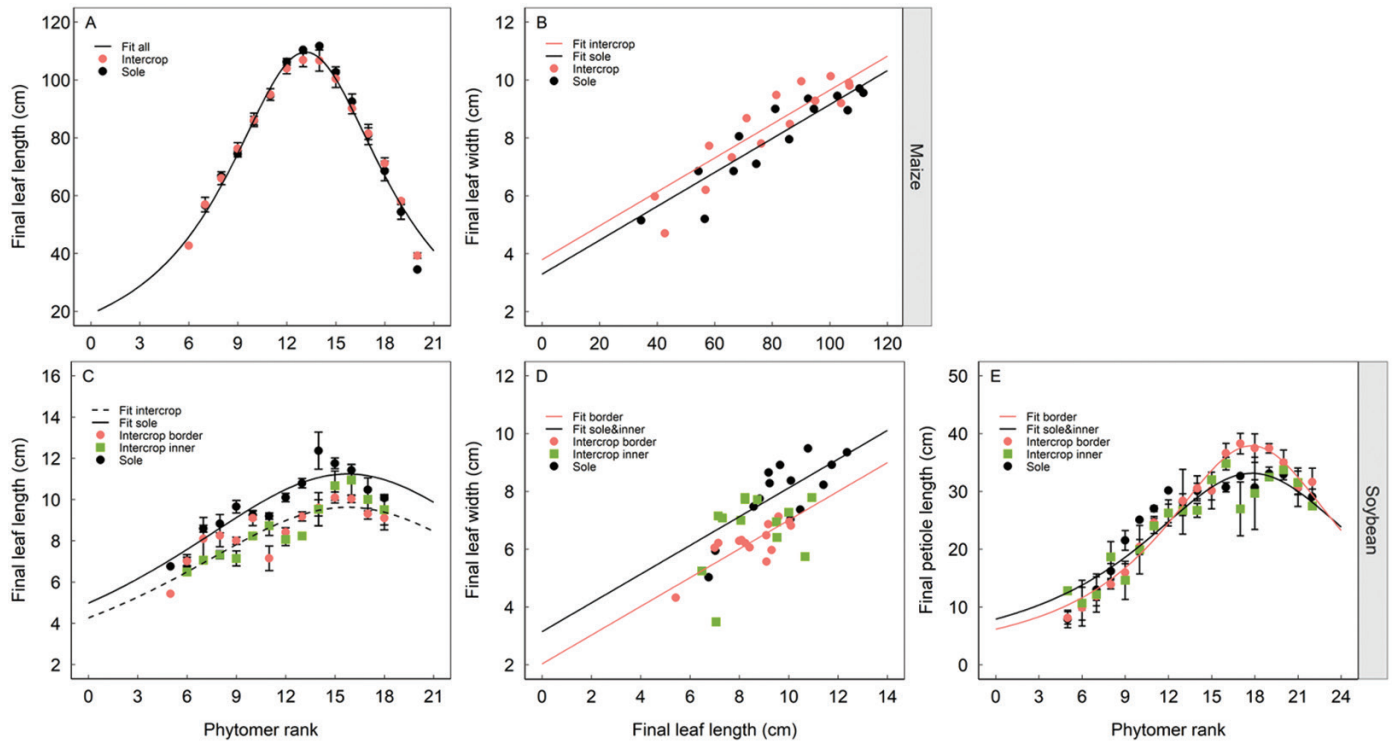
Fig. 3. Final leaf length (A, C), relationship between leaf length and width (B, D), and final petiole length (E) for maize (A, B) and soybean (C, D, E) in sole crop and intercrop during the 2013 growing season. Values are the means ±SE (n=2 in sole crops and intercrop inner row, and 4 in the intercrop border rows).
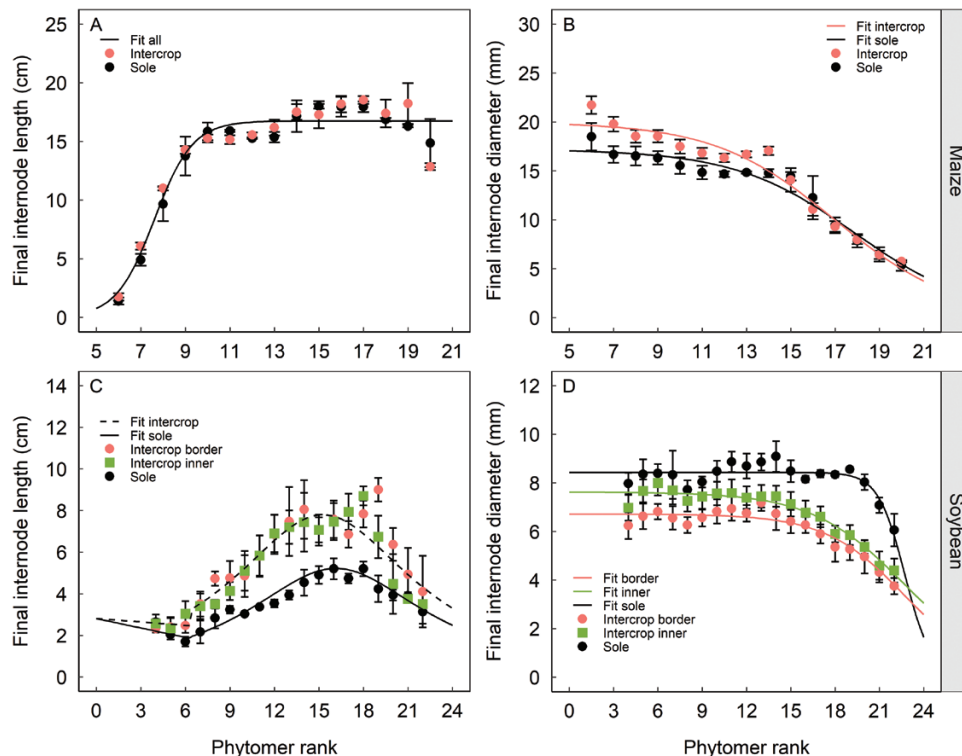

Fig. 4. Final internode length (A, C) and diameter (B, D) related to phytomer rank of maize (A, B) and soybean (C, D) in sole crop and intercrop during the 2013 growing season. Values are the means ±SE (n=2 in sole crops and intercrop inner row, and 4 in the intercrop border rows).
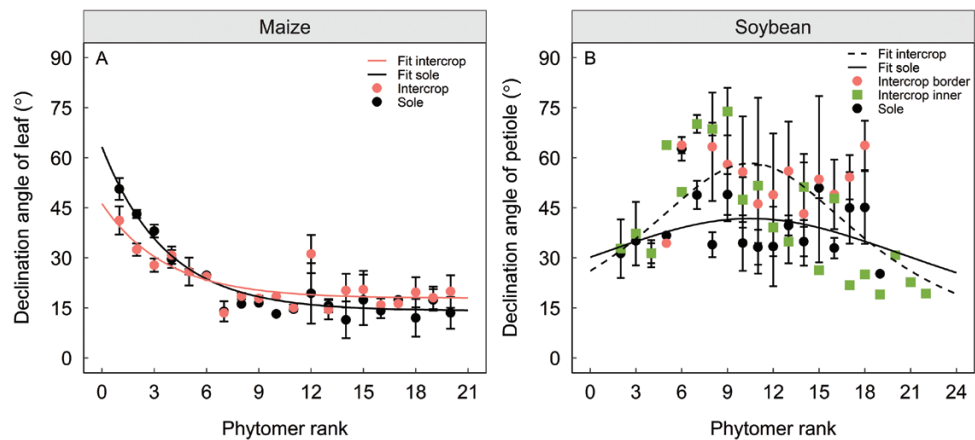
Fig. 5. Declination angle of maize leaf (A) and soybean petiole (B) related to phytomer rank in sole crop and intercrop during the 2013 growing season. Values are the means ±SE (*n*=4 in sole crops and intercrop border rows, and 2 in the intercrop inner row).
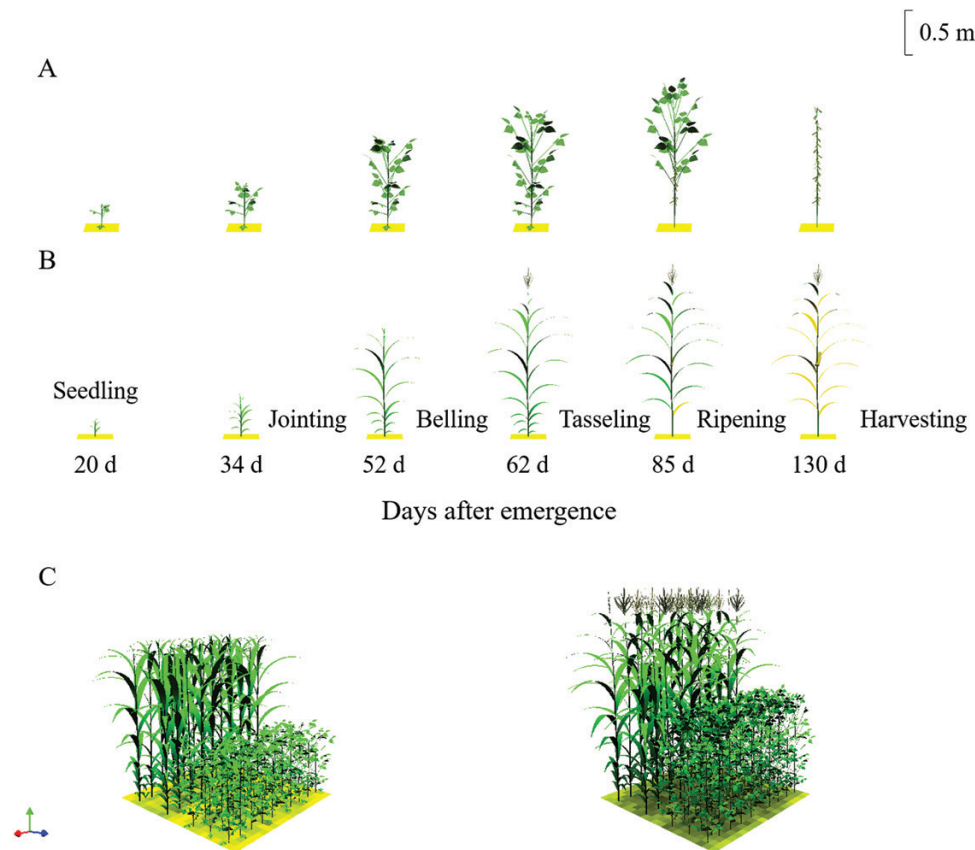

Fig. 6. Visual output of simulated soybean and maize: (A and B) single plant, (C) plot in intercrop [left, 54 days after emergence (DAE); right, 72 DAE]. The colour gradient in (C) represents the proportion of absorbed PAR (increases from black to light green for plant organs, and from black to yellow for the soil surface). The simulations in intercrops were run on 5×10 plants (one maize strip and one soybean strip). The plots were copied 10 times in both the *x* and *y* direction using the replicator functionality of GroIMP to calculate light capture by the centre plants and minimize border effects with respect to the incoming light. Simulations were run using the plant population density of the field experiment (8.3 plants m^{-2} for maize and 16.7 plants m^{-2} for soybean in the sole crops and within the intercrop strips).

used in a sole maize configuration, light capture was increased by 2%, but if the intercrop phenotype of soybean was used in a sole soybean stand, light capture was reduced by 5–10%, compared with light capture with the sole crop phenotype. In the intercrop, the maize intercrop phenotype increased light capture by 3%, but the soybean intercrop phenotype reduced light capture of soybean by 9%, compared with the light capture with sole crop phenotype. Thus, the maize intercrop phenotype contributed to higher light capture, but the soybean intercrop phenotype decreased light capture in both the sole crop and intercrop setting.
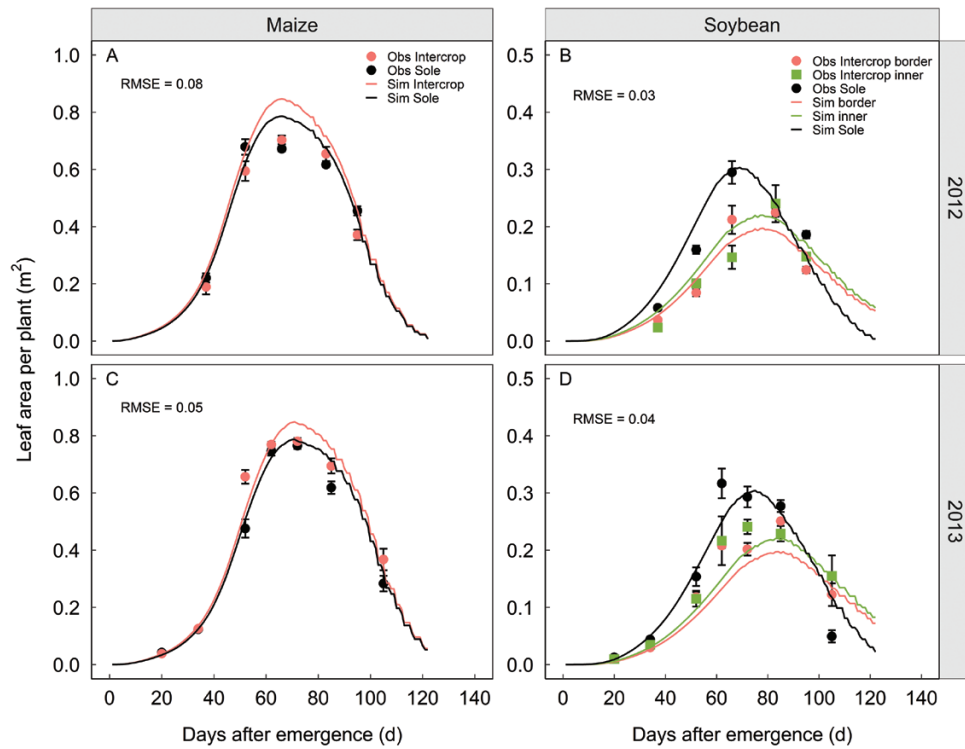
Fig. 7. Model evaluation of leaf area per plant of the sole crops as well as the intercrops using independent data in 2012 (A and B) and 2013 (C and D). All maize rows are border rows as the strips were two rows wide but in soybean there were three rows per strip; thus border rows and inner rows are distinguished. Values are the means ±SE (n=4 in sole crops and intercrop inner row, and 8 in the intercrop border rows).
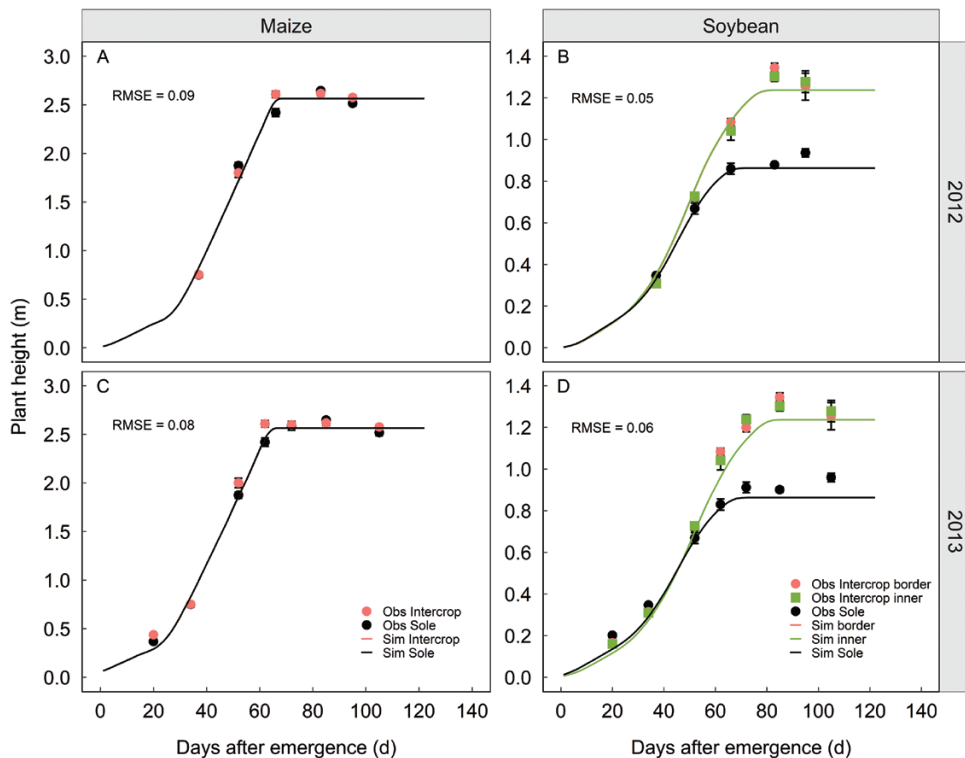

Fig. 8. Model evaluation of plant height in sole crops as well as in intercrops using independent data in 2012 (A and B) and 2013 (C and D). Values are the means ±SE (n=4 in sole crops and intercrop inner row, and 8 in the intercrop border rows).
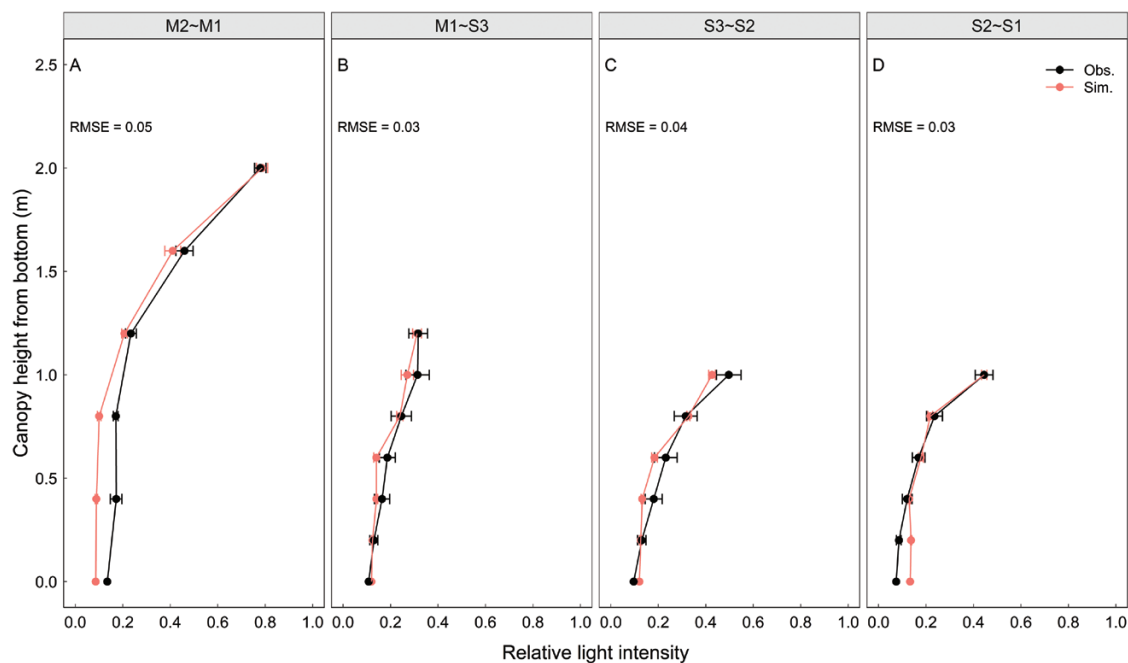
Fig. 9. Simulated and observed relative light intensity in the intercrop canopy in the middle between the two maize rows (M2–M1, A), in the middle between a maize and soybean row (M1–S3, B), and in the middle between two soybean rows (S3–S2, C and S2–S1, D). Values are the means ±SE (*n*=6 for observation, and 20 for simulation).
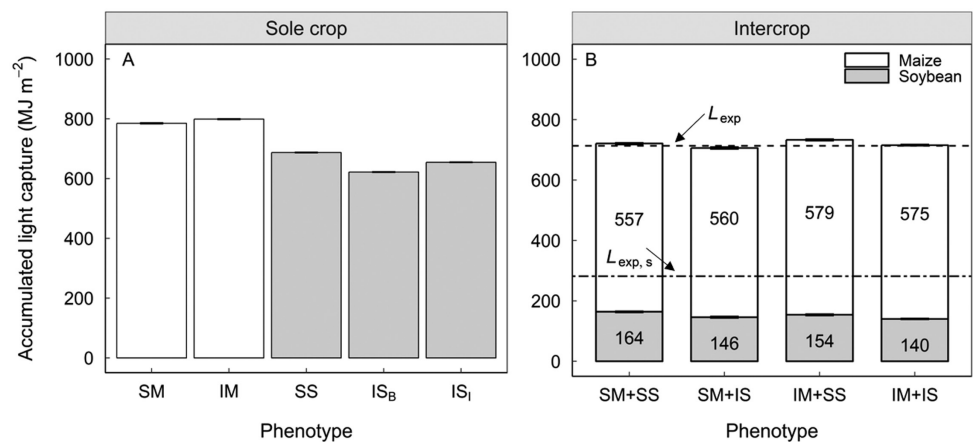

Fig. 10. Light capture of maize and soybean over the growing season in sole configuration (A) with sole phenotype and intercrop phenotype (border row and inner row) and in intercrop (B). SM, sole maize phenotype; SS, sole soybean phenotype; IM, intercrop maize phenotype; IS, intercrop soybean phenotype; IS_B, intercrop soybean phenotype in border row; IS_I, intercrop soybean phenotype in inner row; SM+SS, a strip maize/soybean intercrop with phenotype of sole crops. Light capture in SM+SS represented a pure structure effect without a contribution from plant plasticity. The light capture for species in intercrops was expressed per m^2 of intercrop area. The horizontal dashed lines represent the expected soybean light capture ($L_{exp,s}$) and intercrop light capture (L_{exp}) in an intercrop without the effects of structure or plant plasticity, respectively. In intercrop, $L_{exp}=L_{exp,m}+L_{exp,s}=0.55L_{s,sm}+0.41$ $L_{s,ss}=431.6 + 281.7=713.3$ MJ m^{-2}. The row category was indicated in Fig. 1. Error bars are not shown as they were within 1% of the averaged values. Values are the means ±SE (*n*=10).

In intercropping, the expected light capture based on sole light capture and relative densities in the intercrop (L_{exp}, Equation 14) was 713.3±0.6 MJ m^{-2}, which includes 431.6±0.6 MJ m^{-2} light capture by maize ($L_{exp,m}$) and 281.7±0.1 MJ m^{-2} light capture by soybean ($L_{exp,s}$). Light capture by maize (61% of the total) was thus slightly above the relative density of 55%, while light capture by soybean (39% of the total) was slightly lower than the relative density (41%). This difference is due to the higher leaf area index and higher light capture in sole maize as compared with sole soybean. With the intercrop phenotype of both species in an intercrop configuration (IM+IS), total light capture was 715.7±0.7 MJ m^{-2}, virtually equal to the expected total light capture of 713.3±0.6 MJ m^{-2} based on sole crop light capture and relative densities.
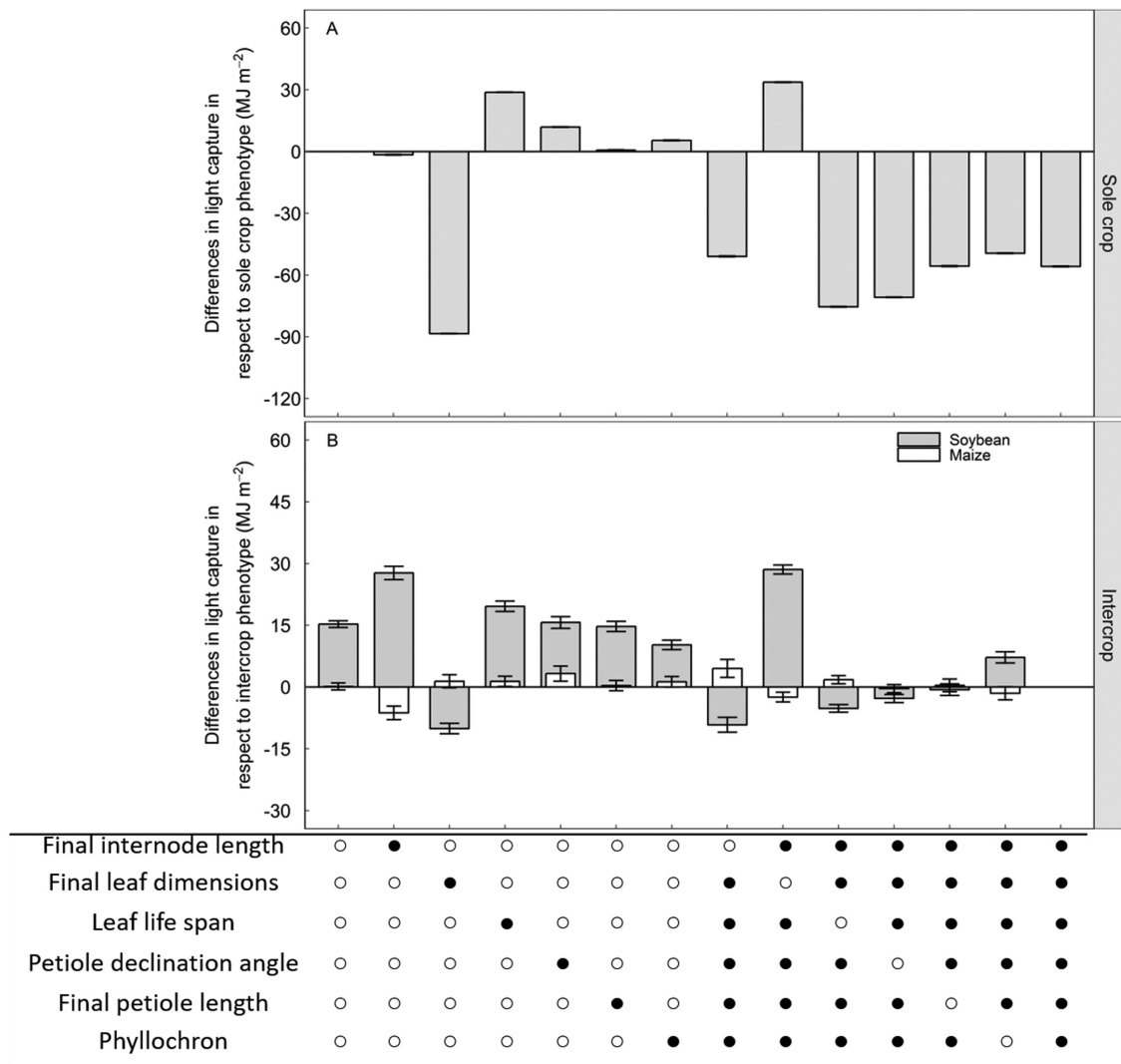
Fig. 11. Differences in light capture with respect to pure sole crop phenotype in sole soybean (A) and pure intercrop phenotype in intercrop (B) when soybean with and without selected single plant traits. Open circles, the value in sole phenotype was used in the simulation. Filled circles, the value in the intercrop phenotype, expressed as a weighted mean value (2/3 border row+1/3 inner row). Further plant traits (growth duration of internode and leaf and internode diameter) came from sole crop (A) or intercrop (B). The combination of different symbols represents the integration of those plastic traits. The light capture of soybean with pure sole crop traits was 687.1±0.2 MJ m^{-2} in sole crop. The light capture of plants with pure intercrop traits was 575.5±1.9 MJ m^{-2} for maize and 140.2±1.5 MJ m^{-2} for soybean in intercrop. Error bars that not shown are within 1% of the averaged values. Values are the means ±SE (n=10).

Simulated intercrop light capture with sole crop phenotypes (SM+SS) slightly increased (1%) system light capture in intercropping (720.3±1.7 MJ m^{-2}), compared with expected (Fig. 10B). Again, the distribution of light capture over the component species was affected considerably: the configuration effect increased the light capture of maize by 29% (556.5 MJ m^{-2} versus 431.6 MJ m^{-2}) and reduced the light capture of soybean by 42% (163.7 MJ m^{-2} versus 281.7 MJ m^{-2}), using sole crop phenotypes (SM+SS). Therefore, these simulations show that configuration changed total light capture very little, but it caused a major increase in the radiation captured by maize and a major decrease in the radiation captured by soybean. These changes were relatively insensitive to whether the

intercrop phenotypes of the two species were used or the sole crop phenotypes.

Relative importance of soybean traits for light capture

Average light capture of soybean in sole crops with intercrop phenotypes (all six traits set to intercrop values) was 8% lower than the light capture with the phenotype of sole soybean (Fig. 11A). Smaller leaf sizes of the intercrop phenotype were the main factor reducing light capture. The light capture with small leaves was 7–13% lower compared with light capture by sole soybean with the sole crop phenotype. The greater internode length and petiole length of the intercrop phenotype did not
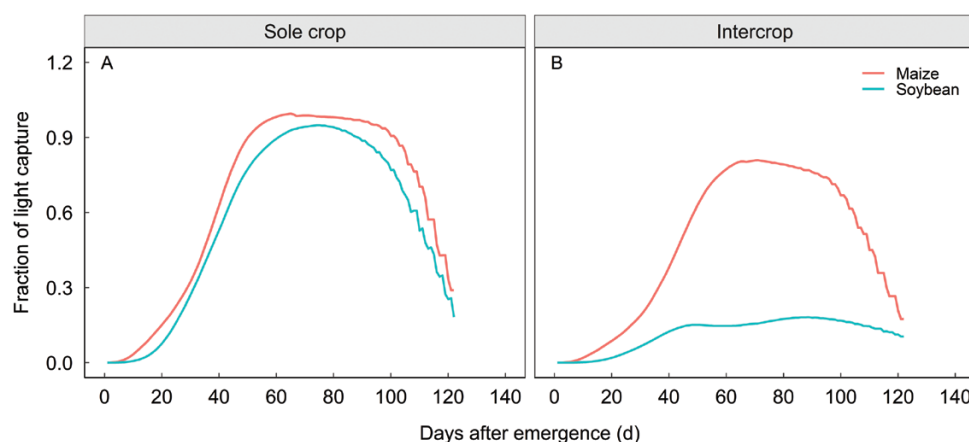
Fig. 12. Fraction of light captured by plants in sole crops (A) and the intercrop (B). Plants had sole phenotypes in the sole configuration and intercrop phenotypes in the intercrop configuration.

affect light capture, whereas the larger phyllochron, petiole angle, and leaf life span increased light capture by 1–4%, compared with the sole phenotype in a sole configuration.

Sole crop phenotypes increased soybean light capture in the intercrop by 11% compared with soybean with the intercrop phenotype (Fig. 11B). When this contribution of sole crop phenotype to light capture by soybean in the intercrop configuration was partitioned in contributions from the six component traits, the shorter internode length of the sole crop phenotype contributed −53%, larger leaves contributed +187%, shorter leaf life span contributed −30%, smaller petiole angle (more erect leaves) contributed −25%, shorter petioles contributed −2%, and shorter phyllochron contributed +46% to this increased light capture resulting from replacing intercropped soybean traits by sole soybean traits (Equation 15).

In most scenarios, except those in which only soybean phyllochron had the sole crop trait value, maize light capture was affected by intercropped soybean, which means maize would capture less light when intercropped soybean captured more light. The relative change in total light capture by the whole system caused by maize was smaller than that caused by trait values of soybean, which means soybean is the main species that affects system light capture, and changes in traits of maize in response to intercropping are not influential but those of soybean are. Intercrop light capture was significantly increased by 3.6% when only sole soybean leaf dimensions trait was added to the intercrop phenotype. There was larger variation in scenarios for the intercrop configuration than for the sole crop configuration, due to the smaller numbers of individual maize and soybean plants in the simulated scene in intercrop simulations as compared with sole crop simulations (Fig. 11).

Discussion

Intercropping had virtually no effect on total light capture compared with the expected value from sole crops. The configuration of the intercrop had a large positive effect on the light capture of maize, but a negative effect on the light capture of soybean. The major difference in plant height between maize and soybean resulted in a major increase in light capture per maize plant, and a corresponding reduction in the light capture per soybean plant in intercropping compared with the light capture that these species realized in the sole crop. Due to this over-riding effect of plant height, trait responses to intercropping contributed only slightly to total light capture and light partitioning.

This is the first comprehensive study to explore the role of soybean plant traits in light capture in simultaneous maize/soybean intercropping. It is of great interest to find out whether traits of soybean can to some extent overcome the limitations, particularly shading, that the plant experiences in intercrops with maize (Liu *et al.*, 2017*b*). Only after knowing the traits restricting soybean performance in intercropping, can related strategies that reduce interspecific competition and improve intercrop system performance, especially for simultaneous systems, be put forward to make soybean more suitable for simultaneous intercropping with maize.

Our current model does not contain the physiological processes that drive growth or belowground competition for resources. For the purpose of this study, those features were not required; however, in subsequent modelling studies, they can be included to be able to assess how phenotypic plasticity responses and the metabolism of carbon and nitrogen affect productivity of intercrops (Gu *et al.*, 2014; Barillot *et al.*, 2018; Evers *et al.*, 2019).

Plant phenotypic plasticity in the field

Maize had greater leaf area and final internode diameter in intercrops than in sole crops due to a favourable position (taller and less intraspecific interaction) in the canopy, which could improve light capture and lodging resistance, and then yield (Crook and Ennos, 1994; Flint-Garcia *et al.*, 2003; Zhang *et al.*, 2014, 2018; S. Li *et al.*, 2020). Since the model is not

mechanistic, difference in final leaf size cannot be simulated, leading to overestimation of leaf area per plant for maize and underestimation of relative light intensity among maize rows (Figs 7A, C, 9A, C).

Our soybean genotype was not shade tolerant, and consequently displayed strong shade avoidance response to maize shading in the form of small leaves, longer and thinner internodes, and less steep leaves (Pierik and De Wit, 2014; Zhao *et al.*, 2019), which leads to lower biomass and yield, especially for plants in border rows (S. Li *et al.*, 2020). Due to the heterogeneous intercrop environment, paraheliotropism (light avoidance) led to a large variation in soybean petiole declination angle compared with a sole crop (Fig. 5B) (Bielenberg *et al.*, 2003; Nagasuga *et al.*, 2013). This response was stronger when closer to maize, similar to the earlier finding in maize/soybean intercropping (Liu *et al.*, 2017b). However, there is a limit to the extent that soybean plants can display shade avoidance, and eventually too much shading will reduce the dry matter production of a subordinate species through a huge reduction of net photosynthesis (Yang *et al.*, 2018). In order to keep sustainable production of soybean in intercropping, the intercropping planting pattern can be designed to improve the light environment for soybean (Khalid *et al.*, 2019).

Intercrop configuration and phenotypic plasticity effects on light capture

Quantifying the role of intercrop configuration and phenotypic plasticity in light capture advantage of intercrop helps to better understand the biodiversity effects on ecosystem functioning (Loreau *et al.*, 2001). Oftentimes the role of plasticity in the realization and utilization of niche differentiation is not considered (Loreau and Hector, 2001; Cardinale *et al.*, 2007). In fact, plasticity contributes a great deal to the net biodiversity effect in relay intercropping systems, especially through phenotypic effects in the border rows of the species strips (Zhu *et al.*, 2015; Wang *et al.*, 2017).

No light capture advantage for the intercrop system as a whole was found in our study. However, both intercrop phenotype and configuration increased light capture for maize, and decreased light capture for soybean. In this system, there was very little complementarity for light capture. Compared with relay systems, the light taken away by maize cannot be captured by soybean in simultaneous systems; that is, there is hardly any 'left-over' light that would otherwise be lost, that could result in complementarity in light capture (Fig. 12), even though soybean showed strong plastic responses to shading. The increased light capture of maize could not complement or improve the reduced light capture of soybean. Additionally, in the studied intercrop system, the overall number of plants per unit of area in the intercrop was lower than in the equivalent sole crops (the sum of relative densities was <1), indicating that increasing

the total relative density in intercrops to at least 1 might result in a total relative light capture >1. Also, our system did not have temporal niche differentiation, which is an important contributor to intercrop performance (Yu *et al.*, 2015), leading to the absence of complementarity in light capture in our study.

The intercrop maize phenotype increased maize light capture but the intercrop soybean phenotype reduced soybean light capture in both the sole crop and the intercrop (Fig. 10). Due to the greater performance of maize in intercrop, maize intercepted almost 79% of the light. In contrast, maize shading led to less performance of soybean, resulting in 21% of light capture in which 63% was attributed to the two border rows and 37% to the inner row. The two species benefit from temporal complementarity in a relay system (Yu *et al.*, 2015), but only the dominant species benefited in our simultaneous system at the expense of the subordinate species. Therefore, without temporal complementarity in our intercrop system, the phenotype of species affected the light partitioning from subordinate species to dominant species greater than that in a relay system (Zhu *et al.*, 2015).

The yield advantages in simultaneous intercropping systems, such as maize/soybean (S. Li *et al.*, 2020) and maize/peanut (Gao *et al.*, 2020; Wang *et al.*, 2020) have been found to be smaller than in relay systems (Yu *et al.*, 2016; Xu *et al.*, 2020). Simultaneous cereal/legume intercropping systems may however be advantageous under low input conditions due to complementarity for nitrogen acquisition (Bedoussac *et al.*, 2015). While there is no doubt that many cases of overyielding in intercrops happen at a low input level, the benefits may be even greater if stresses are relieved, and intercropping is exploited to enhance resource capture and mitigate nutrient losses at higher input levels (C. Li *et al.*, 2020).

Soybean single phenotypic plasticity effects on light capture

Intercropping increased soybean internode length at the expense of diameter, which improved soybean light capture in intercrop. Our simulations showed that this effect on internode dimensions did not affect light capture in sole configurations (Fig. 11). Longer internodes of soybean in intercrops increased light capture because light intensity in the top layer will be increased (Gao *et al.*, 2008; Yang *et al.*, 2015). For most crops, even a slight increase in light interception leads to considerable changes in photosynthetic rates and yield formation (Khalid *et al.*, 2019). Thus, an increase in soybean internode length in maize/soybean intercropping, resulting in higher soybean light capture, probably translates into a yield increase.

Soybean leaves were smaller in intercrops than in sole crops (Liu *et al.*, 2017b). Leaf dimensions were the main trait relevant to light capture in sole crops and intercrops

(Fig. 11). In shaded environments, plants typically have increased specific leaf area (SLA) leading to larger leaf area, to optimize light capture. However, in heavy competition for light, carbon assimilation may be so limited that even an increase in SLA, in combination with enhanced stem extension and thus leaf positioning away from shading, may lead to smaller instead of larger leaf areas (Valladares *et al.*, 2011; Gong *et al.*, 2015). The smaller and thinner leaves lead to lower light interception and photosynthetic capacity, resulting in lower biomass accumulation (Gong *et al.*, 2014). Therefore, even though soybean in intercrops had less steep leaf angles, longer internodes, and longer leaf life span, the effect of these positive changes on light capture could not compensate for the maize shading.

Branching is an important light response of soybean, especially in the absence of light competition and at low plant density (Gulluoglu *et al.*, 2017; Liu *et al.*, 2017b). However, the percentage of soybean with branching was very low (<8%) in intercrop and in sole crops (10%), which could be caused by variety, high plant density, and shading in intercrop as well. Hence, the shade avoidance strategy, which is the responses of plants to the position of its leaves out of shade via a photoreceptor signalling network (Ballaré, 1999; Smith, 2000), is not an optimal option for soybean grown in strip intercropping with a tall dominant companion crop such as maize when no measures are taken on the tall crop.

Soybean is the main factor in the intercrop holding back system performance. Therefore, improvements in soybean leaf dimensions, leaf life span, and internode length under shade could help improve maize/soybean intercrop performance. In the future it will be also worthwhile to study the maize trait effect on light capture in the intercrop. Alternatively, short stature maize genotypes, and management options such as wider gaps between maize rows, or detasseling or maize leaf stripping could improve soybean performance (Raza *et al.*, 2019a, b). It remains to be verified to what extent it is possible to improve soybean yield without concurrently decreasing maize yield. Further studies with FSP models can help to explore the scope for such advantages, integrating them into the current framework of photosynthesis, nutrient uptake, carbon partitioning, and yield formation.

Supplementary data

The following supplementary data are available at *JXB* online.

Table S1. Maize phyllotaxis (angles between consecutive leaves along a stem, °) in sole crop and intercrop.

Table S2. The log-likelihood, parameter number, and AIC values of the nest models for soybean final internode diameter.

Fig. S1. Simulated and observed daily maximum temperature, minimum temperature, and mean temperature in 2012 and 2013.

Fig. S2. The shape of a full-grown maize leaf and soybean leaflet by plotting normalized margin to midrib distance (0.5× the width measured) versus normalized distance to leaf tip.

Fig. S3. Comparison of observed and simulated daily global radiation in the growing season of 2012 and 2013.

Fig. S4. Light capture of maize and soybean over the growing season in intercrop.

Author contributions

Methodology, SL, JBE, WW, YM, YG, and BL; data analysis, SL, JBE, WW, and YG; model construction, SL, JBE, JZ, and BL; writing, SL, JBE, WW, JZ, and YM; experiment design and conduct, YM, YG, and BL.

Data availability

The data supporting the findings of this study are available from the corresponding author upon request.

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